# A MONOGRAPH OF THE FERN GENUS MICROSORUM (POLYPODIACEAE)

## including an attempt towards a reconstruction of the phylogenetic history of the microsoroids

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CONTENTS

*(contents continued)*

## 1. SUMMARY

This revision is a monographic treatment of the fern genus *Microsorum* (Polypodiaceae). To elucidate the problematic generic delimitation and systematic position of this genus an additional selection of 26 possibly related species was also studied. Most of these related species are traditionally placed in *Colysis, Leptochilus, Neocheiropteris, Paraleptochilus, Phymatosorus* (*'Phymatodes'*), and *Podosorus*. In order to produce a natural classification an attempt is made to recognize monophyletic groups of species through cladistic analysis. The methods and underlying theories which have been employed are made explicit as much as possible. A suitable selection of intrinsic characters is used for analysis with the computer programs CAFCA, PAUP and HENNIG86. The resulting cladograms are very inconsistent with the datamatrix. They need many ad hoc hypotheses, such as homoplasies, to explain the pattern of distribution of character states among the species. Even when the number of species to be analysed is artificially reduced by using representative species of inferred monophyletic subgroups of *Microsorum*, the resulting cladograms are to be rejected because of their low consistency indices.

The conclusion is reached that the evolution of the microsoroids has resulted in a complex pattern, which cannot be understood sufficiently with the present set of data and available methods. Additional analyses of other characters and species, microsoroids as well as other Polypodiaceae, field observations, cytological and isozyme studies are needed. The results presented here form a good basis for the selection of problematic or promising groups of species.

In the absence of an acceptable hypothesis concerning the genealogical relationships among the microsoroids, a temporary formal classification is constructed. Because of this temporary nature of the classification, stability of nomenclature, and recognizability of the taxa, have in this treatment priority over a maximum of phylogenetic information. Thus the classification may contain para- and polyphyletic groups.

This results in the recognition of *Microsorum* in a restricted sense, comprising 20 species (including *Dendroconche* and *Diblemma*) and of five other microsoroid genera: *Colysis* (including *Paraleptochilus*), *Leptochilus* (emended), *Neocheiropteris, Phymatosorus*, and *Podosorus*. Two species of *Microsorum* are newly described, namely *M. cinctum* and *M. sopuense*, and two newly transferred. Nine species, initially thought to belong to *Microsorum*, are fully described and included in the key, but are finally classified under one of the other microsoroid genera, resulting in seven new combinations and one new species (*Phymatosorus biseriatus*). Many other species of *Microsorum* (84 names) are excluded but, because of the temporary character of this classification, the formal new combinations, necessary for most of these 84 names, are not formally made.

## 2. INTRODUCTION AND ACKNOWLEDGEMENTS

This monograph deals with the revision of *Microsorum*. Especially the generic boundaries and the systematic position of *Microsorum* appeared to be problematic. Therefore a number of other microsoroid species were also included in this study. These have been usually placed in: *Colysis* (*C.*), *Leptochilus* (*Lc.*), *Neocheiropteris* (*N.*) *Paraleptochilus* (*Pa.*), *Phymatosorus* (*Ph.*), and *Podosorus* (*Po.*). Additionally one species of *Lepisorus* (*Lp.*) has been studied as a possible 'outgroup' (see chapter 6). The abbreviations employed above will be used in most instances in this revision.

This is the first monographic treatment of *Microsorum*. A few regional revisions have been carried out before, the most extensive of which is that of Ching (1933b) for the Chinese species.

This monograph was prepared as a Ph.D. thesis at the Rijksherbarium/Hortus Botanicus of the Rijksuniversiteit Leiden and forms part of the Polypodiaceae Project supervised by Prof. Dr. E. Hennipman (Rijksuniversiteit Utrecht). A preliminary study of this group, a character analysis of the venation pattern and related structures, was carried out in the same project by W.L.A. Hetterscheid and E. Hennipman (1984).

The aim of this study is twofold:

1. To produce a natural classification, which is as informative, practical and stable as possible. As will be explained, this entails a classification including only monophyletic groups which are assigned formal ranks on the basis of practical considerations. At present the phylogenetic method seems the best way to achieve this aim.
2. To produce a revision in which the methods and underlying theories are made explicit directly, or indirectly by reference to other authors. This may seem obvious but, unfortunately, especially in 'classical' systematics it is still a rare phenomenon.

A vast amount of herbarium material was used for detailed species descriptions and character analyses, which together form the necessary basis for a phylogenetic analysis. Additional information from cultivated living material was used incidentally.

The first aim, to produce a natural classification, has not been fully attained, as the complex genealogical relationships of the microsoroid ferns cannot be unravelled with the data and methods used in this study. However, the results of the present investigation form a firm basis for a well-founded choice of species and methods for further research (as indicated in chapter 8). This is partly reflected by the accepted classification, which is probably not completely natural and which is therefore temporary and only partly formalized.

Whether I succeeded in fulfilling the second aim is to be judged by unbiased readers, especially those who are not familiar with the subjects discussed.

This revision is my first encounter with pteridological research. It took some time to get accustomed to the idea that ferns do not bear flowers, nor produce fruits, but that they show many other characters which are biologically informative, although they are not always easily observed. In some respects ferns may even be as beautiful as the most elegant flowering plants, although this needs some persuasion when working for several years on the very plain-looking *Microsorums*.

From my systematic experience with ferns as well as with higher plants I have gained the impression that the evolutionary biology of ferns is generally more complex than that of flowering plants and consequently their systematic study is often more problematic, interesting and time-consuming.

I have learnt at least one thing: never think too lightly of innocent and plain-looking phenomena, they may hide swamps, jungles and paradises from which it is difficult to escape without sweat, scratches and sins.

***Acknowledgements***

The assistance of keepers and directors of the herbaria listed in chapter 3 who have been so kind as to put their collections at my disposal, often for a considerable time, is gratefully acknowledged. For their help during my stay, I also wish to express my gratitude to the staff members of the herbaria I visited (B, BM, K, P). They made me feel welcome and comfortable. My visit to the herbarium in Paris was made possible by financial support from the Netherlands Organization for the Advancement of Pure Research (Z. W. O.).

I wish to mention Wilbert Hetterscheid for his kind permission to use his photographs of venation patterns. Gerda van Uffelen provided the photograph of the spore of *M. linguiforme* and gave helpful suggestions on interpretation and terminology of spore surface sculpture. Gerda Bosman-van den Heuvel kindly corrected the English text of the general chapters in the first version of the manuscript and Monique Smits, apprentice technician, helped in scanning the spores.

The diagnoses of newly described species were translated into Latin by Peter Hovenkamp. The habitus drawings were made by Joop Wessendorp; the other drawings were made from my own sketches by Jan van Os. The lay-out and setting were done by Emma van Nieuwkoop. Peter van Welzen assisted me whenever problems with computers and computer programs occurred.

## 3. MATERIAL AND METHODS

### 3.1. Material

A fairly large selection of the dried material of *Microsorum* and some allied genera present in the following herbaria was studied: A, B, BISH, BM, BO, C, CAL, G, K, L, LE, M, MICH, NY, P, PR, PRC, S, SING, UC, US and Z (abbreviations following Index Herbariorum). Of other herbaria, i.e., E, FAN, MA, NANCHUAN, NSW, PE, TI, U, UPS, only one or a few specimens (often types) were studied.

Occasionally living plants, cultivated in the botanical gardens of Leiden and Utrecht, were studied. Unfortunately it was not possible to obtain representatives of all species, nor to raise gametophytes and (fertile) sporophytes from spores of all specimens in cultivation in the above mentioned gardens.

For each species described, all available specimens were studied for morphological characters that did not require any special preparations. Rhizome scales, sporangia, paraphyses, and spores were studied from a small, representative selection of specimens (preferably 4 to 15 per species). For anatomical and electron microscopic observations at least two specimens per species were examined.

For each species not described but included in the phylogenetic analysis, a representative selection of specimens was examined but only for the characters in question.

In chapter 7 all species studied are listed.

### 3.2. Methods

#### Preparations

*Rhizome scales* — From a selection of specimens several rhizome scales were detached. These were preferably taken several centimetres behind the apex of the rhizome to obtain full-grown scales. Occasionally, for purposes of comparison,

younger stages were also taken from the apex of the rhizome or from lateral buds. The rhizome scales were wetted with a solution of photographic detergent and very carefully detached from the rhizome by placing one leg of a pair of finely pointed tweezers between the scale and the surface of the rhizome and the other on top of it, near the point of attachment, and breaking off the stalk in the direction of the basal part of the scale. Thus also the basal part, which is necessary to decide whether a scale is pseudopeltate or peltate, came off intact. After rinsing in water the scales were embedded in glycerine jelly for preparing semi-permanent slides.

Occasionally cross sections of scales were made by hand with sharp single-edged razor blades, simply by resting the scale horizontally on a slide and by cutting it vertically into very thin slices.

*Sori* — From a selection of specimens preferably several mature sori (with closed sporangia) from different parts of the lamina were removed. These sori were also wetted with a solution of photographic detergent before they were taken off. With a pair of fine tweezers with curved ends the sporangia and paraphyses were scraped off the lamina, including (part of) the receptacle, if possible. They were rinsed in water and under a binocular the sporangia and paraphyses, often in small clusters, were separated from each other and from the receptacle. They were finally embedded in the same way as the rhizome scales.

*Rhizome and stipe* — For anatomical studies small pieces of rhizome or stipe were boiled in water for several minutes, until they sank when transferred to cold water. Preferably at least two specimens per species were selected: one specimen with relatively thin and one with relatively thick rhizome and stipes. Cross sections of rhizomes were made at the internodes and cross sections of stipes within 1 cm from the phyllopodia. This was done by hand with a sharp single-edged razor blade or with a Reichert slide microtome using a double-edged razor blade. Sections were embedded in glycerine jelly.

*Lamina* — The anatomy of the lamina was studied in sections of fronds of some cultivated plants, made in a similar way as those of the rhizomes, but pressed between two pieces of elder pith.

*Venation* — In order to study venation and innervation patterns it was sufficient for most species to wet the lamina with some alcohol 95% and study this in transmitted light with the aid of a binocular. Additional observations were made on cleared and photographed material supplied by W.L.A. Hetterscheid (for clearing procedures see: Hetterscheid & Hennipman, 1984).

*Spores* — Spores studied with the scanning electron microscope were mounted with silver-containing conducting glue on aluminium stubs and subsequently covered with gold (using a Polaron E 5100 series II sputter-coater).

*Gametophytes and juvenile sporophytes* — From cultivated specimens fresh spores were taken and sown on an Agar medium in a sterile petri dish sealed with parafilm and placed in a phytotron. In various stages of their development gametophytes and juvenile sporophytes were fixed in FAPA until they were observed.

### Observations

Most observations were made with a Leitz binocular. Light-microscopical observations were made with a Leitz Laborlux microscope with drawing device. Electron microscopic observations were made with a JEOL JS35 scanning electron microscope.

In microscopic observations measurements were made with an eye piece micrometer (μm). All measurements presented in the descriptions were taken from herbarium specimens. Those concerning anatomy or microscopic structures (such as spore sizes) are based on relatively few observations (usually 5–10). Observations and measurements on macroscopic structures involved large numbers of specimens, if available.

## 4. TAXONOMIC HISTORY

Before Link (1833) established the genus *Microsorum,* many species to be subsequently transferred to it had already been described under *Polypodium* and a small number of other genera. Thus the 'prehistory' of the genus started eighty years before Link's publication, with the description by Linnaeus (1753) of *Polypodium heterophyllum,* which served as basionym for *M. heterophyllum* (Linnaeus) Hawkes [= *Microgramma heterophylla* (Linnaeus) Wherry]. Ten years later Linnaeus (1763) described another species, *Acrostichum punctatum,* which became the basionym of the most widespread species of *Microsorum, M. punctatum.*

In the following years several authors (i.a. Thunberg, Forster, Swartz, D. Don, Blume) described species of *Polypodium* which would later be transferred to *Microsorum.* Particularly many of the *Polypodium* species described by Blume (1829) are still accepted as basionyms of microsoroids, e.g., *P. heterocarpum, P. musifolium, P. insigne, P. pteropus, P. superficiale,* and *P. zippelii.*

The genus *Microsorum,* which Link (1833) described for only one species, *M. irregulare* (= *M. punctatum*), was enlarged by Fée (1852) with three new combinations and two new species. Two of these he placed in the section *Dissidentes,* not being completely sure of their generic identity [*M. palmatum* = *Colysis insignis* and *M. trifidum* = *Tectaria trifida* (Fée) Price]. The other three, together with *M. irregulare,* made up the section *Eumicrosorum.*

Despite the erection of this genus, for many years many of its species, or species to be, were newly described or combined in other genera, such as:

- *Phymatodes* (C.B. Presl, 1836),
- *Drynaria* (J. Smith, 1841; Brackenridge, 1854),
- *Pleopeltis* (Moore, 1857; Beddome, 1865–1892; Alderwerelt, 1909–1924),
- *Polypodium* (Mettenius, 1856b; W.J. Hooker, 1864; Baker, 1868–1896; Christ, 1896–1910; Copeland, 1905–1914; Hayata, 1915; Takeda, 1915), and
- *Colysis* (J. Smith, 1875).

It was Copeland (1929a) who, almost a century after Link's publication, revived the genus. While dismembering the genus *Polypodium* in the preceding years, he had not yet handled this group because he was "satisfied of the affinity of this group

to that of *Polypodium vulgare* and because of doubt as to the proper number and size of the fragments." He now estimated the size of *Microsorum* at "probably two hundred species" and he included 12 "phyletic groups", among which are, apart from microsoroids s.s.: *Lepisorus, Paragramma, Phlebodiopsis, Arthromeris,* and *Phymatopsis.* Awaiting a monographic study he fortunately refrained from making all the necessary new combinations.

Subsequently Ching (1933b) made an "attempt to draw a more clear-cut line of demarkation between *Microsorum* Link and some other phyletically related genera." He excluded *Lepisorus, Colysis, Phymatodes* (all of which he thought closely related to *Microsorum*) and the above-mentioned groups of Copeland that are now considered as non-microsoroid. Thus Ching estimated *Microsorum* to comprise c. 40 species, and included 17 new combinations.

In the next ten years a small number of species were added by, i.a., Itô (1935), Copeland (1938), Christensen & Tardieu-Blot (1939), and Ching (1941).

In 1947 Copeland dealt with the difficult issue of the generic distinction between *Microsorum* and *'Phymatodes'* (= *Phymatosorus,* see Pichi Sermolli, 1973: 457). He stated: "The types of *Microsorum* and *Phymatodes* look too unlike for inclusion in any natural genus [...]. Expecting to find somewhere a line between them, I have left this as the last genus for final description, but am unable to separate them by any character, or to assign a considerable number of species with any confidence to one rather than to the other. As a matter purely of convenience, *Microsorum* and *Phymatodes* can be retained as descriptive names of sections." Apart from this he followed Ching in reducing the scope of his over-large *Microsorum* of 1929, by excluding *Colysis* and all non-microsoroid members. The inclusion of *Phymatodes* entailed approximately 40 new combinations.

Copeland's act was the last major taxonomic change for *Microsorum*; in the next 40 years or so only 21 species were added by various authors, bringing the total number of combinations in *Microsorum* up to about 120 (of which a very small number, namely six, is subspecific). In the present study only 16 of these 120 names are accepted, and 55 are excluded (mostly as *Phymatosorus*), while the others are regarded as synonyms.

Whereas the number of additions of new names and combinations after 1947 was small, the discussion on the generic delimitation and the taxonomic position of *Microsorum* has been going up to the present, including this monographic treatment.

In this discussion neither a definition of terms, nor an indication of methods chosen and arguments used are as a rule explicitly given. Thus, the reader is forced to guess the meaning of statements such as "This group represents the nearest approach to *Crypsinus*" (Copeland, 1947: 196). Moreover, the lack of consistency in choosing a well-defined method or choosing no method at all may cause a number of flaws, such as:

- circular arguments, for instance that of Pichi Sermolli (1977) who, in his discussion of the relationships between polypodiaceous genera, defined primitive characters as those possessed by primitive groups and primitive groups as having primitive characters;

- internal contradiction, for instance that of Pichi Sermolli (1977), who stated that the *Microsorum* group is nearer to the group of *Pleopeltis* (*Lepisorus*) than to any other, but proposed a scheme showing the presumed relationships of genera of the Polypodiaceae in which these two groups are at the far end of two distinctly separated lines;
- a cocktail of pragmatic and other arguments, such as that of Copeland (1929a), who kept *Dendroconche* apart from *Microsorum* because of "pure convenience to not complicate the definition of *Microsorum* against *Drynaria*" and "to have a few genera which can be recognized as in the act of evolution, to exemplify the fact that all genera have originated in this manner."

Therefore a complete review of all these ideas concerning the position of *Microsorum* and allied genera would perhaps be equally confusing as it would be interesting. In order to spare the reader these 'pleasures' and in order to avoid long-windedness in the following, I summarize only some of the more prominent opinions.

One of the most troublesome points of discussion has been, and still is, the generic delimitation of *Microsorum* and *Phymatosorus* (called *'Phymatodes'* by most authors). As mentioned above, Copeland (1929a, 1947) was the first to unite these under one genus. This example was followed by some authors (i.a. Sledge, 1960; Nayar, 1961; Tagawa & Iwatsuki, 1989), while many others, although often hesitantly, chose to keep them apart (i.a. Ching, 1933b, 1978b; Christensen, 1938; Holttum, 1946, 1949, 1954; N. Pal & S. Pal, 1964; Bir & Trikha, 1968b, 1979; de la Sota, 1973; Pichi Sermolli, 1977; Hetterscheid & Hennipman, 1984; Baayen & Hennipman, 1987; Hennipman et al., 1990).

Another point of controversy is the origin of *Microsorum*, and with it the position of the microsoroids within the Polypodiaceae. Holttum (1946, 1949, 1954) and Bir & Trikha (1968b, 1979) considered *Lepisorus* or a *Lepisorus*-like group as the most probable ancestor of *Microsorum*, mainly because some microsoroids also have peltate paraphyses. This opinion was probably shared by Ching (1933b), although he only spoke in terms of relationships, 'intermediates', without indicating direction: "*Microsorum* is related to *Lepisorus* and *Neocheiropteris* on the one hand and to *Colysis* on the other hand." The genus *Neocheiropteris* is associated with this lepisoroid ancestor. Holttum (1946, 1949, 1954) considered *Neocheiropteris* (*palmatopedata*) because of, i.a., its frond shape and venation, a relatively primitive genus from which *Lepisorus* is most probably derived. According to Bir & Trikha (1979) *Neocheiropteris* is derived from *Dipteris* and ancestral to *Lepisorus*. Consequently, they related the lepisoroids and microsoroids to what is generally thought the most primitive element in the family (or at the origin of the family, when *Dipteris* is placed in the Dipteridaceae).

Christensen (1938) and Pichi Sermolli (1977), on the other hand, regarded *Phymatosorus* as the 'direct' ancestor of *Microsorum*. However, Pichi Sermolli (l.c.) remarked that some species of *Microsorum* resemble some species of *Neocheiropteris* and *Neolepisorus*, which he placed in a different line together with *Lepisorus*. The 'phyletic line' which includes *Microsorum* "appears to have diverged early from the other groups" of the Polypodiaceae, but he still considered *Polypodium* with its

free venation the most primitive element in the family. As a consequence reticulate venation would have had to originate three times in his scheme.

Finally, Copeland (1947) regarded the *Microsorum–Phymatosorus* group as "probably more primitive than *Pleopeltis*." Besides, he regarded a small group of "austral species" (his *M. pustulatum, M. diversifolium* and *M. novae-zealandiae*) as the most probable common ancestor of this *Microsorum–Phymatosorus* group.

The following genera, alphabetically listed, are often considered to be derived from *Microsorum*:

- *Colysis* (Ching, 1933b; Christensen, 1938; Holttum, 1946, 1949, 1954; Copeland, 1947; Bir & Trikha, 1968b, 1979; Tagawa & Iwatsuki, 1989);
- *Dendroconche* (Copeland, 1929a, 1947; Christensen, 1938);
- *Diblemma* (Copeland, 1928, 1929a, 1947);
- *Drynaria* (Copeland, 1929a, 1947; Holttum, 1946, 1949, 1954; Pichi Sermolli, 1977; Bir & Trikha, 1979; Chandra, 1982; Tagawa & Iwatsuki, 1989; but opposed by Ching, 1978c, who thought of common ancestry or convergent evolution);
- *Kaulinia* (Nayar, 1964: parental to *Colysis*, relationship with *Microsorum* doubtful);
- *Lepidomicrosorum* (Ching & Shing, 1983);
- *Leptochilus* (Copeland, 1928, 1947; Christensen, 1938; Tagawa & Iwatsuki, 1989);
- *Nistarika* (Nayar, 1985);
- *Paraleptochilus* (Copeland, 1947);
- *Phymatosorus* (Bir & Trikha, 1979; opposed by Holttum, 1946, 1949, 1954: also derived from *Lepisorus* but via a different line);
- *Podosorus* (Holttum, 1967: probably related; opposed by Zamora & Chandra, 1978);
- *Tricholepidium* (Ching, 1978a).

Again, of these genera *Colysis* is regarded parental to:

- *Dendroglossa* (Copeland, 1929a, 1947);
- *Leptochilus* (Ching, 1933b; Holttum, 1946, 1949, 1954);
- *Paraleptochilus* (Bir & Trikha, 1979);
- *Selliguea* (Copeland, 1929a),

and the following genera were said to have been derived from *Phymatosorus*, or that part of *Microsorum*:

- *Arthromeris* (Christensen, 1938; Holttum, 1946, 1949, 1954; Bir & Trikha, 1979);
- *Crypsinus* (Copeland, 1947: "the nearest approach to");
- *Dictymia* (Copeland, 1929a);
- *Lecanopteris*, incl. *Myrmecophila* (Copeland, 1929a; Christensen, 1938; Holttum, 1946, 1949, 1954; Tagawa & Iwatsuki, 1989);
- *Polypodium* (Holttum, 1946, 1949, 1954; Bir & Trikha, 1979).

In this study I refrain from reviewing the different formal names and ranks the group of microsoroid genera has received from various authors who discussed the subdivision of the Polypodiaceae, such as tribe Microsoreae or Microsorinae, subfamily Microsorioideae. Firstly, this falls outside the scope of this study, which does not include a revision of all microsoroids. Secondly, these distinctions are only of importance when the systematics of the family as a whole are discussed.

## 5. CHARACTERS

For an explanation of the abbreviations of genera used in this chapter I refer to the first paragraph of chapter 2.

### 5.1. Rhizome

The rhizomes of 11 microsoroid species were studied by Nayar (1963a). Nayar (1963b) also compared the rhizomes of *Lc. axillaris* and *Pa. (C.) decurrens*. Zamora & Chandra (1978) paid much attention to the rhizome of *Podosorus* and Nayar et al. (1985) described the morphology and anatomy of the rhizome of *Nistarika*. Both monotypic genera are usually considered to be microsoroids, but the latter is not further discussed in this monograph as no material of it was studied. A comparative survey of (literature on) rhizome anatomy and morphology of Polypodiaceae, including microsoroids, was recently made by Kaur (1984).

#### Morphology

The rhizome of the microsoroids varies from short- to long-creeping and is dorsoventrally flattened or approximately cylindrical. At least the younger parts, but sometimes also the older parts, are more or less densely set with scales. The surface is smooth to finely wrinkled after drying and varies from green to brown to blackish. Sometimes it is covered by a thin, probably waxy layer, which gives the surface a glaucous hue (e.g., in *M. glossophyllum, M. punctatum, M. steerei, M. (N.) sarawakense,* and *Ph. scolopendria*). As in *Drynaria* (Roos, 1985) the waxy rhizomes usually bear relatively few persistent scales, which suggests that in these rhizomes the wax layer 'has taken over' some of the possible functions of the scales (see paragraph 5.2).

In most species branching can be observed in relatively few herbarium specimens. Usually only short rhizome fragments are collected, which makes it difficult to establish the actual frequency of branching. However, in a few species relatively many branches are found even in short fragments (e.g., in *M. samarense*), while in others even longer fragments are rarely branched (e.g., in *N. ningpoensis*). All branches develop from lateral buds ('accessory branching').

*Phyllopodia* — Phyllopodia are usually placed in two alternating rows, although sometimes three rows seem to be present (in *M. congregatifolium, M. longissimum, M. pentaphyllum,* and *M. samarense*). However, this may be the result of a distor-

tion during the drying process and should be checked by anatomical observations on living material. Nayar & Madhusoodanan (1977) reported only one row for adult specimens of *M. linguiforme,* but two for juvenile plants. As in this species fairly stout fronds and stipes are sometimes borne on thin rhizomes, this seems to be a case of secondary displacement.

The phyllopodia vary in distinctness. They are more or less densely set with scales. Colour and diameter may differ from or resemble those of the stipes. They are usually short, in the species examined up to 4 mm long, but in a few species they may reach 6–10 mm (e.g., in *M. membranaceum, M. musifolium,* and *M. punctatum*).

The distance between two successive phyllopodia varies considerably even within a single plant and may attain 10 cm (e.g., in some vining branches of *M. linguiforme*), although it usually does not exceed 5 cm. In some species the fronds are more or less tufted (e.g., in *M. congregatifolium*).

As in *Pyrrosia* (Hovenkamp, 1986), lateral buds are usually borne close behind each phyllopodium or somewhere halfway between two phyllopodia on one side of the rhizome, and sometimes they may be positioned even further back.

*Roots* — Roots are borne ventrally or also more or less laterally and may vary from short to long and from sparsely to densely set, in the latter case often forming a dense, spongy mass covering the rhizome. Roothairs are usually brown and lax, but may be more or less stiff, bristle-like.

### Anatomy

*Stele* — The stelar structure of the microsoroids can best be called a highly perforated dictyostele, following Schmid (1982). By his definition, the perforations in this type of stele are discontinuities other than leaf, branch, or root gaps. This usually results in the presence of a considerable number of vascular bundles in cross section (up to c. 35). In internodal cross sections of all microsoroids studied these bundles are situated more or less peripherically in a ring.

According to Nayar (1963a, b) leaf traces originate from the dorsal (median) and a lateral bundle and branch traces originate from lateral bundles only. He found an exception in *Lc. axillaris* where leaf traces originate laterally and branch traces dorsally.

*Sclerenchyma* — Sclerenchymatic tissue is present in all species except in the rheophytic *C. pteropus*. It may form strands scattered in the ground tissue (fig. 1a, b) or it may form one to several cell layers in circumvascular sheaths (fig. 1c, f), or it may occur in both forms (fig. 1d, e). Where both forms are present, the strands in the apical region of the rhizome differentiate before the cells of the vascular sheath become sclerenchymatic. The strands, however, do not continue into the stipe, whereas the vascular sheath does.

Differentiation of the sclerenchyma sheath may be incomplete, that is, some cells, usually the cortical ones, are sclerified while other cells are more or less collenchymatous. In other species the sheath may be collenchymatous (*C. pteropus*) or not distinctly differentiated (parenchymatous).

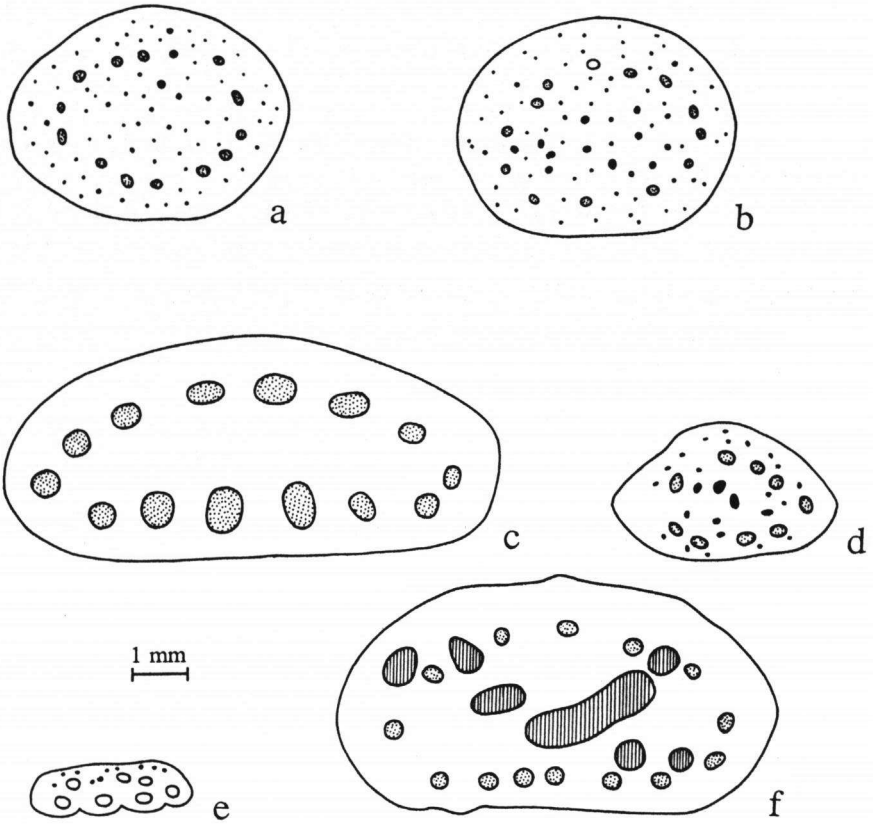


Fig. 1. **Rhizome anatomy.** Transverse sections of internodes. Stippled: vascular tissue; black: sclerenchyma; cross-hatched: intercellular cavities. — a. *M. punctatum*; b. *M. lastii*; c. *M. cinctum*; d. *M. heterocarpum*; e. *N. ningpoensis*; f. *M. linguiforme* (a *van Steenis 3916*; b *Perrier de la Bâthie 15621*; c *Jermy 8111*; d *Iwatsuki B 971*; e *Koidzumi s.n.*, -6-1923; f *NGF 34852*).

According to Ogura (1972), the walls of the sclerenchymatic cells are impregnated by a brown pigment, phlobaphene, which may have the effect of preventing the tissue from decay. Where these cells border parenchyma, they are partly thick-walled and partly thin-walled. In some species the inner wall layers are set with warts, resembling those found in the scales of *M. spectrum*. These warts resemble those mentioned by Frey-Wyssling (1976), which he reported as being quite common in lignified cells, especially in 'primitive groups'.

In quite a number of microsoroid species the presence and position of sclerenchymatic tissue is correlated with the shape of the rhizome.

In 20 out of 25 species with dorso-ventrally flattened rhizomes (e.g., the *M. linguiforme* group and *Leptochilus*) scattered sclerenchyma strands are rare or absent,

whereas the vascular sheath is distinctly sclerenchymatic. Only five species with flattened rhizomes (*M. lastii, M. leandrianum, C. pteropus, M. spectrum,* and *M. (?) latilobatum*) have many sclerenchyma strands and/or a non-differentiated or only slightly sclerenchymatic vascular sheath.

In 13 out of 20 species with cylindrical rhizomes (e.g., the *M. punctatum* group) sclerenchyma is only present in scattered strands and rarely in some cells of the vascular sheath. In the remaining seven species (*M. heterocarpum, N. ensata, N. palmatopedata, M. (N.) sarawakense, C. hemionitidea, Ph. scolopendria, Po. angustatus*) the vascular sheath is distinctly sclerenchymatous and/or sclerenchyma strands are rare or absent.

Many flattened rhizomes are distinctly elongate and contain few (up to c. 15 in cross section) large vascular bundles, which often show their outline on the ventral surface of the rhizome, separated by distinct, fine grooves (fig 1d). In species with such rhizomes, roots are usually sparsely set. Remarkably, in some of these species hairs resembling (and possibly functioning as) roothairs are found on the rhizome scales and even (e.g., in *Lc. buergerianus* and *Lc. axillaris*) directly on the ventral surface of the rhizome. These hairs possibly compensate for the low root density.

Cylindrical rhizomes are usually shorter than flattened ones. They often have more (up to c. 35 in cross section) and relatively smaller vascular bundles and more densely set roots.

*Intercellular cavities* — Intercellular cavities were observed in the ground tissue of a few specimens of *M. congregatifolium* and four species of the *M. linguiforme* group. In most of these species only one or a few cavities per cross section were found. However, in one specimen of *M. linguiforme* seven cavities (fig. 1e) formed a complete system of canals, some of which in serial sections proved to be interconnected in a fixed pattern. Once (in *M. samarense*) a gap connected to the dorsal surface of the rhizome was observed. On the periphery of the cavities the cells have slightly darkened walls and cell-fragments can be observed. These indicate that the cavities are probably formed schizogenously (Ogura, 1972). It is doubtful whether the function of these cavities is similar to that in *Lecanopteris* because the difference in size is considerable and ants have not yet been recorded from these rhizomes. As (initiations of) cavities were found neither in apical fragments of rhizomes of herbarium specimens nor in cultivated plants it was impossible to investigate whether their development resembles that of the cavities in *Lecanopteris* or not.

### 5.2. Scales

Nayar (1963a), Chandra (1962) and Teeuwen (1985) have studied the structure and especially the ontogeny of the rhizome scales of some microsoroid species. Other authors described scales only briefly and often not very precisely.

Müller et al. (1981) suggested some possible functions of rhizome scales: reflection of light resulting in lower surface temperature, reduction of evaporation, water absorption through the cell walls and water transport in capillary spaces between closely appressed scales and the rhizome surface.

In microsoroid ferns scales are found on the rhizome (including the phyllopodia). In some species they are also present on the fronds (including the stipe) but they are always lower in number and often smaller and more simple in structure than those on the rhizome.

The density of the scales is relatively highest on young parts, i.e., on the rhizome apex, lateral buds and developing fronds and, in mature fronds, on the major veins. In older parts this density usually decreases simply by extensive growth of the surface, or because the scales gradually erode or fall off. The scales usually overlap and may be more or less spreading to closely appressed, and are – at least in the two microsoroid species – studied by Teeuwen (1985), viz. *M. punctatum* and *N. palmatopedata*, arranged spirally on the rhizome.

### Morphology

*Shape* — The general outline of the usually small scales (up to c. 10 mm long), is often somewhat irregular and varies from more or less orbicular to ovate and narrowly ovate (fig. 2a) with entire (fig 2b, c, e, g) to dentate (fig. 2a, d, f) margin and acute to acuminate apex. In some scales one or a few marginal, short and approximately triangular lobes are present (e.g. in *C. insignis* and *N. ningpoensis*: fig. 2c, d). These lobes are often terminated by a glandular hair. Distinct dimorphy in scales has been found only in *M. rampans*, where it seems to be geographically correlated (see note under the species).

Most species have basally attached scales which are more or less auricled at base, often with overlapping auricles (i.e., pseudopeltate). A few species have peltately attached scales. In other species both types of attachment may occur, even on the same rhizome (e.g., in *M. linguiforme, M. rampans*, and *M. sopuense*). Pseudopeltate scales are sometimes easily mistaken for peltate ones, especially when the auricles are completely overlapping and closely adhering to another (i.e., only separable by very careful preparation).

In pseudopeltate scales it is difficult to establish whether two auricles are really separate up to the top of the stalk or only for the larger part of the basal half. As, moreover, peltate and pseudopeltate scales are present in closely related species or sometimes even in a single species or specimen, it may be expected that scales with intermediate differentiation (i.e. peltate but with overlapping auricles: pseudobasifixed) are occasionally present.

*Marginal indument* — Glandular, 1–3(–5)-celled hairs are usually present: one at the apex of the scale and very few (many in *M. rampans*: fig. 2e) along the margin, especially on the basal auricles of pseudopeltate scales. Occasionally these hairs are branched and they bear two glandular cells (e.g. in *N. superficialis* en *Lc. buergerianus*) or one glandular and one acicular apex (in *M. longissimum*). Teeuwen (1985) suggested that the glandular compounds may facilitate the movements of the growing apex of the rhizome in or along the substrate or that they may protect the rhizome from insect attacks.

*Superficial indument* — Superficial hairs are usually absent but in some species a tuft of hairs resembling roothairs may be present in the central region above the stalk

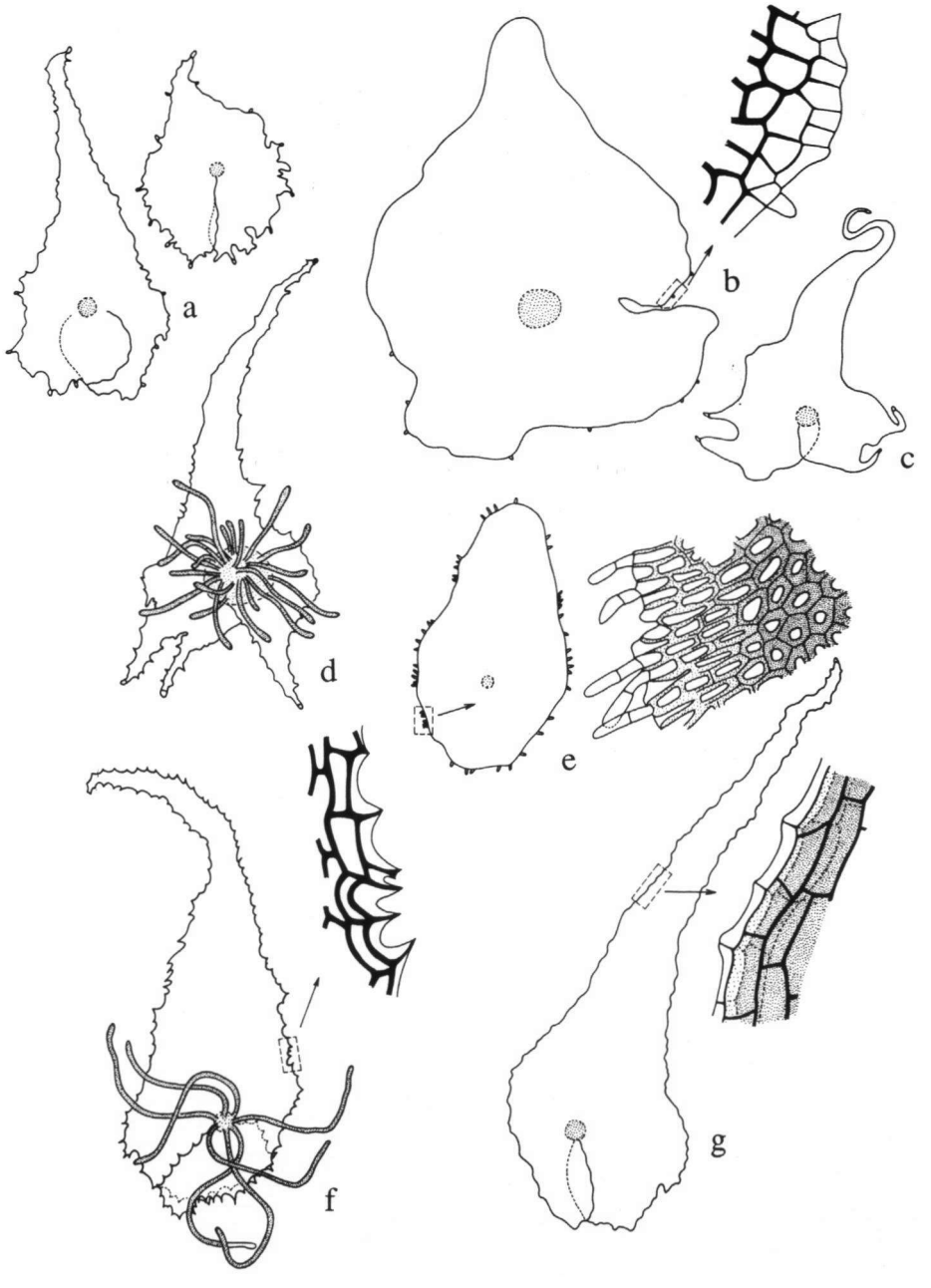


Fig. 2. **Rhizome scales.** Outline, indument and details of margins. Outlines about × 20, details about × 100. Stippled: central region (stalk). — a. *M. punctatum*; b. *M. musifolium*; c. *C. insignis*; d. *N. ningpoensis*; e. *M. rampans*; f. *M. congregatifolium*; g. *M. glossophyllum* (a *Maxwell 76-243*; b *Endert 4022*; c *Hennipman 3607*; d *Tagawa & Iwatsuki 764*; e *Croft 502*; f *Dransfield 3371*; g *Croft 451*).

of the scale (e.g., in *M. congregatifolium* and *N. ningpoensis*: fig. 2f, d). These hairs are lax or stiff, usually long and conspicuous (extending beyond the margin of the scale), but easily abraded. They also occur outside the microsoroids, e.g. in *Polypodium* and *Marginaria* (Ogura, 1972).

Poirault (1893) suggested that these hairs, like roothairs, may function in the process of water absorption. This seems likely as Müller et al. (1981) demonstrated (in *Microgramma* species) that water absorption through the cell walls of rhizome scales is possible. It is therefore interesting to note that these hairy scales are also found on the fronds of the rheophytic *C. pteropus*. On the lateral and ventral side of the rhizome of *Lc. axillaris* the scales (especially the basal half) may be largely or completely reduced, ultimately leaving only the tufts of hair on the epidermis of the rhizome.

### Anatomy

All microsoroid scales (except those of *M. glossophyllum*: fig. 2g) are one cell layer thick, except for the central region around the stalk which is often thicker. In surface view the cells are quadrangular to polygonal with straight to slightly wavy anticlinal walls.

The colour varies from light (greyish or yellowish) to dark brown, sometimes reddish, and depends mainly on the degree of cell wall lignification.

Often all anticlinal walls are thickened and lignified and the superficial walls translucent, thus giving the entire scale a lattice-like appearance (plate 2f). This clathrateness has often been called characteristic for microsoroids. However, this property is not exclusive to this group (cf. *Lepisorus, Christiopteris*, etc.), nor is it equally distinct in all species. The thickening of anticlinal walls is confined (at least in some species) to only a part of the wall, in cross section resembling Caspary's strips of the endodermis (plate 2e). This has also been observed in *Polypodium lepidopteris* and *Polypodium revolutum* (Ogura, 1972).

The margin in fully clathrate scales is usually more or less dentate as a consequence of the marginal anticlinal walls not being thickened and being slightly curved inward between the sharp pointed 'ends' of the thickened walls (fig. 2f).

Some scales are only partly clathrate, i.e., the marginal cells (sometimes only in the basal half of the scales) have thin, translucent anticlinal walls. In a few species all superficial walls are more or less opaque, while the anticlinal walls are thickened; these scales are here called subclathrate (in *M. glossophyllum* and *M. punctatum*).

In most species the scales are either fully clathrate (to subclathrate) or partly clathrate, but in five species (*M. egregium, M. linguiforme, N. superficialis, N. palmatopedata, Ph. nigrescens*) both types have been observed. As the thickening of cell walls in the ontogeny of clathrate scales proceeds from the apex of the scales towards the base and margins, partly clathrate scales resemble juvenile stages of development of fully clathrate scales.

In the central region of the scales of *M. spectrum* some superficial cell walls are opaque and in some cells one of the anticlinal walls is not thickened. The inner layer of the thickened cell walls in this species is distinctly warty (cf. the warts on the inner walls of sclerenchyma cells in some rhizomes).

### Development

Immature scales can be found only on the meristematic growing points of the rhizome (e.g. in *M. punctatum*) or also axillary to mature scales (e.g. in *N. palmatopedata*).

Basally and peltately attached scales both develop from a uniseriate row of cells (a 'hair'), terminated by a glandular cell. A few basal cells develop into a short uniseriate or multiseriate stalk, whereas the apical cells by repeated divisions in one plane develop into the blade of the scale (Teeuwen, 1985; Nayar 1963a, b). The basal part of this blade may develop about equally in all directions around the stalk, thus forming a peltate scale. If the basal half extends beyond the stalk into two separate directions, two rounded or triangular auricles develop which may finally overlap to form a pseudopeltate scale. According to Nayar (1963a) these auricles develop from single initial cells in *C. pteropus* and *C. insignis*, whereas in, e.g., *M. punctatum, M. congregatifolium, N. superficialis,* and *N. zippelii* no specialized initial cells are present.

## 5.3. Fronds

### Morphology

The fronds of the microsoroids are articulated to the rhizome, small to medium-sized and are usually more or less distinctly differentiated into a stipe and lamina.

The frond length is usually correlated with the rhizome diameter so that the two are equally proportioned in size; only *M. monstrosum* and *N. zippelii* have relatively large fronds borne on thin rhizomes (i.e. the maximum frond length in these species is more than 200 times the maximum rhizome diameter).

The angle between frond and rhizome varies from c. 0° to 90°, the fronds thus being either erect (and in vertically scandent species close to the substrate) or more horizontally spreading or pendulous. Some species form loose and shaggy, creeping or climbing colonies; others grow more solitary with the fronds clustered, forming irregular nests (e.g., *M. punctatum*).

Most species are evergreen but a few species (*M. membranaceum, N. zippelii*) are known to shed all fronds in dry seasons (Nayar, 1963a). For *M. membranaceum* this phenomenon was also observed in a specimen cultivated in Leiden: during the winter fronds were absent and the plant seemed to be dead.

*Dimorphism* — In most species of *Microsorum* fertile and sterile fronds are not notably different in size and shape. Only *M. heterocarpum* is usually slightly dimorphic, the fertile fronds being generally longer stipitate and narrower (fig. 4c, d). A local form of *M. linguiforme* in Papua New Guinea, which for this reason was put in a separate genus (*Dendroconche*), has narrowed fertile apices.

In *Colysis* frond dimorphism (i.e., lamina reduction in fertile fronds) is more common and often accompanied by acrostichoidy. In, for instance, *C. hemionitidea* the instability of this condition is pronounced (Hetterscheid & Hennipman, 1984: fig. 14). Some other distinct dimorphic microsoroids are *Lc. axillaris, M. (?) varians,* and *M. (?) latilobatum.*

*Indument* — The indument of the stipe and that of the lamina usually correspond, although scales, if present, are mostly confined to (the basal part of) the stipe and the major veins on the abaxial side of the lamina. These scales resemble those of the rhizome but are somewhat smaller or reduced to basally attached forms. Baayen & Hennipman (1987) reported intermediates between scales and simple hairs on the fronds of *Po. angustatus*. On the fronds of *C. pteropus* they found glandular hairs with roothair-like appendages. These hairs may be interpreted as reduced forms of scales with appendages (superficial hairs) like those found on rhizome scales.

In all species minute 1–3-celled glandular hairs cover the stipe and lamina, though more densely on the undersurface than on the upper surface. In *M. longissimum, M. egregium,* and *M. samarense* these glandular hairs are mixed with more distinct, one-celled, acicular hairs. In *M. longissimum* branched, in part glandular, in part acicular hairs are occasionally found.

### Development

Vernation in microsoroids, as far as it has been observed in living collections, is circinnate. Subsequent leaf growth takes place at or near the apex of the fronds or lobes only, i.e. the leaf growth can be classified as acroplastic (Hagemann, 1984).

The differentiation of the fronds into stipe and lamina is usually indistinct in the very first stages of ontogenetic and blastogenetic development, the lamina being only slightly narrowed towards the base, as shown in the many drawings of Mitsuta (1982, 1984a, b). In pinnatifid species the first-formed fronds are always simple.

## 5.4. Stipe

The morphology and anatomy of fern stipes were recently studied and discussed by Lin & DeVol (1977, 1978). Although these authors included some microsoroid species in their survey, few details on the species level were given. Nayar (1963a, b), too, included only very scanty information on stipes in his morphological studies of microsoroids.

In many microsoroid species a distinct, though often short stipe is present in at least some specimens. Only in *M. musifolium, M. congregatifolium,* and *M. sopuense* the stipe is always very short or absent.

### Morphology

*Shape* — The shape of transverse sections varies from approximately round to oval or slightly angular. In some species it is characterized by a distinct adaxial gutter and/or an abaxial keel (fig. 3). However, caution is required with respect to observations on this character in herbarium specimens because the shape may be influenced by the drying process. In most species the length of the stipe is rather variable and often cannot be precisely determined because the base of the lamina usually tapers very gradually, leaving narrow lateral ridges on both sides of the stipe. The length of the stipe has therefore been measured up to the arbitrarily chosen point where the lamina on both sides is c. 0.5 mm wide.

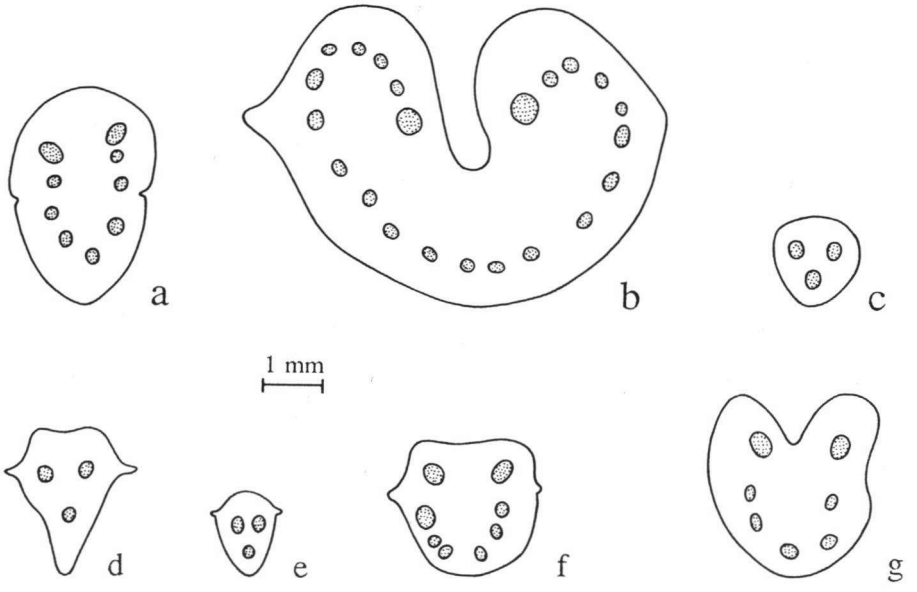


Fig. 3. **Stipe anatomy.** Transverse sections of base. Stippled: vascular tissue; black: sclerenchyma (circumvascular sheaths). — a. *M. egregium*; b. *Ph. biseriatus*; c. *M. heterolobum*; d. *M. sopuense*; e. *Lc. subhemionitideus*; f. *M. heterocarpum*; g. *M. lastii* (a *Nedi 274*; b *Croft 1870*; c *Loher s.n.*, -3-1897; d *Darnaedi 1739*; e *Tsai 53101*; f *Endert 3022*; g *Perrier de la Bâthie 15621*).

No distinct correlation was found between the length of the lamina and the length of the stipe, apart from the fact that the stipe is always shorter than the lamina or at most equals it (as in *M. spectrum*).

The maximum stipe length may reach 55 cm in *Ph. alatus* and 85 cm in *C. insignis* but in most species it lies between 10 and 20 cm.

The maximum stipe diameter varies from 1–10 mm and is positively correlated with the maximum rhizome diameter as well as with the maximum lamina length. The stipes are usually 1–3 mm narrower than the rhizomes.

*Surface* — The colour of the stipe, when dry, varies from light brown (straminеous) to dark, sometimes reddish, brown; the surface may be polished and shining or more rough and dull.

### Anatomy

The anatomy as observed in transverse sections is rather simple and uniform in all species. Below the epidermis several layers of collenchyma are found which stand out more or less distinctly from the ground tissue parenchyma. In *M. egregium, M. rampans, M. glossophyllum, M. lastii,* and *M. leandrianum* this collenchyma is abaxially somewhat darker than adaxially.

In the *M. linguiforme* group the subepidermal collenchyma is often interrupted laterally by grooves (fig. 3a). These grooves are easily observed on the outer surface and ultimately grade into the laminal ridges towards the apex of the stipe. They are reminiscent of, and possibly homologous to, the aeration lines observed in other fern families (Lin & DeVol, 1978; Hennipman, 1977), but a detailed comparison of morphology and function of these structures has not yet been made.

In the ground tissue up to 14 vascular strands are arranged in an arc, with two relatively large strands on both adaxial ends. The strands are round or oval in cross section and are always surrounded by sclerenchyma sheaths, also in species where such sheaths are not present in the rhizome. The number of strands is usually highest at the base of the stipe but occasionally increases by 1 or 2 in the first centimetre just above the phyllopodium (for instance in *C. insignis*). Towards the apex of the stipe the number of strands gradually decreases by 1–3, sometimes leaving only one strand at the base of the lamina, as for instance in *M. pentaphyllum.*

The maximum number of strands in the stipe is positively correlated with that in the rhizome. Usually the number of strands in the rhizome is 2–2.5 times as high as in the stipe. Only in *Ph. biseriatus* the numbers are almost equal, but this is based on only one observation. Moreover, the number of strands is positively correlated with the diameter of the stipe, although this holds most convincingly for larger fronds. Wide stipes (over 5 mm) bearing large laminas (over 80 cm long) usually show six or more strands (in, e.g., *Ph. biseriatus*: fig. 3b). In less robust fronds the maximum number of strands may be much lower (down to three) as, e.g., in *M. heterolobum, M. sopuense* and *Lc. subhemionitideus* (fig. 3c, d, e), but it may also be as high as seven or eight in, e.g., *M. heterocarpum* and *M. lastii* (fig. 3f, g).

Sclerenchyma strands scattered in the ground tissue of the stipes of *Pa. (C.) decurrens* are reported by Nayar (1963b). This observation could not be confirmed, nor have such strands been found in any of the other microsoroids studied. When present in the rhizome, these strands always end rather abruptly at the articulation between the phyllopodium and the stipe. As the articulation in this species is sometimes rather indistinct, it seems likely that Nayar mistook a section of the phyllodium for that of the stipe.

## 5.5. Lamina

### Morphology

*Shape* (figs. 4 & 5) — In most species of *Microsorum* the lamina is simple. Only in the *M. linguiforme* group the pinnatifid condition is more common, some species having both simple and pinnatifid fronds, while others are exclusively pinnatifid. In *M. cinctum* (fig. 5p) the basal part of the lamina is pinnate and the apical part pinnatifid. *Microsorum spectrum* has uniquely shaped fronds which are pinnatifid but with very wide triangular lobes (fig. 5q). Other microsoroid species are either exclusively simple or pinnatifid or both, and occasionally pedately dissected, as in some specimens of *C. pteropus* and *M. spectrum.* In *Phymatosorus* the pinnatifid condition seems to be the most common.

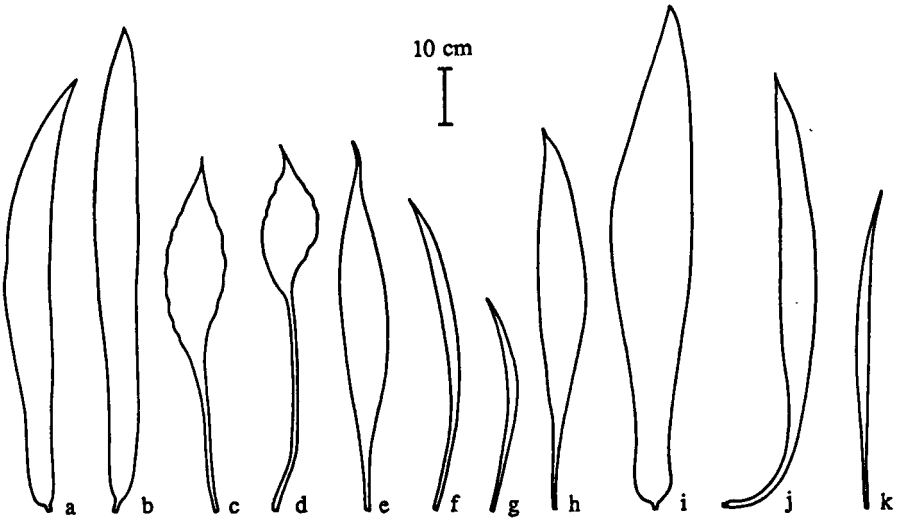


Fig. 4. **Frond shape.** Outline of 'typical' fronds. — a. *M. congregatifolium*; b. *M. glossophyllum*; c. *M. heterocarpum*, sterile; d. idem, fertile; e–g. *M. longissimum*; h. *M. membranaceum*; i. *M. musifolium*; j. *M. punctatum*; k. *M. sopuense* (a *Iwatsuki S 767*; b *Brass 29786*; c *Iwatsuki B 4162*; d idem; e *Williams 2210*; f *Bartsch 531*; g *Iwatsuki P 1200*; h *Rock 1504*; i *Williams 2831*; j *Korthals 196*; k *Hennipman 5619*).

In one species, *M. rampans*, a correlation was found between the dissection of the lamina and the altitude at which the plants had been collected: specimens from low altitudes almost exclusively show simple fronds, whereas plants at higher altitudes also bear pinnatifid fronds.

In most species aberrant specimens are occasionally found which bear fronds with an irregularly lobed base, margin or apex (furcate or cristate), which some authors have described as varieties. *Microsorum heterolobum* (fig. 5g) even derives its name from the fact that irregular marginal lobes are often present.

Size and shape of the lamina often varies considerably within one species (figs. 4e–g, 5a–e) and is thus in most cases only of limited use as a diagnostic character.

Simple laminas are usually widest at or near the middle and may be obovate, ovate, oblong, or lanceolate. They vary from relatively broad, with indices up to 10, to very long and narrow (indices up to 30–60).

Pinnatifid fronds are generally somewhat larger than simple ones of the same species. The lateral lobes, placed more or less alternately on either side of the rachis, may occur in up to 10–15 pairs (e.g., in *C. insignis* and some *Phymatosorus* species), but do not exceed four or five pairs in *Microsorum*. The greatest width is usually at or just above the base of the lobes. Their length decreases somewhat towards the apex of the frond, the longest lobe being, at least in *Microsorum*, at the first or second position from the base. The apical lobe is in most specimens slightly or distinctly larger than the upper lateral lobes, but in *C. insignis* it is also occasionally smaller.

The base of the simple and pinnatifid lamina is in most species long and attenuate and often slightly unequal. In *M. musifolium* and *M. punctatum* it may vary from obtuse to truncate and in *M. linguiforme* even to cordate.

The margin of the lamina is usually entire, but in some species, especially of the *M. heterocarpum* group, a sinuate margin is quite common.

The apex of the lamina varies from acute to (long-)acuminate, except in *M. punctatum* and *M. linguiforme* where it may also be more or less obtuse.

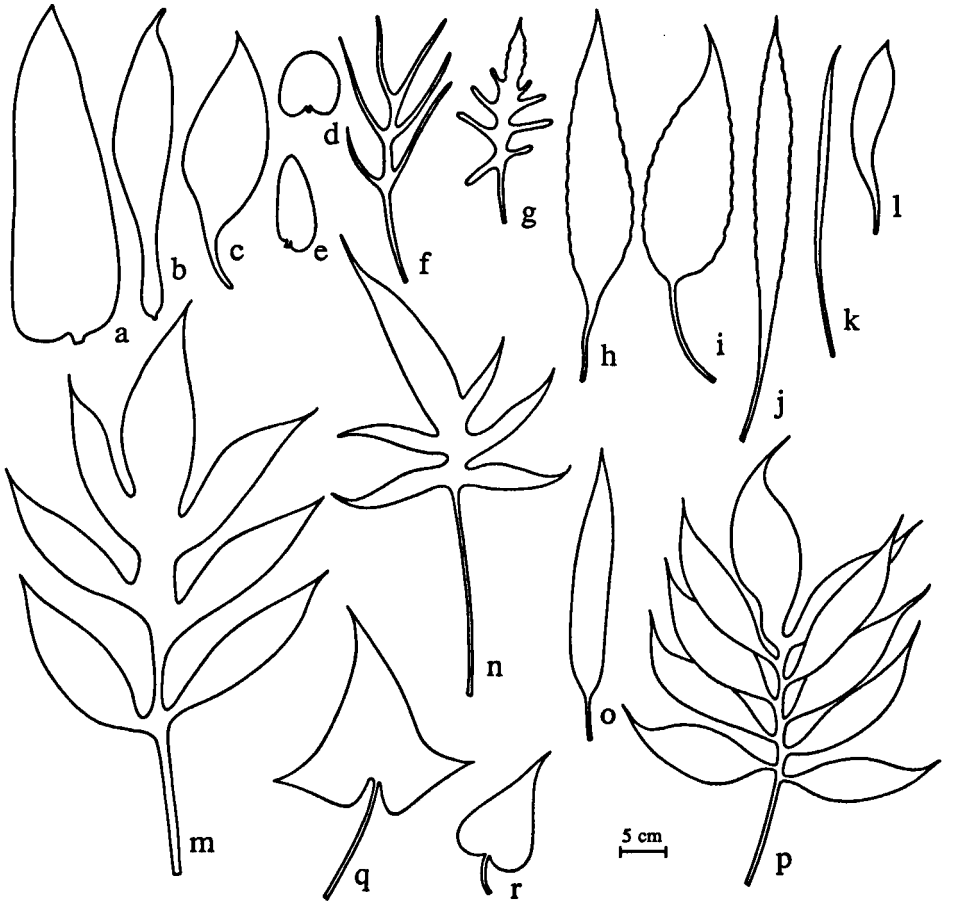


Fig. 5. **Frond shape.** Outline of 'typical' fronds. — a–e. *M. linguiforme*; f. *M. pentaphyllum*; g. *M. heterolobum*; h. *M. leandrianum*; i. *M. lastii*; j. *M. monstrosum*; k. *M. samarense*; l. *M. steerei*; m. *M. egregium* (partly reconstructed); n. *M. rampans*; o. idem; p. *M. cinctum*; q. *M. spectrum*; r. idem (a *A.C. Smith 8450*; b *A.C. Smith 5253*; c *Craven & Schodde 433*; d *King 387*; e *Lam 1137*; f *Iwatsuki P 261*; g *BS 9427*; h *Léandri 810*; i *Perrier de la Bâthie 7493*; j *Williams 1589*; k *Weber 1159*; l *Colani s.n.*, -4-1924; m *Ledermann 7542*; n *Brass 25048*; o idem; p *Jermy 8111*; q *Cowan s.n.*, 7-9-1944; r idem).

*Texture* — The texture of the lamina of most species varies from thin- to firm-herbaceous and seems to be influenced to some degree by the conditions under which the plant grows. Some species diverge distinctly in texture from the majority of species: e.g., *M. membranaceum, M. lastii,* and *M. leandrianum* have an extremely thin, membranaceous lamina, whereas e.g. *M. punctatum, M. glossophyllum, M. steerei,* and *M. samarense* are more or less coriaceous (in dried material this may be less obvious than in living specimens). In most species the lamina is flat, but in some (e.g., *M. longissimum* and, to a lesser extent, *M. musifolium*) the surface is somewhat uneven, i.e., between the veins it is slightly raised towards the adaxial side.

**Anatomy**

The general anatomy of the lamina in some microsoroids was studied by Nayar (1963a, b) and Bir & Trikha (1979). Extensive studies of the epidermis and, especially, the stomata (including a revision of the terminology) were made by Van Cotthem (1970, 1973) and for the Polypodiaceae by Sen & Hennipman (1981). All these studies on laminar anatomy include only a selected number of microsoroid species. To these data only some observations on sterile fronds of living specimens of *M. punctatum, M. musifolium,* and *C. pedunculata* are added in this revision.

*Epidermis* — In the microsoroids studied the epidermis cells contain many chloroplasts and, in surface view, have sinuate anticlinal walls, except for the cells overlying the veins, which are more angular with straight walls. This undulation of cell walls is, according to Van Cotthem (1970), quite a variable character, apparently influenced by a number of ecological factors. The outer and inner periclinal walls are approximately of the same thickness.

Stomata are only found abaxially, i.e., the fronds are hypostomatic (Van Cotthem, 1970); they are placed at the same level as the epidermis cells. Following the terminology of Sen & Hennipman (1981) all microsoroids show both polocytic and copolocytic stomata, or, in some *Colysis* species, *Lc. buergerianus,* and *Po. angustatus,* exclusively copolocytic stomata. Van Cotthem (1970) observed pericytic stomata in *M. samarense,* but this was not confirmed by Sen & Hennipman (1981) who found only polocytic and copolocytic stomata in this species.

*Hydathodes* — Hydathodes are found on the upper surface of all microsoroids at the tips of the free veins or there where two of those tips meet, and are usually lighter or darker in colour than the lamina The epidermis cells above the hydathodes are smaller than the surrounding cells. They have straight anticlinal walls and are arranged in irregular concentric circles (Nayar, 1963a; here confirmed for *M. musifolium*).

The structure and function of hydathodes were studied by Sperry (1983). He concluded that root pressure is directly responsible for the secretion of water (and salts) through the subepidermal and epidermal apoplast and the cuticle. This activity is most prominent in young tissues where the endodermis surrounding the veins and hydathodes is still absent or incomplete. Secreting hydathodes usually protrude somewhat above the epidermis, whereas non-functioning ones become gradually depressed. Guttenberg (1934) recorded so-called calcium scales, residues of calcium-oxalate secretion (Ogura, 1972), for *M. punctatum* and *Ph. scolopendria,* but

his illustration of the 'hydathodes' of the first species show a sorus in a very early stage of development. The presence of calcium scales in *M. punctatum* could not be confirmed in this study.

*Mesophyll* — The mesophyll in microsoroids is composed of 3–5(–10 in *M. punctatum*) layers of spongy parenchyma. Collenchyma is only found in the rachis or costa as a subepidermal sheath surrounding the ground tissue (in *M. punctatum*) or as abaxial and adaxial subepidermal layers (in *M. musifolium* and *C. pedunculata*). In *C. pedunculata* collenchyma was also found at the margin of the lamina. Palisade tissue (Bir & Trikha, 1979) or 'more compact' subepidermal cells (Nayar, 1963a) are only recorded for *Phymatosorus*; in other microsoroids the mesophyll is not further differentiated.

### 5.6. Venation

In the taxonomy of the microsoroid ferns venation patterns have received relatively much attention. The most recent and elaborate studies are those of Mitsuta (1982, 1983, 1984a, b), who included many observations on the development of the patterns, and those of Hetterscheid & Hennipman (1984), who concentrated on the microsoroids. The only aspect that has been seriously neglected by most authors is that of the anadromous versus catadromous architecture of venation and dissection, although already more than a century ago Von Ettingshausen (1864) demonstrated that it was, at least for venation patterns, a feature of taxonomic importance, even in microsoroid ferns. Kramer (1987), who discussed and revived the subject of the so-called dromy patterns in ferns, stated that the Polypodiaceae seem to represent a special case as the character is often not observable or only weakly and/or inconsistently developed. As far as dissection is concerned, Kramer is of the opinion that it even may have been lost in the simple fronds, from which the dissected fronds are assumed to have developed. Indeed, dromy patterns in the venation of microsoroids are not always very straightforward and need careful and multiple observations, but then, as will be shown in this study, they may prove to be a character of great taxonomic importance.

In most microsoroid species all veins are readily observable using a binocular, sometimes combined with transmitted light and some droplets of alcohol 96% on the dried lamina. Further clearing is required for only a few coriaceous species and is necessary when photographs are to be made.

The venation of simple and pinnatifid fronds can best be compared by treating the venation of the lobes of the latter as if it were that of a simple lamina, because these are essentially the same (Hetterscheid & Hennipman, 1984). In comparing fronds of different sizes it has to be taken into account that the venation pattern in narrow and small fronds is generally a simplified version of that in larger fronds of the same species. Venation of fertile fronds, which in some species may differ slightly from that of sterile fronds, is discussed in connection with the innervation of sori. The terminology applying to veins and areoles, as adopted here, is summarized in figure 6. This terminology follows that of Hetterscheid & Hennipman (l.c.), except for some details: their A3 and A4 main areoles are here referred to as marginal areoles and they

do not distinguish tertiary and quaternary veins, which are important when discussing the innervation of sori.

*Primary veins* — The primary or main veins, i.e., the rachis of simple fronds and the costae of lateral lobes, are always distinct for most of their length. They are raised and rounded, angular or slightly keeled on the abaxial side of the lamina, and usually flatter and in some species slightly grooved on the adaxial surface. Their colour often corresponds with that of the stipe (at least in dried material): light to dark, sometimes reddish brown, or green.

*Secondary veins* — The secondary veins branch off alternately from the primary veins. They run parallel at distances of up to (5–)10–20(–30) mm and are straight or slightly zigzag. The angle between primary and secondary veins is rather variable in most species (30–90°), but generally smaller in the *M. punctatum* group (never above 70°) than in the *M. heterocarpum* and *M. linguiforme* groups (never below 50° and up to 80° or 90°). There does not seem to be a distinct correlation between the lamina width and the angle between the primary and secondary veins. In species with broad fronds or lobes the angle may reach up to 90° (as in *M. linguiforme*) or may reach only 65° (as in *M. spectrum*), whereas in narrower fronds, as for example those of *M. samarense*, the angle reaches 80° and in *Lc. subhemionitideus* only 70°.

In most species the secondary veins are distinct, at least near the primary vein, sometimes becoming ± immersed towards the margin in fronds of firmer texture.

The relative length of the secondary veins depends on the point where they 'dissolve' into tertiary venation by dichotomous branching. In the *M. punctatum* and *M. heterocarpum* groups and in most species of *Colysis* and *Neocheiropteris* this is near the margin of the lamina, whereas in the *M. linguiforme* group the secondary veins branch into relatively prominent tertiary veins that border the main areoles at c. 1/2–2/3 of the lamina width. In many species of *Phymatosorus* (excluding *Ph. alatus*, *Ph. biseriatus* and *Ph. commutatus*) the secondary vein also branches into tertiary veins well within the margin of the lamina, but the general venation pattern (see below) still differs considerably from that of the *M. linguiforme* group.

In some species, especially in those in which secondary and tertiary veins are almost equally prominent, the secondary veins can be better distinguished from the tertiary veins in fertile fronds, because innervation of sori is always on tertiary or higher order veins, never on secondary veins. In, e.g., *Leptochilus* the length and the course of the secondary vein are not easy to interpret because a prominent tertiary vein branches off basiscopically near the primary vein. Thus it appears as if the secondary vein were dichotomous (ends) at that point, although it really extends almost to the margin of the lamina.

*Tertiary veins* — Tertiary veins branch off alternately from the secondary veins. They run parallel or oblique to the primary veins and connect each pair of secondary veins, thus forming the primary areoles.

*Quaternary and smaller veins* — Quaternary veins, running parallel to the secondary veins, may interconnect the tertiary veins, forming two or more secondary areoles within each primary areole. They usually do not connect the first tertiary vein with

the primary vein, although this may sometimes seem to be the case when the costal areole is very narrow.

Smaller veins may further divide the secondary areoles. These veins anastomose variously but as a rule do not connect the secondary veins with adjacent quaternary veins (except in the *M. linguiforme* group).

Free ending veins are often included in the smallest areoles. They are more or less curved, may be simple or once to three times branched and are, at least in the marginal areoles, mostly recurrent. On the upper surface of the fronds they bear more or less distinct hydathodes at their tip.

The marginal venation is formed by some acro- or basiscopically directed free ending veins and small simple areoles, often with an included recurrent free ending vein. A distinct continuous vein is usually absent.

**Venation patterns**

Within the microsoroids the general venation pattern, formed by the secondary and tertiary veins, can be roughly divided into four types (fig. 6). These differ from the 18 groups distinguished by Hetterscheid & Hennipman (1984), which are roughly divided over two major venation types, but they seem to be more congruent with the distribution of other character states.

*Venation type 1* (fig. 6a, plate 1a–f) — This type is the most common in the microsoroids; it is found in all species of the *M. heterocarpum* and the *M. punctatum* groups, *Colysis, Neocheiropteris,* and in *Ph. alatus, Ph. biseriatus,* and *Ph. commutatus*. In most species, except in some of *Neocheiropteris,* the pattern is rather regular: between each pair of adjacent secondary veins one to ten tertiary veins form a series of primary areoles of approximately equal size.

*Venation type 2* (fig. 6b, plate 1g) — The second type, unique for *Leptochilus,* differs from the first in the distinctness of the secondary veins (see above): as these branch off a basiscopic prominent tertiary vein near the primary vein, they seem to be dichotomous at that point. This type often shows irregularities and in some specimens transitions to type 1.

*Venation type 3* (fig. 6c, plate 1h) — The third type, present in most *Phymatosorus* species, differs clearly from the first in that the tertiary veins are not equally prominent. The more prominent tertiary veins border both large, main and smaller, marginal areoles. The main areoles may include two or more primary areoles separated by the less prominent tertiary veins. This usually results in one series of relatively narrow primary areoles bordering the primary vein ('costal areoles'). Each of these is subsequently followed by other primary areoles which coincide with or are included in one large main areole and one or more smaller marginal areoles which decrease in size towards the margin of the lamina. In fertile fronds the main areole and sometimes also the larger marginal ones include one (rarely two) distinct soral vein(s). As the secondary veins branch into tertiary veins well within the margin of the lamina (i.e. at the outer border of the main areoles), the primary areoles are not arranged in a regular row as in the first venation type. Some specimens of *Ph. commutatus,* however, show a transition from the (usual) first to the third type, justifying the

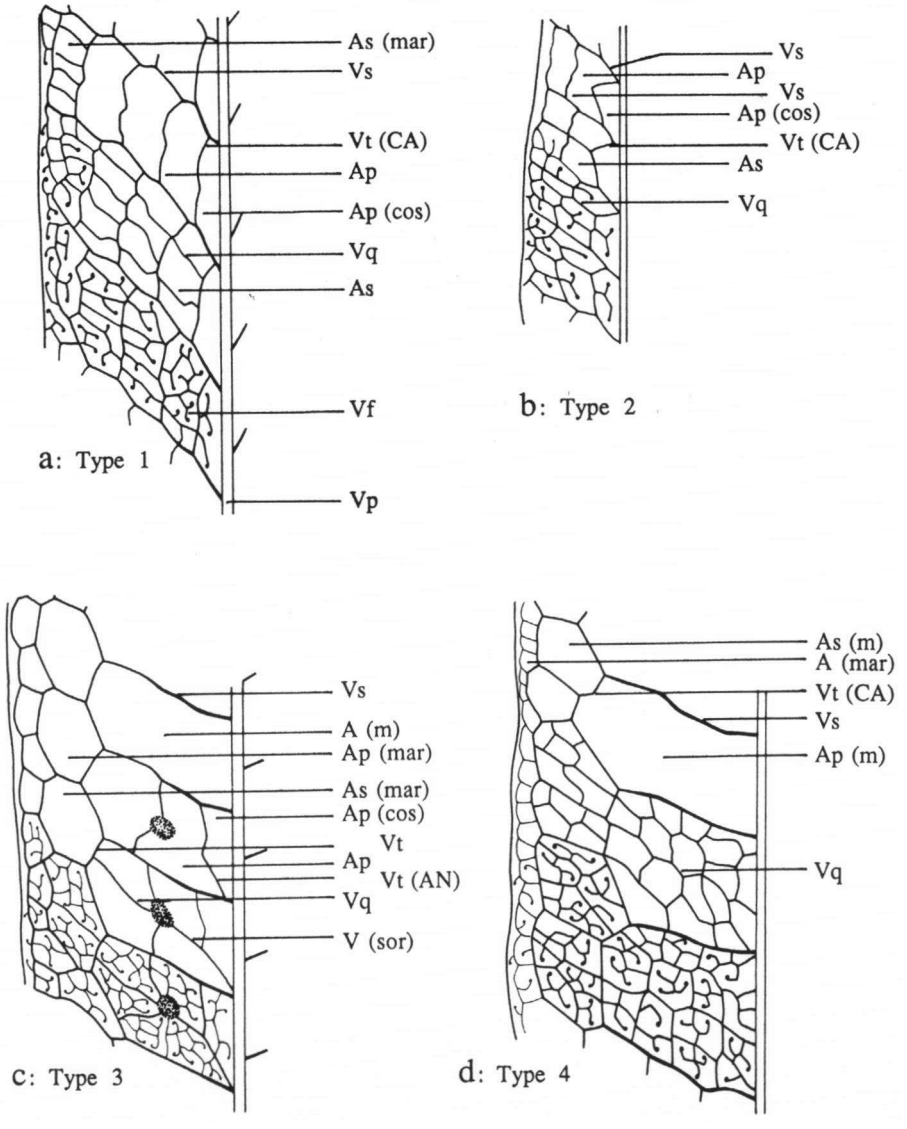


Fig. 6. **Venation.** Descriptive terminology and venation types. Smaller veins in part omitted. Vp and Vf only indicated in a. All × 1.3. V = vein; A =a reole; p = primary; s = secondary; t = tertiary; q = quaternary; f = free ending; sor = soral; cos = costal; mar = marginal; m = main; AN = anadromous (1st tertiary branch on acroscopic side of Vs); CA = catadromous (1st tertiary branch on basiscopic side of Vs); 1 = 1st tertiary branch; 2 = 2nd tertiary branch. — a. Type 1: *M. steerei.* — b. Type 2: *Lc. subhemionitideus.* — c. Type 3: *Ph. nigrescens.* — d. Type 4: *M. longissimum* (a *Bon 1274*; b *Henry 9265*; c *Hoogland 4514*; d *Elmer 12371*).

interpretation of the unequally prominent tertiary veins as being of equal order, bordering primary areoles.

*Venation type 4* (fig. 6d, plate 1i) — This type, which is exclusive for the species of the *M. linguiforme* group, superficially resembles the third type in having larger main areoles near the primary vein, bordered by some smaller marginal areoles. It differs, however, essentially from the third type in lacking included, regular and distinctive, primary areoles within the main areoles and narrow primary ('costal') areoles bordering the primary vein. Instead, the smaller veins are variously anastomose, sometimes with the secondary and primary veins as well. In fertile fronds no distinct soral veins are present as the sori are scattered on the smallest veins.

*Anadromy versus catadromy* — An important but much neglected aspect of venation patterns in microsoroid ferns is that of anadromy versus catadromy. These dromy patterns are best observed at the first tertiary branches of secondary veins in the apical part of the lamina or lobes and in as many specimens per species as possible, as in some species irregularities may occasionally disturb the general trend.

In the first, most common venation type both anadromous and catadromous tertiary veins occur. All species of the *M. punctatum* and *M. heterocarpum* groups and some species of *Neocheiropteris* show catadromous venation (plate 1a, d, e). Other microsoroids with the first venation type, i.e., some species of *Neocheiropteris,* all of *Colysis,* and the three of *Phymatosorus* (*Ph. alatus, Ph. biseriatus, Ph. commutatus*) have anadromous tertiary veins (plate 1b, c, f). Elsewhere this anadromy is found only in the third venation type including all other species of *Phymatosorus.*

*Leptochilus* species, all with the second venation type, are distinctly catadromous, as are the species of the *M. linguiforme* group (with the fourth type), although the dromy pattern in this group can only be read when the secondary vein is interpreted as being continued in acroscopic direction after its dichotomy. Observations on the ontogeny of the venation patterns in the *M. linguiforme* group are needed to confirm this interpretation.

It can be concluded that each of the microsoroid genera as here delimitated, except *Neocheiropteris,* shows only one dromy pattern. *Microsorum* and *Leptochilus* are catadromous, as is *Lepisorus* (which is therefore marked by Mitsuta, 1984b: 137, as microsoroid); *Colysis* and *Phymatosorus* are anadromous. Thus, in contrast to the suppositions of Kramer (1987), careful observations on 'dromy patterns' in Polypodiaceae may reveal a promising taxonomic character on genus level.

### Development

The heteroblastic development of venation patterns was studied extensively by Mitsuta (1982, 1983, 1984a, b). The most important conclusions to be drawn from his illustrated observations on microsoroids can be summarized as follows.

Complexity of venation increases from the first-formed to the later-formed and mature fronds. In the first-formed fronds the venation consists of a simple primary vein. This vein soon becomes pinnately branched with few (up to 4–6) simple free branches (secondary veins), the ends of which are sometimes curved and acroscopically or basiscopically directed.

In later fronds these free veins may become forked or not and anastomose with adjacent veins, often producing a free recurrent vein in the resulting areole and/or an excurrent vein which again anastomoses to form subsequent areoles. In contrast, in *Drynaria,* the venation of which has often been compared with that of *Microsorum,* the first tertiary branch of each secondary vein does not anastomose but is free and acroscopic.

The second and subsequent series of areoles are usually not formed before the first series, immediately bordering the primary vein, is completed. In later stages the included free veins branch and anastomose in various ways to produce a ± complex pattern of quaternary and smaller veins and free-ending veins pointing in all (but mostly recurrent) directions. Only in the areoles bordering the primary vein this process is often less elaborate, leaving the areoles with few, hardly anastomosing included veins.

Most of the differentiation towards the adult venation types that are here distinguished seems to take place in the later stages of development. However, examination of more blastogenetic series is needed to elucidate this part of the development and to permit a more elaborate comparison of the four types of venation patterns.

## 5.7. Sori

Position, size and shape of sori in microsoroid ferns have generally been described only superficially. Usually the sori in *Microsorum* are said to be numerous, small, round, and irregularly scattered. Closer study, especially in relation to venation patterns, yields taxonomic useful characters (Hetterscheid & Hennipman, 1984).

### Morphology

*Size and shape* — In *Microsorum* the sori vary from light to dark brown. They are usually round in circumference, with a diameter of up to 2.5 mm (up to 3 mm in *M. linguiforme*). In most species of the *M. heterocarpum* and *M. linguiforme* groups, few to many elongate sori also occur alongside the round ones; especially in the first group this is a rather common phenomenon. The length of these elongate sori does not exceed 5 mm, except in *M. samarense* and a few specimens of *M. rampans* where they always run parallel to the margin of the lamina and may reach up to 40 and 35 mm, respectively. The same range of sizes and shapes is found in *Neocheiropteris* and *Leptochilus,* although most of their species have relatively large sori. Only *Lc. axillaris* forms an exception, being fully acrostichoid.

In *Colysis* round sori as in *Microsorum* are also found, especially in *C. pteropus, C. insignis* and *C. hemionitidea,* but elongate sori, mostly parallel to the secondary veins, are more common.

In *Phymatosorus* the sori are either round and small (up to 1.5 mm) as in *Ph. alatus* and *Ph. biseriatus,* or larger and sometimes slightly elongate, as, e.g., in *Ph. scolopendria.*

In all species confluent sori are more or less frequently encountered, especially where they are densely set and fully mature. They can often be only distinguished from elongate sori by removal of the sporangia and observation of the receptacles.

**Position**

In all microsoroids the sori are superficial or, in very coriaceous fronds, slightly immersed in the undersurface of the lamina, except in some *Phymatosorus* species where they are deeply sunken in steep-sided depressions, visible as protrusions on the upper surface. The sori are distributed over the whole undersurface of the lamina or absent from the basal parts, in extreme cases confined to 1/10 of the total length of the frond. In most species of *Microsorum* this character is rather variable and both conditions occur, therefore its taxonomic value seems limited. Only in the *M. linguiforme* group the sori are usually found from the apex to the base of the fronds (except in *M. linguiforme*). In the *M. heterocarpum* group the sori usually occupy at least the upper 1/2(–1/3) of the lamina.

Presence or absence of sori in the marginal areoles and the areoles bordering the primary vein varies, sometimes even within species. Only in the *M. linguiforme* group most species bear sori in all areoles (but in *M. linguiforme* they are occasionally absent from the marginal areoles and in *M. samarense* from the costal ones).

*Innervation* — In all microsoroids the sori are innervated on tertiary, quaternary or smaller (free) veins. At first sight they are often irregularly scattered, as is usually the case in the *M. linguiforme* group, but in most species a certain, although not always completely, regular pattern can be discerned.

The sori are predominantly found on either tertiary or quaternary veins; the number per tertiary vein may vary from one, two or two to several, resulting in an equally different number of rows of sori parallel to the secondary veins. Finally, the sporangia in some microsoroid species may be confined to a few large sori, often situated on more prominent tertiary ('soral') veins, or to acrostichoid patches.

In this way eight types of sorus distribution patterns are recognized (see chapter 7: table 3, character 22). Round, elongate, and acrostichoid variants are often included in one type because of the more or less regular occurrence of transitions (especially in atavistic fronds) between these variants.

Within *Microsorum* only a single type (type 1) is found (plate 1a, i). In this type the sori in each species are irregularly scattered or (but not exclusively) arranged in two to several rows parallel to each secondary vein and may be situated on tertiary or smaller veins. This is in contrast with the types found in *Leptochilus* (excluding *Lc. axillaris*) and *Neocheiropteris*, which of all microsoroids are most similar to *Microsorum* in sorus distribution: in the species of these two genera the sori are predominantly situated on tertiary veins and are almost exclusively arranged in one to two or two to several rows parallel to each secondary vein (type 2: plate 1c & g, and type 3: plate 1d).

*Phymatosorus alatus* and *Ph. biseriatus* also show rows of sori parallel to each secondary vein, but, in contrast to types 2 and 3, these sori are predominantly innervated on quaternary veins (type 4: plate 1e).

The other four types include more solitary sori and acrostichoid distribution: species of type 5 (the larger part of *Colysis*) show a single row of sori (or one elongated sorus) or acrostichoid patches parallel to each secondary vein (plate 1f); type 6 (e.g. in *Lc. axillaris*) includes elongate sori and acrostichoid patches exclusively parallel to

the margin of the lamina; type 7 (the larger part of *Phymatosorus*) includes solitary sori on distinct soral veins (plate 1h) and type 8 has been distinguished to accommodate the very peculiar sori of *Podosorus* which are stipitate on veins extending beyond the margin of the lamina. Atavistic fertile fronds may help to decide whether fully acrostichoid species belong to type 5 or 6.

*Density* — Excluding the acrostichoid species, the density of sori on the lamina can be estimated by counting the number of sori per square cm in fully fertile areas (excluding parts without sori, which may be the marginal areoles and the areas near the primary and secondary veins). Within *Microsorum* this density varies from one to about 65 sori per square cm, with the maximum value per species starting at six.

Not surprisingly, this density proves to be correlated to sorus size, shape, and position, but only to a certain degree. It is also, but to a lesser extent, correlated to the size of the lamina. A density of 40 or more is only found in *M. longissimum, M. samarense, M. pentaphyllum, M. musifolium,* and *M. punctatum,* in which all sori are scattered on the smaller veins and not more than 1.5 mm in diameter. Other species with similar size and distribution of sori (e.g., *M. congregatifolium, M. egregium, M. heterocarpum, M. sopuense, M. lastii, M. leandrianum, C. insignis,* and *C. pteropus*) have much lower densities (the maxima per species varying from 6 to 30). And species with relatively large sori (up to 2 or 2.5 mm) as, e.g., *M. glossophyllum* and *M. membranaceum* still show higher densities (up to 20 or 25, respectively) than do species with smaller sori (up to 1 mm), e.g., *M. lastii* and *M. leandrianum* (density of up to 8).

Comparing the three groups within *Microsorum* the highest densities are reached in the *M. linguiforme* group (three species with a value over 40) and the *M. punctatum* group (two species with a value over 40), and the lowest densities occur in the *M. heterocarpum* group (two species below 10 and no species above 30).

### 5.8. Paraphyses

In the present work I follow the definition of paraphyses of Baayen & Hennipman (1987) for the sake of conformity, leaving the discussion on this theme to these and other authors [Wagner (1964), R.M. Tryon (1965), A.F. Tryon (1965), and Wagner (1965)]. This means that all sterile organs within the sorus are included even if they do not differ from the other frond indument.

Nayar (1963a, b) studied the morphology of the paraphyses of some microsoroids only superficially. Martens (1952) made an extensive study of the development of sori, including paraphyses, of *Ph. nigrescens*. Baayen & Hennipman (l.c.) were the first to study the paraphyses (and other trichomes) of many microsoroids and other Polypodiaceae extensively. Most of their observations (l.c.) on microsoroid paraphyses are confirmed in this revision. Of the many, often only slightly differing types of paraphyses which they recognized, about ten occur in the microsoroids. To simplify this survey these types are here distributed over four categories: simple uniseriate hairs with a glandular top-cell, branched hairs with glandular or acicular top-cells, clathrate paraphyses, and biseriate non-clathrate paraphyses.

The most common type of microsoroid paraphyses is the simple uniseriate hair with a glandular top-cell. These often resemble the regular frond indument and are usually 2–4 cells long and reach up to 0.2–0.3 mm (fig. 7a–c). Exceptions are, e.g., the very short paraphyses of *M. linguiforme* (1–3 cells, up to 0.1 mm long: fig. 7d) and the relatively long and many-celled paraphyses of *M. congregatifolium* (fig. 7e) and *N. superficiale* (both 3–8 cells, 0.2–0.5 mm long).

As expected, the number of cells is correlated with the length of the paraphyse. An exception was found in *M. lastii* which has rather long paraphyses (up to 0.65 mm) with relatively few, large cells (up to 4).

In most uniseriate paraphyses the cells are all approximately of the same size. Occasionally the top-cell is slightly longer or shorter. Distinct differences in cell-shape and -size are found in *M. steerei* (fig. 7f) where the top-cell is always much larger than the other cells, and in *M. (N.) sarawakense* where the top-cell is large and pyriform. Baayen & Hennipman (l.c.) also found considerable cell-size differences in *Ph. cromwelli, Ph. scolopendria,* and *Ph. subgeminatus,* resulting in variously tapering paraphyses.

A few species occasionally have a few branched paraphyses among the simple uniseriate ones. For instance, in *Po. angustatus* and *M. leandrianum* some paraphyses bear a second glandular cell laterally on one of the cells of the main axis.

In *M. longissimum* (fig. 7g) and *M. egregium,* which both bear acicular hairs on the sterile parts of the lamina, branched paraphyses with one glandular top-cell and one or two acicular lateral cells occur among simple glandular paraphyses.

Clathrate, long-stalked, scale-like paraphyses are found in a few microsoroid species, but not in *Microsorum* itself. They occur in *N. ensata* (fig. 7h) and *N. palmatopedata, Lc. normalis, Lc. subhemionitideus, Lc. buergerianus, C. wrightii, C. hemionitidea,* and *Po. angustatus.* The blade of these scale-like paraphyses is either peltate or basally attached. Scale-like paraphyses are usually most distinct in immature sori; in older sori their number is often relatively low (also because their blade breaks off easily). They always occur together with simple uniseriate paraphyses and sometimes also with intermediates of the two: apically biseriate and clathrate paraphyses. These 'intermediates' are also incidentally present in *M. spectrum* (fig. 7i), although scale-like paraphyses have not been found in this species.

In *Ph. nigrescens* (fig. 7j) and *Ph. longissimus* a seemingly different form of (apically) biseriate paraphyses is common (see also Baayen & Hennipman, l.c.). These are not clathrate and do not occur together with scale-like paraphyses.

The single observation of sporangial indument in *M. sopuense* (their *M. spec.*) reported by Baayen & Hennipman (l.c.) could not be confirmed.

### 5.9. Sporangia

Sporangia of microsoroid species are essentially similar in structure to those of most other Polypodiaceae. A spherical or ellipsoid capsule is borne on a biseriate, apically triseriate stalk. This capsule has a vertical annulus which is interrupted by the stalk and consists of indurated cells and a few non-indurated cells above and below the two stomial cells.

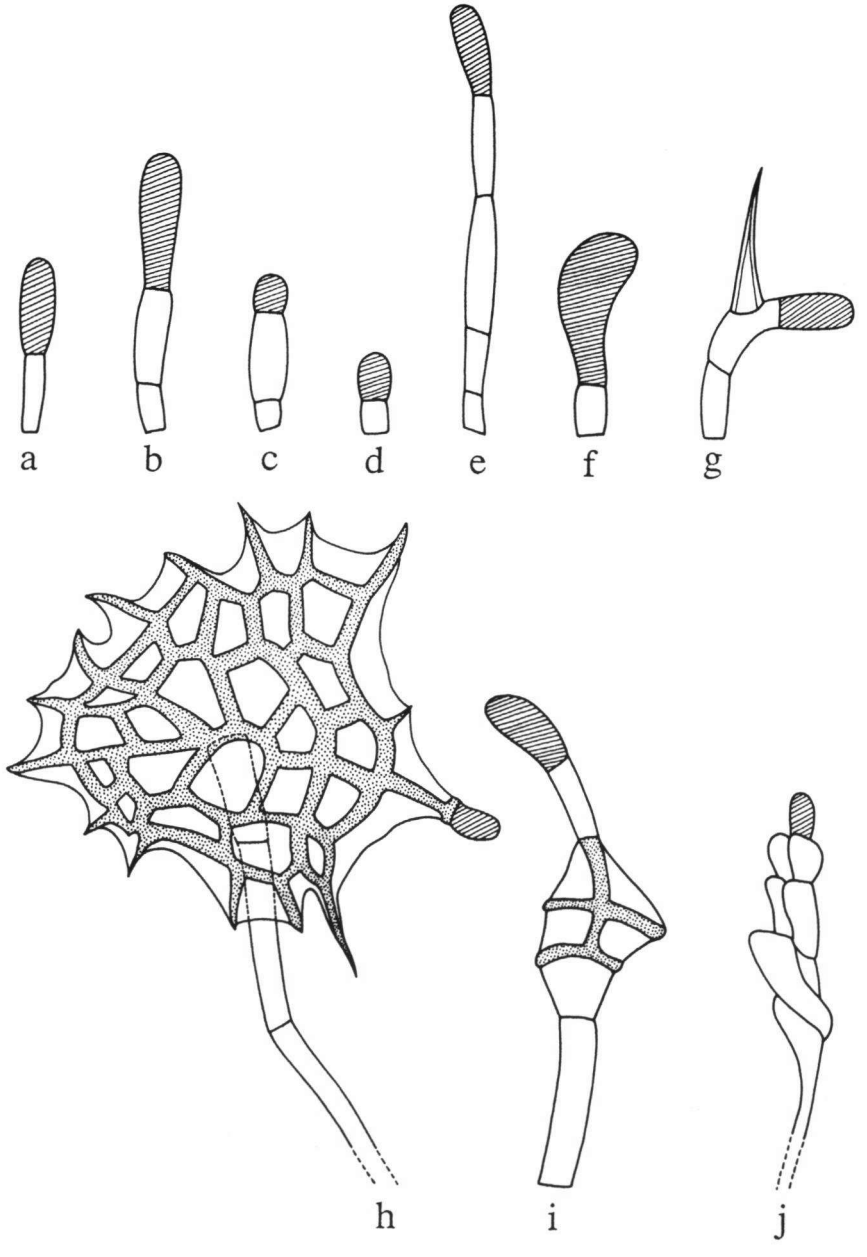


Fig. 7. **Paraphyses.** All about × 175. Cross-hatched: glandular cell; black: lignified cell-walls. — a. *M. punctatum*; b. *M. membranaceum*; c. *M. glossophyllum*; d. *M. linguiforme*; e. *M. congregatifolium*; f. *M. steerei*; g. *M. longissimum*; h. *N. ensata*; i. *M. spectrum*; j. *Ph. nigrescens* (a *Maxwell 76-243*; b *Meebold 6114*; c *Brass 29786*; d *Brass 15818*; e *Bünnemeijer 6884*; f *Ching 5431*; g *PNH 20241*; h *Copeland s.n.*, 1908; i *Heller 2438*; j *S 19058*).

The capsule measures up to 0.25–0.35 by 0.25–0.3 mm in most species. Considerably larger capsules have been found in *M. linguiforme* (0.3–0.6 by 0.25–0.4 mm) and *M. spectrum* (0.35–0.5 by 0.25–0.35 mm). The total number of annulus cells usually varies from 18 to 23, but occasionally lower (down to 15) or higher numbers (up to 28 or, occasionally in *M. linguiforme*, even 37) are found. The number of indurated cells lies around 14 (11–20), exceptional numbers occurring again in *M. linguiforme* (up to 25). Although *M. linguiforme* has both large capsules and a high number of annulus cells, in other species no such obvious correlation between capsule size and number of annulus cells could be found. Also, the members of the three species groups of *Microsorum* did not differ significantly in these characters.

Wilson (1959) studied the cell arrangement on the capsule faces of sporangia and found these essentially similar in most polypodiaceous genera. In microsoroids 10 cells are arranged in a rather regular pattern on the proximal face: four elongated cells in an upper row, three approximately quadrangular cells in the middle row flanked by another elongated cell on the annulus end, and two elongated basal cells, tapering towards the stalk. On the distal face only eight cells are found and these are not as regularly arranged as those on the proximal face, but usually three upper, three median and two basal cells can be distinguished. The walls of the capsule cells are more or less straight instead of wavy as in *Drynaria*.

The length of the stalk of the sporangia varies considerably within a sorus, depending on its position and its stage of development. The maximum length of stalks of mature (but not empty) sporangia for most species lies between 0.3 and 0.6 mm. Longer stalks (up to 0.7 mm) are found in *M. membranaceum, M. linguiforme, N. ningpoensis*, and *N. zippelii* and even longer stalks (up to 0.85 mm) in *N. superficialis, Lc. subhemionitideus*, and *Lc. buergerianus*.

The number of spores per sporangium was counted only for some sporangia with normal spores. It invariably came up to the regular number of 64.

In most species few to many aborted tannin-filled sporangia in various stages of development are mixed with normal sporangia.

### 5.10. Spores

The spores of microsoroid ferns were studied by Nayar & Devi (1964). They concentrated on Indian species and examined only one specimen per species. Hennipman (1990) analysed and discussed exo- and perispore characters of a representative collection of species of Polypodiaceae. He distinguished four exospore types of which the *Blechnum spicant* type is the most common for the microsoroids. The *Belvisia* type, which occurs in the lepisoroids and polypodioids is in the microsoroids only recorded for *Neocheiropteris* (*'M. pappei'*). For the spores of *M. membranaceum* Hennipman distinguished a separate type: the *M. membranaceum* type. Additional LM and SEM studies of spores of all species described in the taxonomic part of this thesis are discussed below.

*Size* — Most microsoroid spores measure in lateral view 50–75 by 30–45 µm. Larger spores are found in *M. glossophyllum* and in most species of the *M. lingui-*

*forme* group (up to 105 by 60 μm). Especially in *M. longissimum, M. linguiforme* and *M. rampans* a large range of sizes is found, the largest being twice that of the smallest. This may be the result of higher ploidy levels. Barrington et al. (1986) supported the hypothesis that ploidy level and spore size are correlated, e.g., spores of tetraploids are twice as large as those of their diploid ancestors.

*Shape* — The monolete, bilateral spores of the microsoroids are usually slightly concavo-convex or plano-convex in lateral view. Only in *M. samarense* and *M. pentaphyllum* the concavo-convex shape is very pronounced, the spores being relatively long and narrow. The colour of the spores usually varies from hyaline to yellowish; only in *M. membranaceum, M. lastii* and *M. leandrianum* it is distinctly yellow.

*Surface sculpture* — The surface of the spores was studied with a scanning electron microscope. Most species showed some or many globules scattered over the surface. The presence or absence of these globules varies considerably even per specimen and seems therefore not a very useful diagnostic character.

Although the sculpture of the spore surface (i.e., in microsoroids, the perispore) in most species is not very impressive, nevertheless five different types could be distinguished among the described species. For a definition of terms I follow Van Uffelen & Hennipman (1985) (colliculate, verrucate) and Harris (1955) (gemmate) (see also chapter 17: glossary).

Smooth surfaces occur in five species of *Microsorum* (in all three groups) and in *Ph. alatus*. A colliculate surface in which the rounded and not very prominent elevations are small (i.e., 0.5–2(–3) μm wide) is the most common type for *Microsorum*. This type occurs also in *C. insignis, C. pteropus, Lc. axillaris, N. superficialis,* and *Ph. biseriatus*.

*Microsorum musifolium* is unique in having distinctly larger, though still not very prominent elevations (c. 5 μm wide). Four species, *Lc. buergerianus, Lc. subhemionitideus, N. ningpoensis,* and *N. zippelii* have colliculate spores in which the elevations taper and are 1.5–2 μm wide. Finally, *M. membranaceum, M. lastii,* and *M. leandrianum* share spores which are very different from all other microsoroids. These may best be described as verrucate-gemmate.

Spines have been found only in *M. membranaceum* (small ones, c. 0.5 μm high) and in *M. pteropus* (larger ones, c. 1 μm high).

*Development* — Abortive spores were found in all species, often in high percentages. This may indicate a high incidence of hybridization but only if it correlates with distinct interspecific intermediacy, because there are several other possible sources of abortion, such as the metabolic condition of the plant which may be influenced by, e.g., cold or drought shocks during spore development (Hennipman, 1977; Wagner, 1986). Putative cases of hybridization are discussed in chapter 8 (see also chapter 6 for theoretical considerations on this subject).

### 5.11. Gametophyte

Gametophytes of microsoroids were studied by S. Pal & N. Pal (1960), N. Pal & S. Pal (1962), S. Pal (1962), Nayar (1962, 1963a, b) and Nayar & Madhusoodanan

(1977). The studies of Pal (& Pal) include *Ph. scolopendria, Ph. banerjianus, Ph. nigrescens,* and *M. punctatum,* while Nayar (& Madhusoodanan) described the gametophytes of *Pa. (C.) decurrens, C. elliptica, C. hemionitidea, C. insignis ('M. hancockii'), C. pedunculata, C. ('M.') pteropus, Lc. axillaris, M. congregatifolium, M. linguiforme, M. membranaceum, M. punctatum, N. ('M.') superficiale, N. ('M.') zippelii, Ph. nigrescens ('M. alternifolium' & 'M. rubidum'), and Ph. scolopendria.*

Apart from minor differences in the development of the apical meristem and the rhizoids, the indument and the massiveness of the mature prothalli, two major types of gametophytes are found among the microsoroid ferns: the heart-shaped prothalli and the ribbon-shaped perennial prothalli (the *Drynaria* type and the *Kaulinia* type of development, respectively, as defined by Nayar & Kaur, 1971).

The ribbon shape is reported for *Colysis, Paraleptochilus* (= *C.*) and *Leptochilus,* while the other species have a heart-shaped prothallus. For a full description of the development and morphology of both types and the minor differences between species I refer to the cited literature.

From incidental observations on cultivated gametophytes I am able to confirm the presence of heart-shaped prothalli in *M. punctatum* and *M. membranaceum*; to this group can be added *M. linguiforme, M. heterocarpum,* and *Ph. commutatus.* None of the three available specimens of *M. linguiforme* produced gametophytes as described by Nayar & Madhusoodanan (1977). They observed in this species a ribbon-like prothallus, though broader and shorter (with lobe-like branches) than those typically found in *Colysis,* etc. On the other hand, I did find gametophytes similar to those described by Nayar & Madhusoodanan (l.c.) in *C. wrightii* and *C. elliptica*: irregularly shaped and branched thalli with broad lobes and often with some approximately heart-shaped apices. Thus, in *Colysis* and *Microsorum* the two defined types are possibly not a stable character in all species.

Incidental infections of other species in some cultures may easily lead to wrong observations. Besides, a large amount of plasticity in thallus shape probably occurs, often under the influence of environmental factors, such as overcrowding of cultures (N. Pal & S. Pal, 1962). More observations are needed to judge the reliability of gametophyte morphology as a taxonomic character in the microsoroids. Therefore, this character plays only a minor role in the taxonomic considerations of this revision.

### 5.12. Chromosomes

For a concise enumeration of the chromosome numbers, see the genus description, note 1 (chapter 11).

### 5.13. Chemistry

Very few details on this subject are known from literature. The extensive surveys of Hegnauer (1962) and Berti & Bottari (1968) do not mention any microsoroids while a more recent survey of Soeder (1985) only includes a remark on *M. punctatum.* Incidental references encountered during this study are given in notes added to some of the species descriptions (chapter 13).

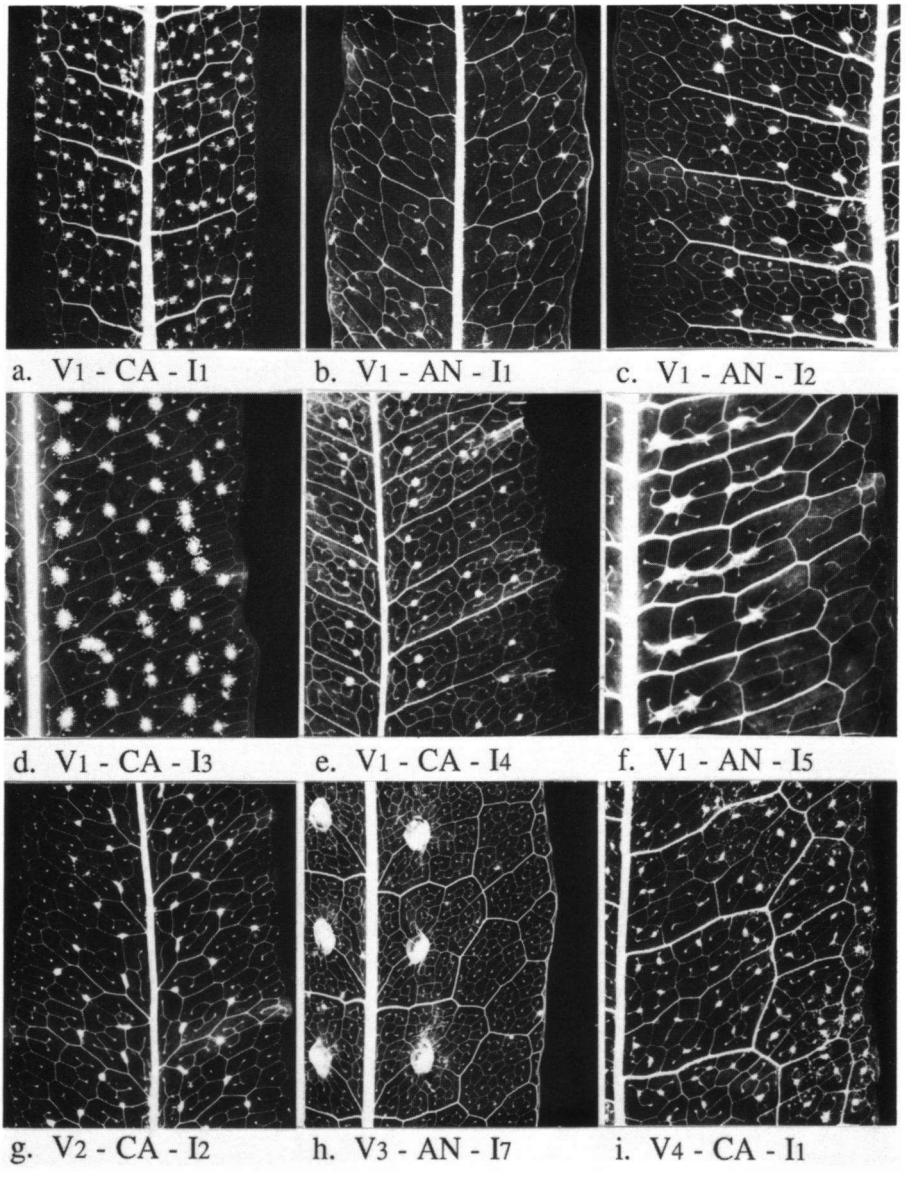


**Plate 1. Venation and innervation.** Examples of different types. All × 1.3. V = venation type; I = innervation type; AN = anadromous tertiary veins; CA = catadromous tertiary veins. — a. *M. sopuense*; b. *C. insignis*; c. *N. ensata*; d. *N. superficialis*; e. *Ph. alatus*; f. *C. hemionitidea*; g. *Lc. buergerianus*; h. *Ph. nigrescens*; i. *M. longissimum* (a *Meijer 9567*; b *Copeland 51*; c *Tagawa 3011*; d *Hooker s.n.*, U55248B; e *Daniel s.n.*, s.d., P; f *Faurie 6193*; g *Cavalerie 112*; h *Surbeck 574*; i *Elmer 12371*).

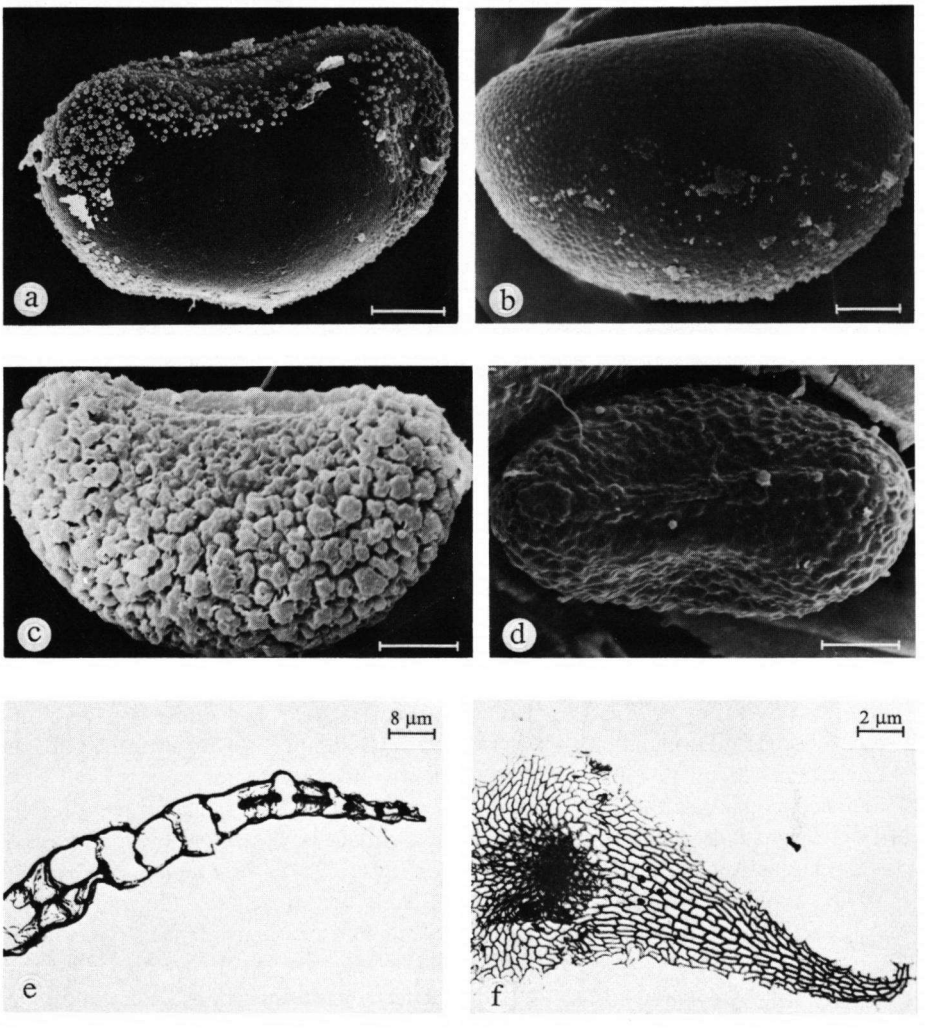


Plate 2. **Spores and rhizome scales.** Spores of different types of perispore sculpture; SEM, bar = 10 µm; a–c. lateral view, d. proximal view. Scales with LM, e.& f, as given. — a. *M. linguiforme:* smooth, globules present. – b. *M. rampans:* colliculate, the elevations not very prominent and rounded. – c. *M. membranaceum:* verrucate-gemmate. – d. *N. zippelii:* colliculate, the elevations tapering. – e. *M. musifolium:* cross section of clathrate part of rhizome scale. – f. *M. congregatifolium:* fully clathrate rhizome scale (a *Anonymus*, HBL 6478; b *Brass 25439*; c *Phusomsaeng BKF 46336*; d *Elmer 22339*; e *King 885*; f *Bünnemeijer 1128*).

# 6. TAXA

"To improve their image it might help if systematists became explicit about the theoretical and practical criteria they use to delimitate their taxa."

D.J. Kornet (1988) 529.

## 6.1. Theoretical concepts and practical consequences

### Species

In analysing and describing the diversity of nature most systematists use the species as the basic element. Therefore a good understanding of what species are and how they can be recognized is essential to this discipline. Yet, extensive and seemingly everlasting discussions suggest that this is a problem which takes more than 'one night's sleep' to solve. Especially in Pteridophytes many problems are encountered when an attempt is made to arrive at a theoretically sound and practically useful species concept. Rampant hybridization, a high incidence of polyploidy, asexually reproducing taxa and cryptic species, and a considerable amount of phenotypic plasticity blur the picture here even more than in higher organisms (Haufler, 1989; Paris et al., 1989).

In this survey I, at least theoretically, adopt the evolutionary species concept as formulated by Wiley (1981: 25): "An evolutionary species is a single lineage of ancestral-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate."

This concept agrees with the notion and opinion of an increasing number of modern systematists that, philosophically, species should be considered as individuals, not as classes (Ghiselin, 1975; Hull, 1978; Wiley, 1981). This means that species exist in nature, independently of man's ability to recognize them. Moreover, they are not defined by characteristics but by ancestor-descendant relations (Geesink & Kornet, 1989).

Wiley (l.c.) discussed extensively the various consequences, in theory and practice, of this definition. I would like to make two additional remarks.

First, the crucial and unfortunately most ambiguous part of the definition is that the lineage has to maintain its identity. The occurrence of hybrids between species may or may not threaten their identity, but Wiley (1981: 29) did not indicate where the boundary lies between a "narrow hybrid zone between two species" and a "wide zone between two geographic variants of the same species." In other words, what the definition lacks is a circumscription of the quality of species identity. This is especially important when the definition is applied in practice.

Second, a related but more theoretical problem arises in exploring the exact beginning of a lineage. To envisage this problem the discussion and the idealized and simplified scheme of Geesink & Kornet (1989) helps considerably. Even for adherents of the historical species concept, the moment of isolation will not automatically be the beginning of a species (as Geesink & Kornet suggested). As each species has to

attain its own identity, the beginning of a species must include not only a moment of splitting (isolation event), but also a process of at least some differentiation. If no differentiation takes place and/or the splitting is of very short duration (but how short?), the essential condition to become a species, i.e. achieving identity, is not fulfilled. Of course, theoretically this can only be determined some time after the isolation event.

Until these two problems are solved or agreed upon, morphological, genetical and other circumstantial evidence has to be judged both subjectively and explicitly in recognizing species. I refer to the key to the species and the notes added to the descriptions for diagnostic information on each species. When relevant, the putative hybrid character of a species is also discussed in these notes. As chromosomal evidence is not yet available, no formalized hybrids have been recognized.

In absence of genetical and genealogical evidence, the species in this thesis are based on a morphological concept. They are recognized by a combination of at least two unique, structurally independent characters or by a unique combination of such characters. In judging the suitability of those discriminating characters and thus the width of the species, Van Steenis' (1957: CCXXIII) suggestion that "a comparatively wide specific concept has yielded the most permanent results" was borne in mind.

### Subspecific taxa

Formal subspecific taxa are not recognized. Major variations found within the species studied are accommodated in either the descriptions or in additional notes. To formalize minor subspecific variations would be, as Geesink (1987: 99) states, merely "a sign of uncertainty and ignorance rather than a representation of Natural Order." As there is always considerable intergradation between the extremes found within the described species a demarcation would be very arbitrary. Moreover, if the extremes of a species are formalized there is a good chance of these extremes starting 'a taxonomic life' of their own, simply by being raised to the rank of species.

### Supraspecific taxa

Supraspecific groupings are merely a passive historical result of the hierarchical cladogenetic genealogy: each monophyletic group within the cladogram represents such a grouping. Formalizing these groups at proper ranks (genera, etc.) is mostly a matter of practicality. Pragmatic criteria as to the size of the group, stability of nomenclature, recognizability of taxa and tradition may play a role, but may, whenever a phylogenetic hypothesis is accepted, not overrule the first criterion of monophyly.

For the practical consequences of this statement on the classification of the species of *Microsorum* and other microsoroids I refer to chapter 8.

## 6.2. Selection of taxa for revision and analysis

When starting this revision the basic elements of study, namely species, had to be delimited. This immediately brought forward the problem of how to select these elements and how to set the delimitations of the group under investigation.

As has become apparent after an initial survey of herbarium material and literature, the microsoroid ferns comprise a rather large, variable, and not well-defined group of ferns (see chapter 4). In this study at least *Microsorum* should be delimited from the other microsoroid ferns, and preferably its systematic position within this group should also be clarified.

A selection of microsoroid species probably belonging to *Microsorum* has been made. To delimit this genus in its most restricted sense, so that most species of disputable taxonomic position are at least initially excluded, an in part intuitively selected combination of characters has been used:

- at least two rows of (relatively small and more or less round) sori parallel to each secondary vein (incidentally on part of the frond one row/sorus is allowed, if not innervated on a 'soral vein' as in *Phymatosorus*);
- no distinct frond dimorphy nor acrostichoidy, unless present in only a small sample of a species; it is generally thought these (advanced) characters involve many parallel developments;
- simple or pinnatifid fronds which are more or less articulate to a rhizome with clathrate scales;
- venation reticulate with included free veins which, at least in broader fronds, are pointing to all sides.

Thus the 29 species here described have been selected. After careful description and analyses, especially of venation patterns and sorus innervation, and after a more precise circumscription of *Microsorum* and the other genera studied (see chapter 8), it appeared that nine species (afterwards numbered 21–29) should be accommodated in other genera (see chapter 8).

To establish the systematic position of these species and the monophyletic character of *Microsorum,* some other microsoroids have been studied for a limited number of characters (see datamatrix). In the selection of these additional species I have attemped to gather information on one or two representatives of the most important phenetic groups or genera and to include some problematic species (e.g., *M. (?) varians, M. (?) latilobatum,* and *Po. angustatus*). After analysis a phylogeny of this selection should reflect the phylogeny of all microsoroids. In the resulting tree, the species which were not selected for the analysis should be added to the branches of 'their' representatives. Also one species of *Lepisorus* was selected to function as a possible outgroup of the microsoroids (see chapter 7).

# 7. PHYLOGENY

## 7.1. Methods and algorithms

The most important aim of evolutionary systematics is to produce a natural classification, one that reflects the results of evolution, that is, genealogical relationships, as much as possible. To achieve this aim the supraspecific taxa recognized should be monophyletic, that is, including all descendants of a common ancestor. Hypotheses

on monophyly are based on the possession of shared apomorphic characters (evolutionary novelties) as these reflect the sharing of a common ancestor which first acquired these traits. An hierarchic set of such hypotheses may result from phylogenetic analysis. If these are combined into one general and acceptable hypothesis (a phylogenetic tree), a pragmatic selection of monophyletic groups can be translated as formal taxa of a natural classification.

As can easily be concluded from the above, I may be classified as an adherent of the phylogenetic school. Four factors have played a role in attaining that position:

1) Phylogenetic analysis, developed by Hennig (1966) and advocated by, i.a., Wiley (1981), offers a (at the moment perhaps the only) way to postulate testable hypotheses concerning genealogical relationships between species, which are in conformity with the evolutionary theory. Other schools, i.e., the phenetic and the classical school, do not or not explicitly apply the consequences of the evolutionary theory, or do so inconsistently and/or only partly in their classifications (Geesink, 1987).
2) As this thesis is part of the Polypodiaceae project it seemed desirable to strive for coherence by conforming to at least some extent to the methods used by other participants in this project (Hennipman & Roos, 1982, 1983; Roos, 1985; Hovenkamp, 1986; Rödl-Linder, 1990).
3) Most of my systematic education was based on the 'principles' of the classical school. Fortunately, in the final stage of my M.Sc. studies and the initial phase of this work, some respected and friendly colleagues got involved in the discussions on cladistics. Inevitably I was, just in time, strongly and pleasantly influenced by their ideas (and thus an easy bait for social historians of science).
4) Especially in groups of organisms where classical methods failed to produce a relatively stable, acceptable classification, as is the case in the microsoroid ferns, it is worth trying to analyse and also to solve at least some of the underlying problems through phylogenetic analysis.

The scope of the present study did not permit a profound comparison of the details and implications of all available methods and algorithms, let alone the development of new variations and improvements. Therefore three well-known and more or less commonly used computer programs were selected:

- CAFCA, versions 1.8.6 and 1.9.5 (Collection of APL Functions for Cladistic Analysis; Zandee, 1987);
- PAUP, version 2.4 (Phylogenetic Analysis Using Parsimony; Swofford, 1985);
- HENNIG86, version 1.5 (Farris, 1988).

As PAUP and HENNIG86 do not differ much in their essential elements and the latter is considerable faster in producing results (although less user-friendly), PAUP was used only in some initial analyses.

A short description, relevant literature and a comparison of the three programs and the methods on which they are based are given by Van Welzen (1990). The most important differences are summarized in table 1.

Table 1. Summarized comparison of the computer programs used for phylogenetic analysis.

| | PAUP and HENNIG86 | CAFCA |
|---|---|---|
| Method | character parsimony: Wagner algorithm with branch and bound option | group compatibility: hierarchically mutually including sets of taxa, characterized by a monothetic set of characters |
| Selection criteria | minimal number of steps | 1. minimal no. of homoplasies<br>2. maximal no. of support<br>3. 1 minus 2<br>4. minimal no. of steps<br>5. highest redundancy index<br>6. highest consistency index |
| Outgroup | necessary | not necessary |
| Outgroup character states | all plesiomorphic | plesiomorphic or apomorphic |
| Polythetic groups | allowed | not allowed |

## 7.2. Data

It is stressed that a cladistic analysis, performed with the aid of a computer algorithm, does not reveal more information than is already included in the input: the character state distributions laid down in a datamatrix. The patterns concealed in this matrix are merely reflected in a more conceivable order in the cladograms superimposed on it. It is therefore of great importance to pay careful attention to the construction of the matrix. The selection of taxa and characters, followed by their translation, coding and combining into a datamatrix is the most decisive step in the analysis. Although this step should be as independent as possible from the succeeding steps, certain conditions and restrictions are set beforehand by the chosen method and algorithm for cladistic analysis. Improvement of the results of this analysis is mainly dependent on improving the information content of the datamatrix. Through reciprocal illumination characters may be reformulated or coded differently. Also addition or deletion of characters may improve the value of the matrix for phylogenetic analysis.

### Taxa

As already set out in chapter 6 the following species have been selected for analysis: the species described in the taxonomic part (nos. 1–29, of which nos. 1–20 are now classified under *Microsorum*), a small representative collection of other microsoroids (nos. 30–45) and one species of *Lepisorus* (no. 46) to function as outgroup in some analyses. These species are listed in table 2.

Table 2. Species selected for phylogenetic analysis. Species 30–46 are arranged according to possible monophyletic groups/genera. Necessary new combinations are indicated between brackets but are not made in this revision (see chapter 8).

| Number | Species |
|---|---|
| 1–29 | species described in the taxonomic part |
| 30 | *Colysis ampla* (Bentham) Copeland |
| 31 | *Paraleptochilus (C.) decurrens* (Blume) Copeland |
| 32 | *C. hemionitidea* Presl |
| 33 | *C. wrightii* (Hooker) Ching |
| 34 | *Leptochilus axillaris* (Cavanilles) Kaulfuss |
| 35 | *M. (Lc.) normale* (Don) Ching |
| 36 | *Neocheiropteris ensata* (Thunberg) Ching |
| 37 | *N. palmatopedata* (Baker) Ching |
| 38 | *M. (N.) sarawakense* (Baker) Ching |
| 39 | *Phymatosorus nigrescens* (Blume) Pichi Sermolli |
| 40 | *Ph. commutatus* (Blume) Pichi Sermolli |
| 41 | *Ph. scolopendria* (Burman) Pichi Sermolli |
| 42 | *Ph. scandens* (Forster) Pichi Sermolli |
| 43 | *M. (?) varians* (Mettenius) Hennipman & Hetterscheid |
| 44 | *M. (?) latilobatum* Hennipman & Hetterscheid |
| 45 | *Podosorus angustatus* Holttum |
| 46 | *Lepisorus thunbergianus* (Kaulfuss) Ching |

Phylogenetic analysis should only be performed on an evolutionarily meaningful group of organisms, that is to say that the species included should be more related to each other than to the species explicitly excluded (in case of an outgroup selection). This does not mean that the group concerned has to be completely monophyletic in the sense that it should include all descendants of the most recent common ancestor. Some species, which are for instance extinct, not yet discovered or of which it is still doubtful whether they belong to the group under investigation, may be temporarily excluded as long as these are not included in the outgroup.

This condition is very important in selecting species for an ingroup while the monophyly of that group is still uncertain or when the total number of species is too large to handle and must be restricted for practical reasons. Both circumstances apply in the case of the microsoroids. This group may include species that are more related to other groups, e.g., the drynarioids (Chandra, 1982), the crypsinoids (Nayar, 1970), and possibly also the lepisoroids (especially species of the *Neocheiropteris* group).

Such a supposedly para- or polyphyletic ingroup can be used as long as the method of analysis does not ask for an outgroup. In PAUP and HENNIG86 an outgroup is needed for a priori polarizing the character transformations and this causes a severe problem in selecting the species for the ingroup. To increase the chance of using mutually exclusive in- and outgroups at least once, several possible outgroups have been tried out (e.g., species 15, 37, 38, 41, 46 and combinations of species such as 4 + 15 + 20).

**Characters**

The first selection of characters is made when observing the specimens in order to delimit and describe the species. This selection is usually not explicitly argued, but is influenced mainly by tradition, personal interest, and available time and energy. Further selection (and coding) of characters is usually applied when performing a phylogenetic analysis. This is often done more or less explicitly. Some authors restricted the number of characters rigorously and use a priori established transformation series (e.g., Hovenkamp, 1986). Others included almost all characters studied (e.g., Roos, 1985; even this author omitted some characters, for instance frond size). Riggins (1987) criticized some aspects of this seemingly objective approach. I have here tried to find the golden mean.

In selecting the characters for use in phylogenetic analysis, the following arguments and techniques have been used:

1) Only characters that may be informative on a genealogical level are permitted. Characters of a presumed mainly phenotypic nature, such as, e.g., lamina size which shows ample variation in most taxa, have been omitted. Presumed autapomorphies (unique to one species) are also not included.
2) To arrive at a set of maximally independent characters and to get a more or less balanced selection with respect to the number of characters pertaining to each structural part or organ, some structurally correlated and often hierarchically ordered characters should be combined: e.g., those pertaining to venation and innervation patterns (Riggins, 1987).
3) Obviously, only characters are allowed which include two or more mutually exclusive states, i.e., characters which do not form a continuous range (see below: range coding).
4) Characters described as an index are only allowed if they consist of two structurally correlated characters, such as the length-width ratio of rhizome scales (cf. Pimentel & Riggings, 1987).
5) Characters which appear in some species as polytypism (more than one state present) may be used, but only if this polytypism is described as a separate state.

Hypotheses concerning homologues, i.e. decisions about which states are part of a transformation series of the same character, did not cause any serious problems.

Topographic and ontogenetic arguments have usually been considered sufficient, although even the most obvious homologues may, of course, hide convergencies or parallelisms.

In handling the apparently continuous ranges of some characters, none of the several gap coding procedures as surveyed and discussed by Archie (1985) has been used, because sample sizes were usually considered too small to give a good estimation of population means and variances.

Instead, a simple range coding procedure similar to that of Baum (1988) is followed. In this procedure the ranges of each species are first ranked by their maximum (or minimum) values and when these are equal they are also ranked by their midpoints. A separate character state does not, as in Baum's method, consist of all ranges with the same values, as this often leads to as many states as species. Only when the highest extreme of one group of species shows a gap to the lowest extreme of the next group which is larger than the gaps between the extremes within the group, two separate states have been recognized (see e.g. character 8: Maximum index of rhizome scales).

All characters have been coded as multistate (one column per character) instead of binary (one column per character state), as the latter coding can only be properly handled by CAFCA and not by PAUP and HENNIG86.

It was preferred not to order the characters a priori, because each such ordering can be seen as an ad hoc statement which renders the cladogram based on it less parsimonious. Only in some initial analyses the states of some or all characters were ordered a priori.

For most characters the multistate coding reflects the sequence and polarity of the supposed transformation series. However, only for characters 14, 22 and 23 additive binary coding was necessary.

One or several arguments have been used to establish each transformation series. Most often trends towards increasing complexity, differentiation and specialization and the dubious common = primitive arguments have been followed. Whenever available, additional information on ontogenetic (heteroblastic) sequences (e.g., in character 4, 9 and 11) and atavisms (in character 17 and 22) has been used. Most of the resulting transformation series are rather weakly sustained, because the arguments used are debatable, especially when reduction of complexity and differentiation and secondary reversals through neoteny are involved. Moreover analyses with ordered characters did not result in more acceptable trees than those with unordered ones. Therefore in the final analyses all character states are treated as unordered.

In initial analyses, including only the first 29 species, 29 characters with 83 states were used. When species 30–46 were added to the matrix several characters had to be removed, either because the states were no longer mutually exclusive (especially those with range coded states) or because many data were missing (e.g. spore sculpture: no SEM-studies of the additional species have been made). The final datamatrix consists of 23 characters with 69 character states distributed over 46 species (table 3).

Table 3. Final datamatrix; all characters are coded multistate; additive binary coding which was used in some initial analysis is added between brackets (characters 14, 22, 23).

CHARACTER STATE DISTRIBUTIONS:

| Species \ Character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *M. cinctum* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 1 | 3 | 1 | 3 | 1 | 1 | 4 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 |
| 2. *M. congregatifolium* | 2 | 1 | 1 | 1 | 4 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 1 | 1 |
| 3. *M. egregium* | 2 | 1 | 2 | 1 | 4 | 1 | 2 | 2 | 2 | 1 | 3 | 2 | 1 | 4 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 |
| 4. *M. glossophyllum* | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 |
| 5. *M. heterocarpum* | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 1 | 1 | 1 |
| 6. *M. heterolobum* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 2 | 1 | 1 | 1 |
| 7. *M. lastii* | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 1 |
| 8. *M. leandrianum* | 2 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 3 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 1 |
| 9. *M. linguiforme* | 2 | 1 | 1 | 1 | 4 | 2 | 2 | 2 | 2 | 1 | 1 | 1 | 1 | 4 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 |
| 10. *M. longissimum* | 2 | 1 | 1 | 1 | 4 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 4 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 1 |
| 11. *M. membranaceum* | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 3 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 |
| 12. *M. monstrosum* | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 |
| 13. *M. musifolium* | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 |
| 14. *M. pentaphyllum* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 4 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 1 |
| 15. *M. punctatum* | 1 | 2 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 2 | 2 | 1 | 1 |
| 16. *M. rampans* | 2 | 1 | 2 | 1 | 4 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 4 | 1 | 1 | 2 | 1 | 1 | 3 | 1 | 1 | 1 |
| 17. *M. samarense* | 2 | 1 | 2 | 1 | 4 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 4 | 1 | 1 | 2 | 1 | 1 | 3 | 2 | 1 | 1 |
| 18. *M. sopuense* | 2 | 1 | 2 | 1 | 4 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 3 | 3 | 1 | 1 | 1 |
| 19. *M. spectrum* | 2 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 2 |
| 20. *M. steerei* | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 3 | 1 | 1 |
| 21. *C. insginis* | 1 | 1 | 1 | 1 | 4 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 3 | 2 | 1 | 1 | 1 |
| 22. *C. pteropus* | 2 | 1 | 1 | 2 | 4 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 3 | 1 | 1 |
| 23. *Lc. buergerianus* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 2 |
| 24. *Lc. subhemionitideus* | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 1 | 1 | 3 | 3 | 2 |
| 25. *N. ningpoensis* | 2 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 2 | 1 | 3 | 1 |
| 26. *N. superficialis* | 2 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 3 | 1 |
| 27. *N. zippelii* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 1 |
| 28. *Ph. alatus* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 4 | 1 | |
| 29. *Ph. biseriatus* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 3 | 1 | 3 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 3 | 1 | 3 | 4 | 1 |
| 30. *C. ampla* | 2 | 1 | 1 | 1 | 4 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 1 | 3 | 2 | 5 | 1 |
| 31. *Pa. (C.) decurrens* | 1 | 1 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 1 | 2 | 2 | 3 | 1 | 1 | 3 | 1 | 5 | 1 |
| 32. *C. hemionitidea* | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 3 | 1 | 2 | 3 | 3 | 5 | 2 |
| 33. *C. wrightii* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 3 | 1 | 2 | 2 | 2 | 1 | 2 | 3 | 1 | 5 | 1 |
| 34. *Lc. axillaris* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 4 | 2 | 1 | 1 | 3 | 1 | 2 | 3 | 1 | 6 | 1 |
| 35. *M. (Lc.) normale* | 2 | 1 | 2 | 1 | 4 | 1 | 2 | 2 | 3 | 3 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 2 |
| 36. *N. ensata* | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 2 | 2 |
| 37. *N. palmatopedata* | 1 | 1 | 1 | 2 | 4 | 1 | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 |
| 38. *M. (N.) sararawakense* | 1 | 2 | 2 | 2 | 3 | 1 | 3 | 2 | 3 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 1 |

| | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 39. | *Ph. nigrescens* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 3 | 1 | 1 | 3 | 2 | 2 | 1 | 2 | 3 | 1 | 1 | 7 | 3 |
| 40. | *Ph. commutatus* | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 2 | 3 | 3 | 3 | 1 | 1 | 3 | 2 | 1 | 1 | 2 | 3 | 1 | 1 | 7 | 1 |
| 41. | *Ph. scolopendria* | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1 | 3 | 2 | 1 | 2 | 2 | 2 | 2 | 1 | 7 | 1 |
| 42. | *Ph. scandens* | 2 | 1 | 2 | 1 | 4 | 1 | 3 | 1 | 3 | 1 | 2 | 1 | 1 | 3 | 2 | 2 | 2 | 1 | 2 | 3 | 1 | 7 | 1 |
| 43. | *M. (?) varians* | 2 | 1 | 2 | 1 | 4 | 1 | 1 | 2 | 3 | 1 | 3 | 1 | 4 | 3 | 2 | 1 | 3 | 1 | 1 | 3 | 1 | 6 | 1 |
| 44. | *M. (?) latilobatum* | 2 | 2 | 2 | 2 | 4 | 2 | 1 | 1 | 3 | 1 | 3 | 1 | 4 | 3 | 2 | 1 | 3 | 1 | 1 | 3 | 1 | 6 | 1 |
| 45. | *Po. angustatus* | 1 | 1 | 2 | 2 | 3 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 3 | 2 | 2 | 1 | 1 | 1 | 3 | 3 | 8 | 2 |
| 46. | *Lp. thunbergianus* | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 3 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | 3 | 1 | 1 | 5 | 2 |

CHARACTERS:

**Rhizome:**

**1** — Shape of transverse section:

1. round or slightly flattened
2. exclusively dorsoventrally (slightly) flattened

**2** — Appearance of surface:

1. not waxy
2. at least sometimes waxy

**3** — Density of roots:

1. more or less high
2. low

**4** — Differentiation of vascular bundle sheaths:

1. exclusively sclerenchymatous tissue
2. collenchymatous or occasionally partly sclerenchymatous tissue
3. absent

**5** — Number and position of sclerenchyma strands:

1. ≥ 30 and scattered in ground tissue
2. < 30 and confined to dorsal part of cortex (and pith)
3. < 30 and scattered in ground tissue or occasionally absent
4. always 0

**6** — Presence of cavities in ground tissue:

1. absent
2. occasionally present

**Rhizome scales:**

**7** — Type of attachment:

1. exclusively pseudopeltate (or basifixed with small auricles)
2. peltate or pseudopeltate
3. exclusively peltate

8— Shape: maximal index:

1. ≥ 3.5
2. ≤ 2.5

9— Clathrateness:

1. exclusively throughout clathrate, or more or less opaque (subclathrate)
2. clathrate throughout or partly clathrate
3. exclusively clathrate, except for the hyaline marginal region (partly clathrate)

10 — Indument type of central region:

1. glabrous
2. lax hairs or glabrous
3. stiff or lax hairs or glabrous

**Fronds:**

11 — Shape: type of dissection:

1. exclusively simple
2. simple or pinnatifid
3. exclusively pinnatifid (to pinnate) or pedately dissected

12 — Type of indument:

1. excluding acicular hairs
2. including acicular hairs

13 — Frond dimorphy:

1. absent
2. occasionally present
3. usually faintly present
4. always or usually distinctly present

**Venation** (of sterile and non-dimorphous fertile fronds):

14 — General pattern:

1. (000) (type 1) veins forming (a row of) ± equally sized areoles between two adjacent secondary veins and no prominent vein situated parallel to the secondary veins
2. (100) (type 2) veins forming (a row) of ± equally sized areoles between two adjacent secondary veins and one prominent vein situated parallel to the secondary veins (i.e. secondary vein seemingly dichotomous near the primary vein)
3. (010) (type 3) as type 4, but the large(r) areoles bordered by the second tertiary vein and including a distinct soral vein; marginal areoles sometimes absent; costal areole formed by the first tertiary vein

4. (001) (type 4) veins forming one row of large areoles parallel to the primary vein, bordered by the first tertiary vein between each pair of secondary veins and bordered by several smaller areoles; included venation variously anastomosing; costal areole, if present, not formed by tertiary but by smaller veins

**15** — Dromy pattern: predominant type in tertiary veins (in the upper half of the lamina):

1. tertiary veins catadromous
2. tertiary veins anadromous

**16** — Forking of included free veins:

1. simple, once or twice forked
2. simple or once forked but never twice forked
3. not forked (simple)

**Sori:**

**17** — Shape:

1. exclusively ± round
2. ± round or elongate
3. ± round, elongate, or sporangia more or less acrostichoid

**18** — Position to surface of lamina:

1. superficial
2. more or less sunken, visible as protrusions on upper surface

**19** — Distribution: limitation to an apical part of the lamina:

1. limitation absent (or limited to basal part)
2. limitation sometimes present
3. limitation always present

**20** — Presence in the very marginal areoles (or on their bordering veins):

1. never present
2. sometimes present
3. always present

**21** — Presence in the costal areoles (or on their bordering veins):

1. always present
2. sometimes present
3. never present

**22** — Distribution pattern and position on veins (innervation):

1. (0000000) (type 1) irregularly scatttered or in 2–more rows parallel to each secondary vein
2. (1010000) (type 2) (almost) exclusively in at most 2 rows parallel to each secondary vein, predominantly on tertiary veins

3. (1100000) (type 3) (almost) exclusively in 2–more rows parallel to each secondary vein, predominantly on tertiary veins
4. (1000000) (type 4) (almost) exclusively in 2 or 2–more rows parallel to each secondary vein, predominantly on quaternary veins
5. (1011000) (type 5) in one (ir)regular row parallel to each secondary vein or in acrostichoid patches (or a single large sorus) between two adjacent secondary veins or fully acrostichoid
6. (0000001) (type 6) elongated or in acrostichoid patches (parallel to the margin of the lamina) or fully acrostichoid
7. (1011100) (type 7) 1 (or 2) per larger areole on a soral vein, not stipitate
8. (1011110) (type 8) stipitate on veins extended beyond the margin of the lamina

**Paraphyses:**

23 — Shape:

1. (00) exclusively uniseriate (not clathrate)
2. (10) biseriate to peltate and clathrate, or uniseriate
3. (01) apically biseriate (protruding cells) and not clathrate

## 7.3. Cladistic analysis

### Initial analyses

In the process of cladistic analysis, c. 50 different computer 'runs' have been made. The initial ones were mostly executed with CAFCA and PAUP, while in the final stage HENNIG86 prevailed. The runs differed in the number of taxa and characters involved, the ordering of character states, the designated outgroups and the algorithms through which the trees were constructed.

The initial analyses resulted in cladograms which were not very consistent with the datamatrix. Many ad hoc hypotheses of homoplasy had to be accepted even for the best possible trees. CAFCA produced trees consisting mainly of a few large and several smaller polytomies, which is a result not only of the rather low number of characters used, but also of the fact that this program cannot select groups with polythetic sets of characters. CAFCA should therefore preferably be used for biogeographical analysis only (Van Welzen & Zandee, in press). Moreover, usually many (almost) equally parsimonious different trees were possible. None of these cladograms represented *Microsorum* s.s. or any other microsoroid genus as a monophyletic group.

A detailed description and evaluation of all these slightly different analyses and results would have been very long-winded and, as none of the cladograms are accepted here, only the ranges in number of steps (character state changes) and consistency and (for CAFCA runs only) redundancy indices are given (table 4).

Table 4, Summary of results of initial analyses.

| Analysis | CAFCA* | CAFCA* | PAUP** | HENNIG86*** |
|---|---|---|---|---|
| Species | 1 – 29 | 1 – 46 | 1 – 46 | 1 – 46 |
| Steps | 181 – 223 | 272 – 319 | 196 – 238 | 117 – 223 |
| Consistency indices | .25 – .32 | .15 – .17 | .20 – .22 | .21 – .25 |
| Redundancy indices | .39 – .42 | .41 – .42 | | |

Settings:
* Partially Monothetic Sets (PMS), Maximum redundancy indices, characters (mostly) unordered.
** Addseq: closest; Swap: global; Opt.: Farris; Root: outgroup, usually most characters ordered.
*** Hennig*, characters unordered or ordered.

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It can be concluded that the present datamatrix does not contain sufficient information to construct an acceptable cladogram of all species. Many character state distributions are contradictory, resulting in very low consistency indices. This is caused by the fact that not enough characters or the wrong characters are included or by the fact that the evolutionary process in this group actually has been very complicated, including many parallel or convergent developments, reversals and reticulations through hybridization. As the present datamatrix has been corrected and improved many times and as further information on the actual evolutionary process can only be obtained through genetical and cytological investigations, which are not included in the present study, other ways have been sought to get as much information out of the present data matrix as possible.

**A final two step analysis**

An artificial way of reducing the number of homoplasies and consequently the number of cladograms to choose from, is to decrease the number of taxa involved. To achieve this, *Microsorum* s.s. as here described is postulated to be monophyletic. First, a cladistic analysis of these 20 species may lead to a number of monophyletic subgroups. Representatives of these groups ànd the remaining 26 microsoroid species may then be subjected to a second analysis. The resulting cladogram of this analysis should:

a) be more consistent with the datamatrix (less homoplasies necessary),
b) reflect the postulated monophyletic character of *Microsorum* in the position of the representative species of the subgroups, and
c) show the genealogical relationships between *Microsorum* or its subgroups and the other microsoroid species.

The analysis of the 20 species of *Microsorum* s.s. has been performed with the computer programs CAFCA (once) and HENNIG86 (seven times, with different settings). Of the original datamatrix some characters are now uninformative, as all

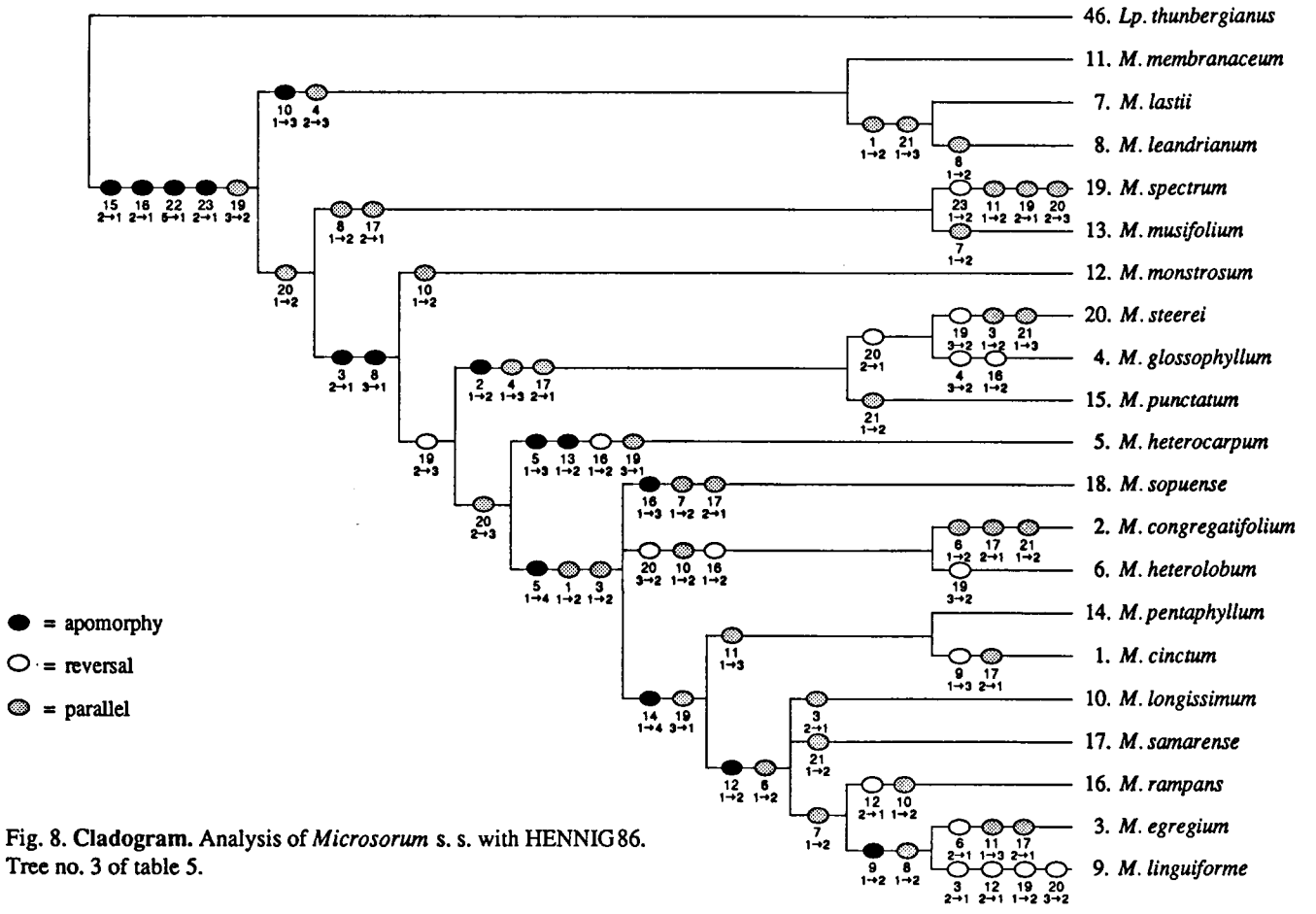


Fig. 8. **Cladogram.** Analysis of *Microsorum* s. s. with HENNIG86. Tree no. 3 of table 5.

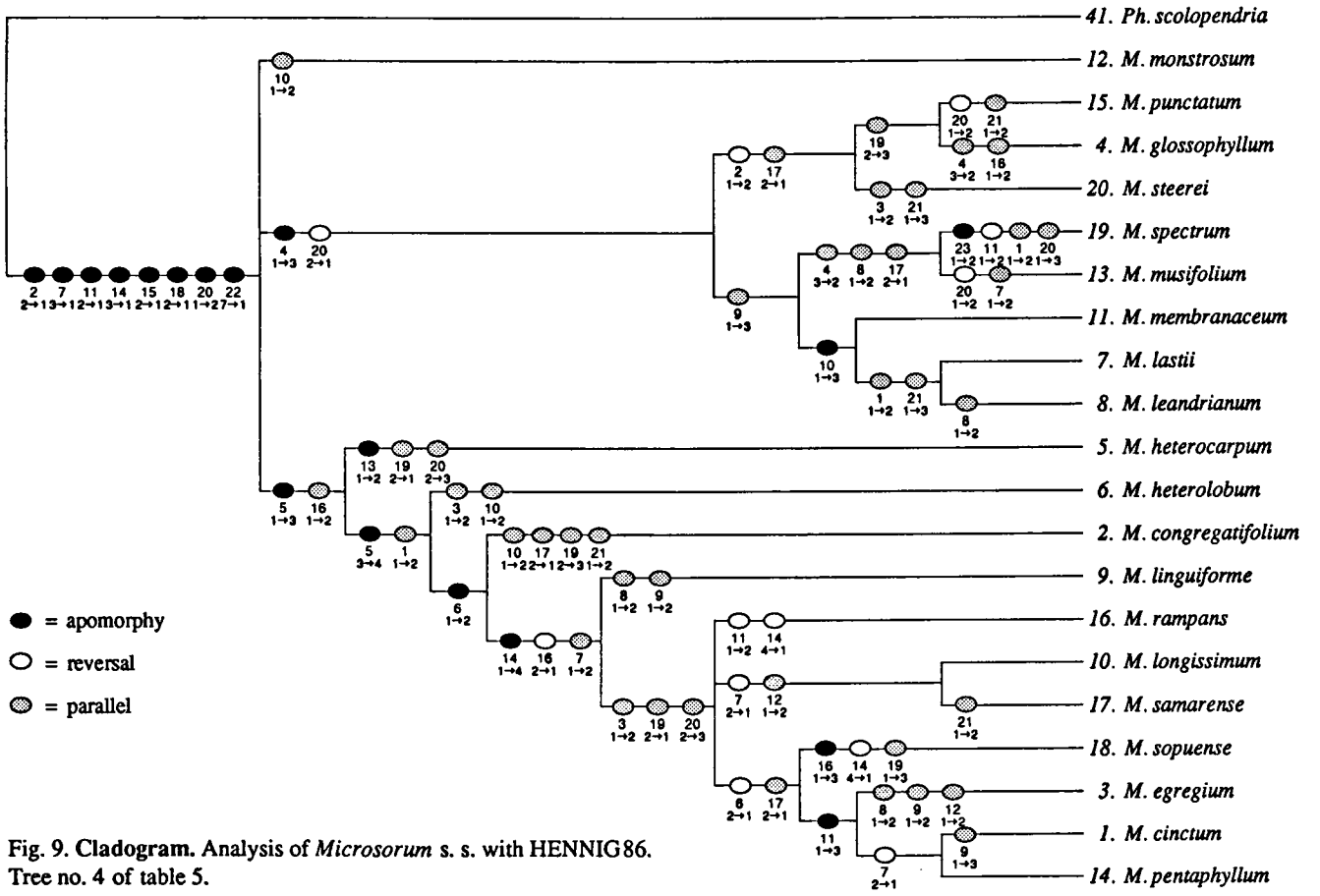


Fig. 9. **Cladogram.** Analysis of *Microsorum* s. s. with HENNIG86. Tree no. 4 of table 5.

selected species show the same state (characters 15, 18, 22) or only one species shows an alternative state (13, 23). All characters in these analyses have been treated as unordered.

The settings and results of the analyses are summarized in table 5. Two of the cladograms constructed and selected via HENNIG86 (number 3 and 4) are given in figures 8 and 9.

Table 5. Settings and results of analyses on *Microsorum* s.s.

| cladogram | settings | steps | c.i. | r.i. |
|---|---|---|---|---|
| CAFCA: 1 | PMS, Max. Red. Ind., No outgroup | 80 | .36 | .47 |
| HENNIG86: | | | | |
| 1 | outgr = 46, hennig* | 72 | .43 | |
| 2 | outgr = 41, hennig* | 73 | .46 | |
| 3 | outgr = 46, mhennig | 73 | .42 | |
| 4 | outgr = 41, mhennig | 73 | .46 | |
| 5 | outgr = 37, mhennig | 74 | .41 | |
| 6 | outgr = 38, mhennig | 71 | .43 | |
| 7 | outgr = 46, mhennig, bb | 71 | .43 | |

Again, HENNIG86 gives better results than CAFCA. The 7 selected cladograms produced by HENNIG86 do not differ much in length and consistency index. All have (with only a few exceptions) four monophyletic subgroups in common:

A) *M. glossophyllum, M. punctatum, M. steerei*
B) *M. musifolium, M. spectrum*
C) *M. lastii, M. leandrianum, M. membranaceum*
D) *M. linguiforme, M. cinctum, M. egregium, M. longissimum, M. pentaphyllum, M. rampans, M. samarense*

*Microsorum punctatum, M. musifolium, M. membranaceum,* and *M. linguiforme* are chosen as representative species because they most often appear at the base of these subgroups. The remaining five species of *Microsorum* s.s. (*M. congregatifolium, M. heterocarpum, M. heterolobum, M. monstrosum, M. sopuense*) are found each time in different positions in the constructed cladograms and will therefore be included as separate species in the second analysis.

It is assumed that the species of each subgroup probably also share other apomorphies apart from those already included in the present datamatrix. It is therefore acceptable to use all characters of the original matrix for the second analysis, as none of these will be needed to supply apomorphies when finally adding the excluded species to their representatives.

Thus the second, final analysis includes 35 taxa, of which 9 belong to *Microsorum* s.s. and 26 to other genera. Of the original datamatrix only character 12 is now uninformative, as all selected species show the same state. *Lepisorus thunbergianus* is chosen as outgroup. Again all characters are treated as unordered. Table 6 shows the length and consistency index of the selected trees of two different analyses executed with HENNIG86.

Table 6. Summarized results of the second, final analyses.

| analysis | setting | length | c.i. |
|---|---|---|---|
| 1 | hennig* | 152 | .29 |
| 2 | mhennig | 153 | .29 |

Figure 10 (see page 58) represents the first of these two trees; the second tree is only slightly different. As the rather low consistency index already suggests, this tree is very ill-supported by synapomophies. Only two characters show unique apomorphic conditions for some groups: 20 and 22. All other character states need one or more homoplasies to explain their distribution over this cladogram.

The nine species of *Microsorum* s.s., as well as those of the other formal microsoroid genera, do not form monophyletic groups and are scattered over the tree. This tree also differs considerably, in the position of quite a number of species, from the trees which resulted from the analysis on all 46 species. If this tree is accepted, then it has to be concluded that all the formal genera are polyphyletic. However, this is only one of the many possible and approximately equally ill supported trees. It is therefore expected that it probably does not show the actual genealogical relationships among these microsoroid ferns, and it is here rejected.

### 7.4. Conclusions

It can be concluded that with the used data and methods no acceptable hypothesis concerning the phylogeny of the microsoroids can be postulated. Additional data on these and other microsoroid species, and more information on the relationships between the major groups of the Polypodiaceae, which can reveal a possible outgroup, may only lead towards better results if the actual evolutionary process is indeed reflected by some orderly pattern of character state distributions. If, on the other hand, homoplasious events, reversals and hybridization have played a major role in the evolution of this group, every new attempt towards a cladistic analysis will lead to similar weakly supported cladograms. These problems probably also underlie the unfortunate efforts on phylogenetic analysis made by Geesink (1984), Kalkman

(1988) and Prance & White (1988), even though their analyses have the additional burden of using supraspecific and possibly paraphyletic groups as terminal taxa (Van Welzen, 1990).

At present a classification of the microsoroids by means of a classical approach is the most reasonable alternative for an ill-founded phylogenetic one.

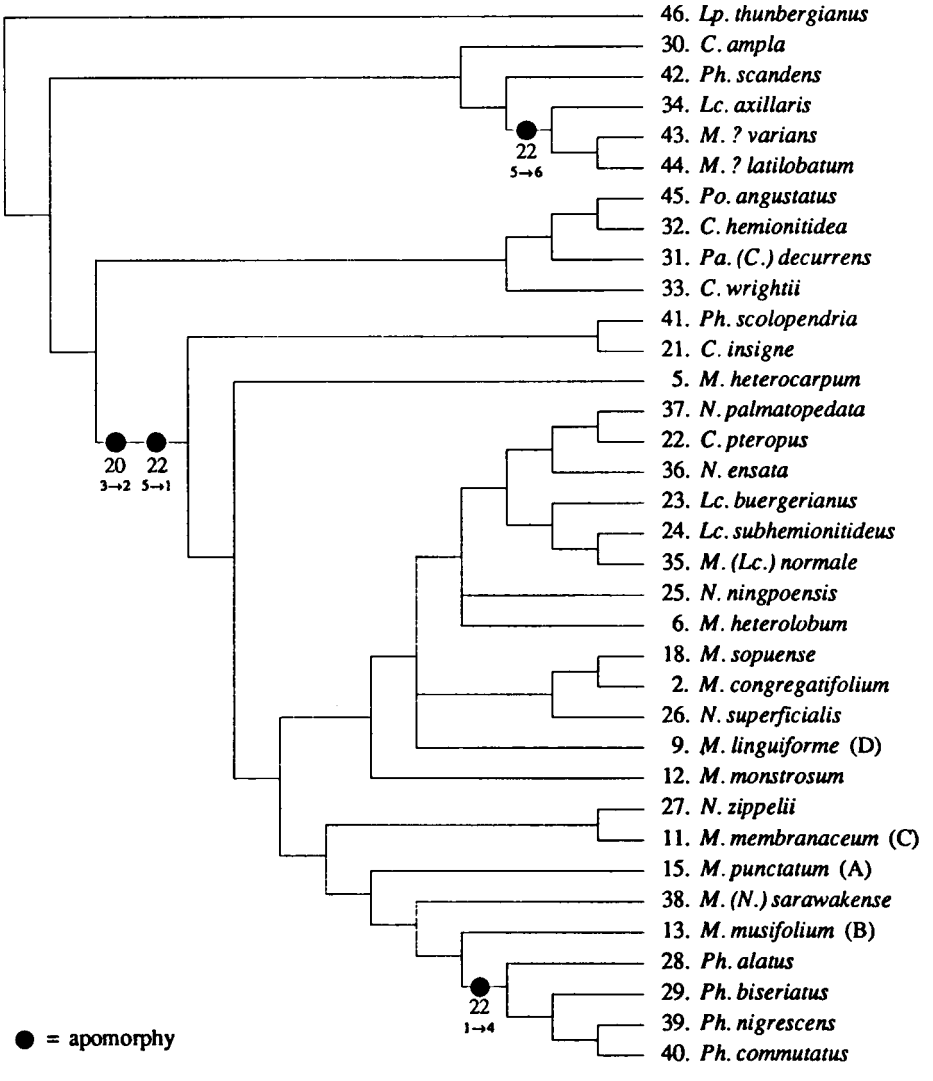


Fig. 10. **Cladogram.** Final analysis of all investigated microsoroids with HENNIG86. Tree no. 1 of table 6. Parallelisms and reversals not indicated. (A)–(D) representative species of four putative monophyletic groups of *Microsorum* s.s.

# 8. CLASSIFICATION

## 8.1. Introduction

In the preceding chapters it has been explained that a classification should be natural, i.e., only include monophyletic groups of species. It has also been demonstrated that the data and methods used in this revision do not lead to an acceptable hypothesis concerning the phylogeny of *Microsorum* and the microsoroids. A more intuitive, practical and incomplete classification of the microsoroids and an informal subdivision of *Microsorum* are therefore reluctantly accepted.

As this monograph is part of a revision of the family Polypodiaceae, the taxonomic decisions taken can be of a temporary nature. A 'final' classification of the microsoroids can and has to wait for the revised classification of the Polypodiaceae, i.e., for the moment that all major groups, or preferably species, have been analysed.

Consequently, the first and major practical criterion will be a temporary stability of nomenclature. This means that only a small number of species are transferred to other genera, resulting in only a few new combinations, and the generally accepted genus delimitations remain preferably unchanged or are only slightly modified. Taxonomic rearrangements which would lead to numerous name changes are proposed merely in an informal manner. These tentative transfers are indicated in chapter 7 (table 2) and chapter 15 (excluded species). A generic subdivision of *Microsorum,* which would lead to new subgeneric names, is also only informally suggested (paragraph 8.3). A second important criterion, especially for further analytical studies of the microsoroids, is the acceptation of easily recognizable groups of manageable size in a clear arrangement. A third criterion, which is at this stage subordinate to the first two, is that the phylogenetic information content must be as high as possible. This may result in a classification that includes para- and even polyphyletic groups, but this is inevitable as all constructed phylogenetic hypotheses are rejected here.

All three criteria, nomenclatural stability, recognizability and informativeness, exclude the most ready solution and perhaps the most logical consequence of the preceding chapters: to accommodate all microsoroid species in a single genus. However, the problem of delimitation of this over-large genus from other Polypodiaceae (especially the lepisoroids) would remain unsolved. The fact that such a genus would neither be very informative nor easily recognizable does not require additional explanation. Moreover, according to the rules of priority, the oldest available name for such a genus would be *Leptochilus*. This would mean new combinations for almost all species.

## 8.2. Delimitation of Microsorum

In this revision it is proposed to circumscribe *Microsorum* in its most restricted sense, that is to say, to exclude all species of *Colysis, Leptochilus, Neocheiropteris,* and *Phymatosorus*. Two smaller genera are included (also suggested by Hetterscheid & Hennipman, 1984):

— *Diblemma,* which is close to *M. longissimum* but in some specimens extreme in its firm texture and much elongated sori, and
— *Dendroconche,* which is a local variant of *M. linguiforme.*

Thus the species of *Microsorum* share a unique combination of characters, all of which are also encountered separately in the other microsoroid genera:

— simple and/or pinnatifid fronds with at most 5 pairs of lobes,
— reticulate venation with catadromous tertiary veins,
— superficial, round or sometimes elongated, but never fully acrostichoid sori, irregularly scattered or in part form 2 to more (ir)regular rows parallel to each secondary vein, but not predominantly on tertiary veins, nor on distinct soral veins, and
— usually uniseriate, incidentally biseriate clathrate but never peltate paraphyses.

As a consequence of this delimitation, nine of the species here described (nos. 21–29) appeared to be better accommodated in one of the other microsoroid genera (resulting in seven new combinations, as *C. insginis* had already been transferred by J. Smith and *Ph. biseriatus* is here newly described).

The other major microsoroid genera differ from *Microsorum* in the following characters (see chapter 8.5 for a provisional key to the genera):

*Colysis* (including *Paraleptochilus,* as also suggested by Hetterscheid & Hennipman, 1984):

— usually more elongate sori or acrostichoid sporangial arrangement,
— anadromous tertiary veins,
— sometimes clathrate and peltate paraphyses.

*Leptochilus* (emended):

— always a low root density, often in combination with 'root-hairs' on the scales or on the ventral surface of the rhizome,
— always a few or no scattered sclerenchyma strands and exclusively sclerenchymatous vascular bundle sheaths in a flattened rhizome,
— exclusively simple fronds of relatively thin texture,
— the secondary vein apparently dichotomous near the primary vein,
— sori (almost) exclusively in 2 or 2 to more rows parallel to each secondary vein, predominantly on tertiary veins or sporangia acrostichoid,
— sometimes clathrate and peltate paraphyses.

*Neocheiropteris:*

— sometimes anadromous tertiary veins,
— sori (almost) exclusively in 2 or 2 to more rows parallel to each secondary vein and predominantly on tertiary veins,
— sometimes clathrate and peltate paraphyses.

*Phymatosorus:*

- — simple and pinnatifid or exclusively pinnatifid fronds with often more than 5 pairs of lobes,
- — always anadromous tertiary veins,
- — sori either on distinct soral veins or (almost) exclusively in 2 or 2 to more rows parallel to each secondary vein and predominantly on quaternary veins,
- — sori sometimes sunken.

### 8.3. Subdivision of Microsorum

In this revision the species of *Microsorum* are informally classified in three subgroups:

1) The ***M. linguiforme group*** includes *M. cinctum, M. egregium, M. linguiforme, M. longissimum, M. pentaphyllum, M. rampans,* and *M. samarense.* This group coincides with subgroup D used in the final cladistic analysis (see chapter 7). These species share a number of characters, the most important of which are the unique venation pattern, the presence of acicular hairs, and a rhizome with sclerenchymatous vascular bundle sheaths, no scattered sclerenchyma strands and, in 4 species, cavities in the ground tissue. Large ranges of spore size may indicate higher ploidy levels in this group (see chapter 5).
2) The ***M. punctatum group*** consists of *M. glossophyllum, M. musifolium, M. punctatum, M. spectrum,* and *M. steerei.* These species are represented in group A and B of the final analysis. *Microsorum glossophyllum, M. punctatum* and *M. steerei* resemble each other very much. They have a more or less cylindrical waxy rhizome with many scattered sclerenchyma strands and unsclerified or only partly sclerified vascular bundle sheaths, exclusively clathrate or subclathrate pseudopeltate scales, simple fronds of usually firm texture with more or less round sori which are often limited to an apical part of the lamina. The position of *M. musifolium* and *M. spectrum* (group B) in this subgroup is less certain, but it is nevertheless better than in one of the other groups, or in a fourth group, comprising only these two species, as they both show a venation pattern and sorus shape which is similiar to that of the other three species.
3) The ***M. heterocarpum group*** comprises *M. congregatifolium, M. heterocarpum, M. heterolobum, M. lastii, M. leandrianum, M. membranaceum, M. monstrosum,* and *M. sopuense.* This is the most heterogeneous, least coherent subgroup. *Microsorum lastii, M. leandrianum* and *M. membranaceum* form a smaller group equivalent to group C of the final analysis, but the position of the other species is very uncertain. All species of this subgroup have two instabilities in common: irregular sorus shape and fronds with an often undulate or sinuate margin, with the irregular lobes of *M. heterolobum* as an extreme example. The lamina is usually simple and of thin texture and the sori are relatively small. Superficially some specimens of *M. heterocarpum* resemble some specimens of *M. membranaceum, M. monstrosum* or *M. congregatifolium,* and hybridization with one or more of

these species does not seem unlikely (see also the note added to the species description of *M. monstrosum*). Karyological and isozyme studies may prove to be helpful in this case.

### 8.4. Classification of the microsoroids

As the cladistic analysis of the selected microsoroids did not result in an acceptable hypothesis concerning the genealogical relationships within this group, this paragraph is, to a certain extent, inevitably subjective and speculative.

From the results of the cladogenetic analysis the suspicion arises that *Microsorum* as described in this revision is not monophyletic. It may include a few monophyletic subgroups, possibly coinciding with some of the informal subgroups of the preceding paragraph, but on the whole it is at most paraphyletic (not including all descendants of a *common ancestor*), but probably even polyphyletic (not including all descendants of *different ancestors*).

Some species of *Microsorum* seem to be very close to other microsoroids. *Microsorum heterocarpum* shows some resemblances to the group of *C. hemionitidea, C. pteropus, Pa. (C.) decurrens,* and *C. pedunculata.* Of all *Microsorum* species it is the only one which has some frond dimorphy and the sori are often slightly elongated, resulting in almost similar patterns as sometimes found in *C. pteropus.* Both tendencies are more prominently present in *Colysis.*

Some superficial resemblances between *M. musifolium* and *C. macrophylla, N. superficiale* and *C. henryi,* and *N. ensata* and *C. hemionitidea* were also found. A closer investigation should reveal whether these resemblances are the result of synapomorphic developments or whether they are convergent tendencies or plesiomorphic traits.

Not only the monophyly of *Microsorum* is questioned but also that of *Neocheiropteris* and *Phymatosorus.*

The former is the only genus studied in which the dromy pattern is not a constant character for all species: tertiary veins are anadromous in *N. ensata* and *N. palmatopedata,* whereas the others have catadromous veins. These two species are also the only species in the genus with clathrate paraphyses. Additional studies should reveal if there is reason to suspect the presence of two separate monophyletic groups and what the relationships between these groups are. Moreover, some species show superficial resemblances – in venation and innervation patterns and the slightly elongated sori – to species of *Colysis* and the relationships between these two genera ask for special attention.

In *Phymatosorus, Ph. alatus* and *Ph. biseriatus* diverge remarkably in some characters from the other species studied. They both have pseudopeltate scales against exclusively peltate in *Ph. scolopendria* and *Ph. scandens,* and innervation type 4 against type 7 in the other species. Together with *Ph. nigrescens* and *Ph. commutatus* they differ from the other two species in the differentiation of vascular bundle sheaths (at most partly sclerenchymatous against exclusively sclerenchymatous), the shape of the rhizome scales (maximum index at most 2.5 against at least 3.5), the

dissection of the fronds (exclusively pinnatifid against simple or pinnatifid), the shape of the sori (exclusively ± round against sometimes elongate) and the absence of the sori in the marginal areoles (against sometimes present). Pal & Pal (1964) listed some additional differences between *Ph. nigrescens* and *Ph. scolopendria*. For *Phymatosorus* also additional information is needed to reveal whether these differences are expressions of the presence of several monophyletic subgroups or whether this genus is polyphyletic.

As has been stated, no phylogenetic classification of the microsoroids is possible at this moment. Even if all traditional genus delimitations are abandoned, only very few and small, possibly monophyletic groups can be postulated with some doubt, the position of the majority of species remaining very obscure (including that of the rather aberrant *M. (?) varians, M. (?) latilobatum,* and *Po. angustatus*).

Intuitively it seems that species groups of *Colysis, Leptochilus, Phymatosorus,* and *Neocheiropteris* are sistergroups of some species of *Microsorum,* while the most primitive elements of the microsoroids are probably found in *Microsorum* itself, as some of its species, e.g. the widespread *M. punctatum,* show very little differentiation in most characters.

As some other authors already suggested, the lepisoroids may be related to some species of *Neocheiropteris,* although the clathrate paraphyses on which this supposition is based also occur in *Colysis, Leptochilus, Podosorus* and even in *M. spectrum,* although in the latter only incidentally and not really peltate.

If an outgroup, or sistergroup, for the microsoroids is needed, the lepisoroids still seem the most probable candidate at the moment, although no characters unique to either of these groups have become apparent. On the other hand, if the microsoroids form a polyphyletic group which should at least also include the lepisoroids and if part of the microsoroids represents the most primitive element of the Polypodiaceae, which has never been suggested up till now but does not seem unreasonable in view of the results of the present study, an outgroup has to be found outside this family. This leads to the conclusion that any sensible, either phylogenetic or 'classical', classification of the microsoroids has to await further studies of other species and genera of the Polypodiaceae.

### 8.5. Provisional key to the genera

Not all microsoroid species were studied. Thus, a key to the genera including all their species cannot be given here. Also, the species included in the cladistic analysis but not described in the taxonomic part of this thesis were only studied for a restricted number of characters and specimens. Therefore the following key to the genera (species) is provisional.

1a. Sori stipitate ..... ***Podosorus*** (*angustatus*)
b. Otherwise ..... 2
2a. Sori 1 (or 2) per large areole on a soral vein, sunken or not; fronds simple or pinnatifid . ***Phymatosorus*** (*commutatus, nigrescens, scandens, scolopendria*)

b. Sori in 2 rows parallel to each secondary vein, predominantly on quaternary veins, superficial; fronds pinnatifid ..... ***Phymatosorus*** (*alatus, biseriatus*)
c. Sorus innervation otherwise; sori superficial or at most slightly immersed; fronds simple or pinnatifid (or pedately dissected) ..... 3
3a. Tertiary veins anadromous ..... 4
b. Tertiary veins catadromous ..... 6
4a. Fronds pinnatifid; sporangia acrostichoid ..... ***M. (?)*** (*latilobatum, varians*)
b. Fronds simple or if pinnatifid (or pedately dissected), sporangia not acrostichoid (at most the sori elongated) ..... 5
5a. Fronds simple (at most irregularly lobed) or pedately dissected; lamina firm-herbaceous; rhizome scales often with superficial hairs; sori present in the costal areoles, in 1 or 2 rows parallel to each secondary vein, round or slightly elongate; (young) sori often with clathrate paraphyses; scattered sclerenchyma strands in cross section of rhizome few (< 30) or absent
***Neocheiropteris*** (*ensata, palmatopedata*)
b. Fronds simple or pinnatifid; lamina (thin-)herbaceous; rhizome scales in most species without superficial hairs (if present, then the sori absent from the costal areoles); sori irregularly scattered or in one row parallel to each secondary vein, round to distinctly elongate, or more or less acrostichoid; (young) sori in most species without clathrate paraphyses (if present then the sori absent from the costal areoles); scattered sclerenchyma strands in cross section of rhizome many (≥ 30) or absent
***Colysis*** (*ampla, hemionitidea, insignis, pteropus, wrightii, Pa. decurrens*)
6a. Venation type 2: one prominent vein situated ± parallel to each secondary vein, i.e., secondary vein seemingly dichotomous near the primary vein
***Leptochilus*** (*axillaris, buergerianus, subhemionitideus, M. normale*)
b. Venation type 1 or 4, i.e., secondary vein not seemingly dichotomous near the primary vein, extending to at least halfway the lamina width ..... 7
7a. Fronds simple; lamina up to 65 cm long, herbacous to coriaceous; sori almost exclusively in (1 or) 2–more rows parallel to each secondary vein, predominantly on tertiary veins
***Neocheiropteris*** (*ningpoensis, superficialis, zippelii, M. sarawakense*)
b. Fronds simple or pinnatifid; lamina up to 175 cm long, membranaceous to coriaceous, sori irregularly scattered or in part in 2–more rows parallel to each secondary vein, on tertiary or smaller veins ..... ***Microsorum***

## 9. DISTRIBUTION AND HABITAT

The distribution of the species of *Microsorum* ranges from tropical and subtropical Africa (from Sierra Leone in the northwest to Natal in the southeast), through India and Southeast Asia (as far as the Himalayas, southern China and Taiwan in the north and Queensland in the south), to the Pacific (up to Tahiti). One species is found in and endemic to Hawaii (*M. spectrum*). If we leave this aside and also the widespread *M. punctatum* and the two endemics of Madagascar (*M. lastii* and *M.*

*leandrianum*), the range of the genus is confined to India, Southeast Asia and the Pacific up to the Fiji Islands, excluding the Andaman and Nicobar Islands, the Marianas and Queensland (fig. 11).

The species of *Colysis* treated in this thesis show more or less the same distribution in Southeast Asia, but they do not reach the Pacific islands and they extend a little further northeast (into the Ryu-Kyu Islands) and they have not (yet?) been found in Sulawesi and northern Luzon (figs. 24, 25).

The two species of *Leptochilus* described in this study are confined to the mainland of Southeast Asia, the Himalayas and southern Japan, with the majority of collections coming from southern en central China (up to Szechwan in the north) (figs. 26, 27).

The species of *Neocheiropteris* described in this study show distribution patterns which overlap those of *Leptochilus* on the one hand (*N. ningpoensis* reaching into southern Japan and Szechwan) and those of *Colysis* and *Microsorum* on the other (*N. zippelii* occurring as far southeast as Sulawesi and the Sunda Islands, with one odd record from New Guinea) (figs. 28, 29).

Finally, the two species of *Phymatosorus* are endemic to New Guinea and the Fiji Islands, respectively.

No representatives of microsoroids are found in the Neotropics. A species previously known as *Polypodium bradeorum* Rosenstock and transferred by Gómez (1977) to a new genus *Pseudocolysis* Gómez, resembles the species of the Old World genus *Colysis* in some aspects. Evans & Mickel (1969), however, studied several collections of both genera and convincingly concluded that the resemblances are the result of parallel developments.

A closer look at the distribution of the species of *Microsorum* (figs. 13–21, 23) reveals that only two widespread species are distributed well outside Malesia (i.e., the Flora Malesiana area): *M. punctatum* and *M. membranaceum*. Of these two, only the former is also widespread within Malesia, whereas the latter only reaches northern Luzon. Other more or less widespread species in Malesia are *M. congregatifolium, M. heterocarpum, M. linguiforme,* and *M. musifolium*. The other 14 species are confined to two islands (*M. longissimum* and *M. egregium*) or a small area (*M. steerei*), or are endemics (ten to Malesian islands, one to Hawaii and two to Madagascar).

The area with the highest number of co-occurring species of *Microsorum* is the Philippines (ten species, including four endemics). If the Philippines are split up into two sub-areas (cf. Hovenkamp, 1986), the northern part (northern Luzon) and the central-southern part, the former is the richest (nine species), closely followed however by the latter (seven species). Moreover, the endemics are also evenly distributed among these two sub-areas.

Other Malesian areas rich in *Microsorum* species are New Guinea, Borneo, and Sumatra (seven, six and five species, respectively). These numbers come very close to those of *Goniophlebium* (table 7), which differs in having fewer species in the Philippines and fewer endemics in the Philippines and New Guinea (Rödl-Linder, 1990).

*Pyrrosia* (Hovenkamp, 1986) and the Drynarioideae (Roos, 1985) are represented in the Philippines by approximately as many species as *Microsorum* but outnumber this genus in other Malesian areas: especially *Pyrrosia* in Sumatra, Java, Sulawesi, and the Lesser Sunda Islands, and the Drynarioids in Java, Borneo, and Sulawesi.

Further west, on the mainland of Southeast Asia, *Microsorum* shows also a relatively low species diversity, compared to both Malesia and the other polypodiaceous taxa. This may be explained by a more restricted preference of the species of *Microsorum* for evergreen lowland or hill forests with relatively high annual precipitation and no dry season or a short one.

All four groups have a relatively high rate of endemism in the Philippines, compared to other Malesian areas: *Microsorum* 40%, Drynarioids 33%, *Goniophlebium* 29% and *Pyrrosia* 30%. This rate is equalled only in Borneo by the Drynarioids (33%) and exceeded by *Pyrrosia* (50%). Surprisingly, no endemics of Borneo are known for *Microsorum*. In other Malesian areas endemism for these taxa does not exceed 17%.

Table 7. Number of species and endemics (before the slash) for four polypodiaceous taxa in the following Southeast Asian areas: Southeast Asia Mainland (SEA), Malesia, i.e. the Flora Malesiana area (MAL), Peninsular Malaysia (PMA), Sumatra (SUM), Java (JAV), Borneo (BOR), Philippines (PHI), Sulawesi (SUL), Lesser Sunda Islands (LSI), Moluccas (MOL), New Guinea (NG).

| area: / taxon | SEA | MAL | PMA | SUM | JAV | BOR | PHI | SUL | LSI | MOL | NG |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Microsorum* | 4 | 16 | 0/4 | 0/5 | 0/3 | 0/6 | 4/10 | 1/4 | 0/2 | 0/4 | 3/7 |
| *Drynarioideae* | 12 | 19 | 0/6 | 0/7 | 0/6 | 3/9 | 3/9 | 0/7 | 0/3 | 0/7 | 0/9 |
| *Goniophlebium* | 14 | 12 | 0/5 | 0/6 | 0/3 | 1/6 | 2/7 | 0/4 | 0/2 | 0/4 | 0/6 |
| *Pyrrosia* | 25 | 23 | 0/7 | 2/12 | 0/9 | 4/8 | 3/10 | 1/7 | 0/6 | 1/6 | 1/7 |

Observed distribution patterns of species are the result of a combination of processes and factors, of which the most important are:

- ecological reasons (within the constraints of historical processes): climate and habitat preferences such as altitudinal range or mean annual precipitation,
- (unintended) selective collecting policies (sampling errors),
- historical processes such as speciation, extinction, vicariance and dispersal.

The majority of species of *Microsorum* have a preference for areas with relatively high precipitation (everwet rain forests or wet pockets in drier areas), or grow in wet and shaded niches as low epiphytes, lithophytes or terrestrials, often in or along streams. Moreover, a relatively high proportion (40%) of species is restricted to low and middle elevations (i.e., not above 1200 m), whereas only 25% may be found above 2000 m. Only two species (*M. pentaphyllum* and *M. heterolobum*) do not

grow below 1000 m, but of these few collections (15 and 11, respectively) have been seen.

The few species growing in seasonally dry areas, at high altitudes or in exposed situations, are relatively firm in texture (e.g., *M. punctatum, M. glossophyllum, M. pentaphyllum)* or seasonally deciduous (*M. membranaceum, M. lastii,* and probably also *M. leandrianum*).

As *Microsorum* species are relatively low in number in the rather well collected parts of the mainland of Southeast Asia and western Malesia and as they are not very inconspicuous (at most a bit unattractive), as they do not grow in less accessible places nor are otherwise difficult to collect, the effect of selective collecting is suspected to be marginal in these areas. On the other hand it is expected that more species may be found in eastern Malesia, especially the wet parts of Sulawesi and New Guinea, as these areas, despite being less well collected, already show more or less the same diversity for *Microsorum* as western Malesia (apart from the Philippines). Moreover, 50% of the species of *Microsorum* newly described in this century are from eastern Malesia (and have not been found elsewhere) and constitute almost half of the total number of *Microsorum* species in that area.

It can be concluded from the notes added to the species descriptions that in certain areas some species have probably not been collected recently. This may be caused by a decrease of collecting activities in those areas, by the rarity of the species, a severe decrease in number, or by extinction. Apart from areas which have recently been inaccessible or hardly accessible in Southeast Asia (Burma, Laos, Vietnam), or where also very few collections have been made in the past (Lesser Sunda Islands, Moluccas), the Philippines (no recent collections of *M. congregatifolium, M. membranaceum, M. heterocarpum*) and Java (*M. heterocarpum*) are worth mentioning.

Historical processes which form the basis of distribution patterns of modern species can be reconstructed to a certain extent with the aid of methods of biogeographical analysis. A prerequisite is a hypothesis concerning the phylogenetic history of the involved species, that is to say, a resolved cladogram. As no acceptable hypothesis resulted from this study, leaving the phylogeny of *Microsorum* and other microsoroids to mere speculation, I had to refrain from any biogeographical analysis. However, if the three subgroups of *Microsorum* as distinguished in chapter 8.3 are monophyletic and the genealogical relationships within the groups are elucidated, the distribution patterns within especially the *M. linguiforme* group are biogeographically interesting, as this group includes a number of allopatric species in the Flora Malesiana area.

In general it can be said of spore-plants such as mosses and probably also ferns (Van Zanten & Gradstein, 1988) that general patterns resulting from vicariancy events are expected to be more disturbed by incidental successful dispersal events than those of seed-plants. This leads to more inconsistencies in the resulting generalized areagrams, which need ad hoc explanations (e.g., Hovenkamp, 1986: 120). Especially small spores 'floating' in moist air-currents may travel at least over the short distances between the islands and continental parts of the Malayan area where the majority of *Microsorum* species is distributed.

## 10. NOTES ON THE DESCRIPTIONS AND THE KEY

All species are treated alphabetically according to accepted genus and species names. Apart from the species of *Microsorum* (nos. 1–20) nine other microsoroid species are fully described: 2 species of *Colysis* (nos. 21 and 22), 2 of *Leptochilus* (nos. 23 and 24), 3 of *Neocheiropteris* (nos. 25–27) and 2 of *Phymatosorus* (nos. 28 and 29). An explanation of this selection is given in chapter 6.2.

### Nomenclature sections

Synonymy is listed in full and chronologically, with each basionym followed by its homotypic synonyms.

Authors and collectors are cited in full. Literature references are shortened to author(s), date and page and are listed in full in chapter 19 (Literature).

The abbreviation q.n.s. (quoad nomen solum) is used where only the name (with its type) of a taxon and not the description and other cited material is meant.

For invalid synonyms the collections on which these names are based are indicated, conform to the indication of types for valid names. These invalid names are included in the index, but not in the chapters 14 and 15 (Doubtful species and Excluded names, respectively).

All types have been examined unless stated otherwise. If attempts to find a type in a particular herbarium were in vain, this is indicated. Lectotypes have been selected only for the names of the accepted taxa. Duplicates of isotypes are only listed when seen.

Collecting localities (of type specimens etc.) are usually cited from the collectors' notes (especially in Southeast Asia fluctuating transcriptions may be more confusing than elucidating).

### Descriptions

Methods of selection, preparation and measuring of parts of specimens for description are discussed in chapter 3 (Material and methods).

Unless otherwise stated in a note, each description is based on more than 10 collections.

Descriptions of new terms and terms which may differ from common usage can be found in chapter 17 (Glossary).

### Distribution, habitat and notes

Areas of distribution are mentioned in the same sequence (namely west–east and north–south) under each species.

The number of collections which have been examined from a certain (sub-)area are placed between brackets after that (sub-)area.

Unless otherwise stated in a note, recent (i.e., dating from 1960 or later) collections have been seen from all (sub-)areas of distribution (as listed under 'Distribution') of a species.

Notes on distribution, habitat, abundance, growth, cultivation, vernacular names and uses have been compiled from the collectors' notes, unless indicated otherwise.

Distribution maps of all described species, except *M. spectrum, Ph. biseriatus,* and *Ph. alatus,* are given in chapter 9.

### References

Primary references to nomenclature are given in the nomenclature sections.

References to recent Floras and regional revisions which deal with the species described in this revision are listed in a note following the description of *Microsorum.*

Special references, usually pertaining to certain aspects of a single taxon, are given in notes following the description of that taxon.

Additional references concerning morphology and taxonomic history can be found in the general chapters on these subjects.

Usually no references are made to publications in which species are merely mentioned or described shortly (check-lists, distributional records, expedition reports, etc.).

### Key

The key is not intended to reflect taxonomic or phylogenetic relationships. All species studied and described in full are included in the key; that is, all species of *Microsorum* and the species described under 21 to 29 which have usually been included in *Microsorum* or may be easily misidentified as belonging to *Microsorum.* A provisional key to the genera is given in chapter 8.5.

Only fully developed and (for most species) fertile sporophytes can be identified with the key to the species.

Descriptions of new terms and terms which may differ from common usage can be found in chapter 17 (Glossary). Different types of venation patterns and innervation of sori are illustrated and discussed extensively in chapter 5. In the key only the necessary characteristics (for the lead concerned) are mentioned.

## 11. GENUS DESCRIPTION

## MICROSORUM

*Microsorum* Link (1833) 110 (orth. variant: *Microsorium,* see note 2). — T y p e: *Microsorum irregulare* Link = *Microsorum punctatum* (Linnaeus) Copeland.

*Diblemma* J. Smith (1841) 399. — T y p e: *Diblemma samarense* J. Smith = *Microsorum samarense* (J. Smith) Bosman.

*Dendroconche* Copeland (1911) 91. — T y p e: *Dendroconche annabellae* (Forbes) Copeland = *Microsorum linguiforme* (Mettenius) Copeland.

*Microsorum* sect. *Eumicrosorum* Fée [(1852) 269, nom. inval. ICBN art. 21.3, 32.1b and 34.1e] — Based on the type species of *Microsorum.*

Herbs, epiphytic, epilithic, or terrestrial, small- to medium-sized. *Rhizome* short with the fronds often tufted, or long with the fronds ± evenly spaced, creeping or climbing, often closely appressed to the substrate and with few or many accessory branches, dorso-ventrally flattened or ± cylindrical, 1–10 mm wide, in very few species waxy (glaucous); roots sparsely to densely set (then forming a thick mat); phyllopodia alternating in two (rarely three) dorsal rows, more or less distinct, contiguous or up to 8 cm apart. Rhizome anatomy (in internodial cross section): vascular bundles 5–23, in a (sometimes flattened) cylinder, bundle sheaths not differentiated, sclerenchymatous or collenchymatous, ground tissue parenchymatous with or without scattered sclerenchyma strands, in a few species with intercellular cavities. *Rhizome scales* ± densely set and overlapping, closely appressed or more or less spreading, usually pseudopeltate, occasionally peltate, usually narrowly ovate with acuminate apex and entire to dentate margin, occasionally more orbicular and rounded, 0.5–10 by 0.3–2.5 mm, fully clathrate or with a hyaline margin (partly clathrate), rarely opaque and in part more than 1 cell thick (in *M. glossophyllum*), light to dark brown, with an apical and often a few (rarely many) marginal short glandular hairs, in some species with long lax (root-)hairs in the central region. *Fronds* articulated to the phyllopodia, monomorphic except for some specimens of *M. heterocarpum* and *M. linguiforme*, in most species consistently simple, in some simple and pinnatifid, or exclusively pinnatifid, rarely irregularly bipinnatifid (in *M. pentaphyllum*) or partly pinnate (in *M. cinctum*), with few to many minute glandular hairs, occasionally with a few small scales and (in the *M. longissimum* group) with small acicular hairs; stipes indistinct or up to 30 cm long, in cross section near the base with 3–9(–14) vascular strands arranged in a U-shaped arc; lamina of simple fronds (ob)ovate or ± lanceolate, sometimes long and narrow (index up to 65), membranaceous to coriaceous, usually (thin-)herbaceous, base usually narrowly angustate, but in some species broader (obtuse, truncate, cordate, auriculate), margin entire, sinuate, or undulate, apex usually acute to acuminate; lamina of pinnatifid fronds conform to that of the simple fronds except in size and shape, 1–4 (or 5) lobes to a side, the longest lateral lobe at 1st or 2nd position from base, the apical lobe longer, shorter or conform to the upper lateral lobes. *Venation* distinct or more or less immersed but usually visible in transmitted light, at least the larger veins often distinctly raised on undersurface and somewhat less on upper surface, sometimes differing in colour from the rest of the lamina; venation pattern: veins either forming a more or less regular row of up to 10 ± equally sized areoles between each pair of adjacent secondary veins (type 1, *M. punctatum* group and *M. heterocarpum* group) or forming one row of main areoles situated parallel to the primary vein and bordered by one or two marginal rows of smaller areoles (type 4, *M. longissimum* group); secondary veins often slightly zigzag, tertiary veins (in type 4 the veins bordering the main areoles) catadromous, quaternary veins interconnecting tertiary veins (in type 1), smaller veins variously anastomosing, free included veins simple, once- or twice-forked, ending in hydathodes, usually pointing to all sides except for some recurrent and occasionally excurrent veins in the marginal zone. *Sori* round to slightly (occasionally much) elongated, often in part a few sori slightly confluent, superficial or rarely

(in some coriaceous fronds) slightly sunken, spreading all over the undersurface of the lamina or confined to the upper 1/10–4/5, in all areoles or absent in the costal and/or marginal areoles, irregularly scattered on the smaller anastomosing veins and the free included veins and/or 1 or 2 per quaternary vein, forming 2–8 irregular rows parallel to each secondary vein, rarely in part on tertiary veins. *Paraphyses* few to many per sorus, uniseriate, occasionally once branched, 1–4(–8)-celled, with a glandular apex, in *M. spectrum* occasionally with a biseriate and clathrate apex and in *M. longissimum* and *M. egregium* sometimes with one or two acicular lateral cells. *Sporangia* of the polypodiaceous type, short- to long-stalked, glabrous; the capsule c. 0.25–0.6 mm high, annulus (15–)18–23(–37)-celled, indurated cells 11–20(–25), the sporangial faces with more or less straigth cell walls in the sporangial faces. *Spores* 64 per sporangium, monolete, bilateral, concavo-convex to plano-convex, usually small, up to 75(–105) by 45(–60) µm, surface smooth to slightly sculptured.

Distribution. Tropical and humid subtropical Africa, Southeast Asia, northern Australia and the Pacific Islands. Fig. 11.

Habitat. Tropical, a few species also subtropical, primary and secondary evergreen or sometimes deciduous rain and monsoon forests. The maximum altitude varies from 200 to 2800(–4000) m, but for the majority of species it lies at c. 1200 m. Most species grow in shady and humid places, often near free water, some species may also grow in more exposed and drier habitats. Most species are low epiphytes, but some may also (i.e. facultatively) grow higher or terrestrial and epilithic.

Notes. 1. Chromosome number: 2n = 72 in *M. linguiforme, M. membranaceum, M. musifolium,* and *M. punctatum* (Löve et al., 1977; N. Pal, 1962; Nayar & Madhusoodanan, 1977). Exceptions are recorded for: *M. punctatum* (2n = 144: Löve et al., 1977) and *M. spectrum* (2n = 148: Wagner, 1963a or 2n = 144?: Löve et al., 1977). Related genera like *Colysis, Leptochilus, Neocheiropteris* and *Phymatosorus* also have 2n = 72 for most species. For four species of *Phymatosorus* 2n = 74 has been reported (Löve et al., 1977).

2. The spelling *Microsorium* has to be regarded as an orthographic variant of the original spelling *Microsorum,* hence it should not be used (Bosman, 1986).

3. *Microsorum* sect. *Dissidentes* Fée [(1852) 269, nom. inval., ICBN art. 34.1e] ex Ching (1933b) 296 = *Colysis.*

4. The following species have been in cultivation for at least some time in botanical gardens: *M. cinctum, M. glossophyllum, M. heterocarpum, M. linguiforme, M. longissimum, M. membranaceum, M. musifolium, M. punctatum, and M. rampans.*

5. Recent Floras and regional revisions (published after 1900) dealing with the species here described (incl. nos. 21–29) are listed below. The species concerned (sometimes described under one of their synonyms) are indicated after each reference by the numbers as used in chapter 13 (species descriptions). Usually these species form only a selection of all species described under *Microsorum* in that publication; the other species are excluded from the genus and not described here. The areas are named as indicated by the authors.

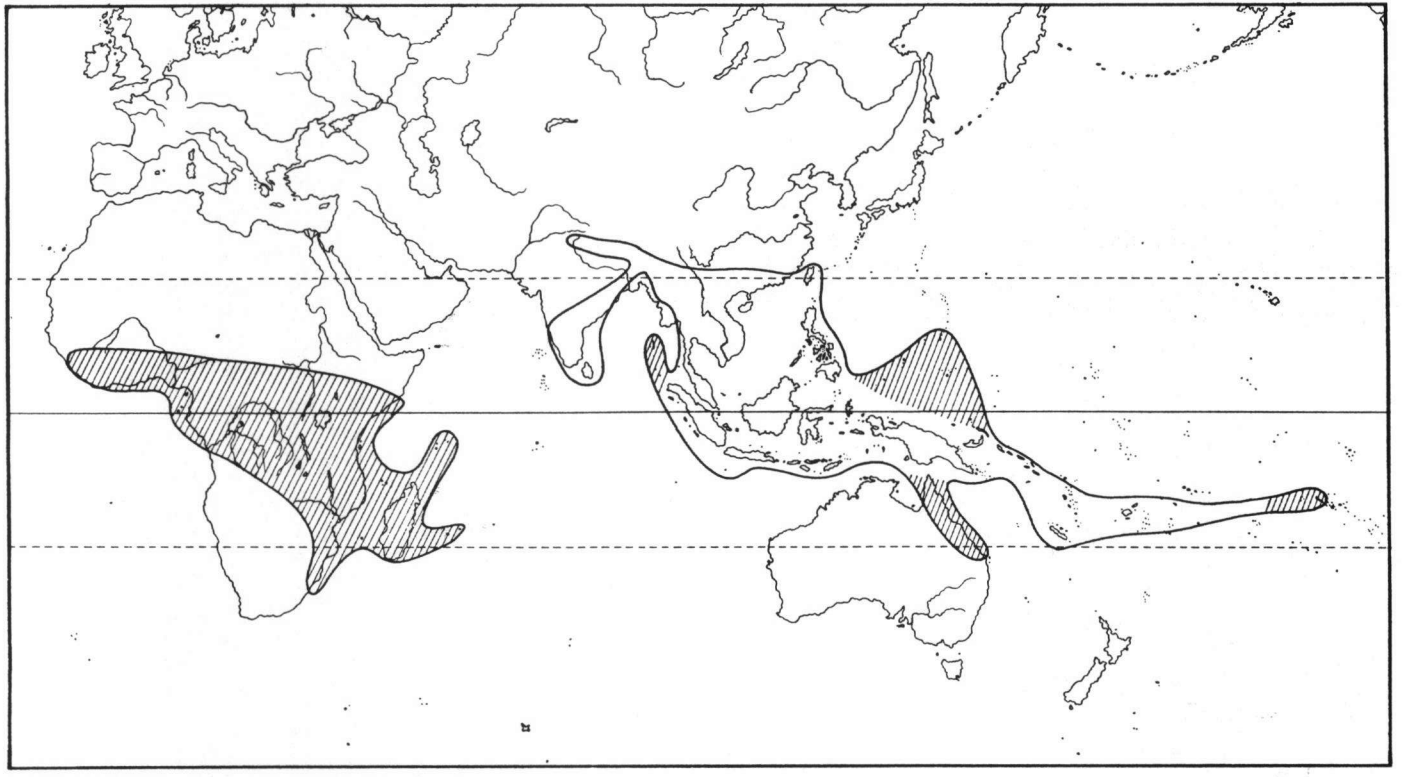

Fig. 11. Distribution of *Microsorum* Link [excl. *M. spectrum* (Kaulfuss) Copeland on the Hawaii Islands].
Hatched areas: exclusively for *M. punctatum* (L.) Copeland.

AFRICA. — South Africa: Jones & Clemesha (1976) 220–225: **15-(26=15)**. — Zambia: Schelpe (1970) 156–158: **15.** — Angola: Schelpe (1977) 121–124: **15.** — Madagascar & Comores: Tardieu-Blot (1960) 114–117: **7-8-15.**

INDIA & SRI LANKA. — India: Bir & Trikha (1968a) 133–148: **11-15-21-22-24-26-27**; Nayar (1961) 1–38: **11-15-21-22-26-27**; Satija & Bir (1985) 72–80: **11-15-21-22-24-26-27.** — Meghalaya State: Baishya & Rao (1982) 67–68: **11-15-26.** — Southern India: Manickam (1986) 153: **15.** — Sri Lanka: Sledge (1960) 142–145: **11-15-21-22.**

(SOUTH) EAST ASIA (excl. Flora Malesiana area). — Japan: Nakaike (1975) 339–347: **21-22-23-26**; Ohwi (1965) 101–102: **25**(*'M. buerg.'*)**-21-22.** — Okinawa & Ryu Kyu Islands: Walker (1976) 113–114: **21-22-25** (*'M. buerg.'*). — Taiwan: DeVol & Kuo (1975) 129–197: **11-15-20-21-22-25.** — China: Ching (1933b) 293–313: **11-15-20-21-22-23-24-25-26-27.** — Kwangsi: Wu et al. (1932) 288–298: **11-15-21-22-26-27.** — Hong Kong: Edie (1977) 125–132: **15-21-22-25-27.** — Thailand: Tagawa & Iwatsuki (1989) 523–534: **11-15-21-22-26-27.** — Indo-China: Christensen & Tardieu-Blot (1939) 193–195: **11-15-20-21-22-23-24-26-27**; Christensen & Tardieu-Blot (1941) 477–486: **11-15-20-21-22-23-24-26-27.**

FLORA MALESIANA AREA. — Malaya: Alderwerelt (1909a) 627–667: **5-9-10-11-12-13-15-21-22-26-27-28**; Alderwerelt (1917) 375–403: **4-5-9-10-11-12-13-14-15-16-21-22-26-27-28**; Holttum (1954) 170–180: **2-5-13-15-21-22-27.** — Malaysia: Piggott (1988) 126–134: **5-13-15-21-22-27.** — Java: Backer & Posthumus (1939) 189–224: **5-13-15-21-22-26-27.** — Philippines: Copeland (1960) 476–487: **2-5-6-9-10-11-12-13-14-15-17-21-22-27.**

PACIFIC ISLANDS. — New Caledonia: Brownlie (1969) 376–379: **9-15-28.** — Samoa: Christensen (1943) 116–117: **15.** — Society Islands: Copeland (1932) 72–74: **15.** — Fiji: Brownlie (1977) 287–288: **15**; Copeland (1929c) 91–94: **9-15-28**; Parham (1972) 64–65: **9-15-28.** — Hawaii: Degener (1940) fam. 17: **19.**

## 12. KEY TO THE SPECIES

0a. Sori irregularly scattered or in 2 or more rows parallel to each secondary vein; if in 1 or 2 rows and on tertiary veins then tertiary veins catadromous and rhizome scales throughout clathrate ..... *Species included in this key and described in chapter 13*

b. Sori in 1 (ir)regular row (or sori elongate) parallel to each secondary vein or 1 (or 2) per large areole on a soral vein or stipitate or sporangia more or less acrostichoid; if sori in 1 or 2 rows parallel to each secondary vein and on tertiary veins then tertiary veins anadromous or, if catadromous, the rhizome scales partly clathrate

*Microsoroid species not included in this key and not described in chapter 13*
(see chapter 8.5 for a provisional key to the genera and chapter 6.2 for an explanation of this selection)

1a. Pinnatifid, bipinnatifid or partly pinnate fronds present; simple fronds present or absent ..... 2

b. Fronds exclusively simple or at most irregularly lobed ..... 10

2a. Index of longest lateral lobe at most 3 *and* many (> 50) scattered sclerenchyma strands present in cross section of rhizome; inner walls of cells in clathrate part of scales warty; endemic of Hawaii ..... **19. M. spectrum**

b. Otherwise; inner walls of cells in clathrate part of scales smooth; not in Hawaii ... 3

3a. Venation pattern type 4 (1 row of larger main areoles parallel to primary vein and bordered by medium-sized and/or smaller marginal areoles); sheaths of vascular bundles in rhizome sclerenchymatous; sori spreading all over the lamina or restricted to a distal part ..... 4

b. Venation pattern type 1 (between each pair of adjacent secondary veins 1–10 small and ± equally sized primary areoles, bordered at the margin of the lamina by a few simple smaller areoles); sheaths of vascular bundles in rhizome collenchymatous or, if sclerenchymatous, the sori restricted to the distal part (1/2–2/3) of the lamina . . . 7

4a. Longest lateral lobe at most 3 cm wide . . . . . 5
b. Longest lateral lobe at least 3.5 cm wide . . . . . 6

5a. Lamina of pinnatifid fronds widest above the middle; index of longest lateral lobe 6–60; sorus density at least 20/cm$^2$ . . . . . **14. M. pentaphyllum**
b. Lamina of pinnatifid fronds widest below the middle; index of longest lateral lobe 3.5–12; sorus density at most 20/cm$^2$ . . . . . **16. M. rampans**

6a. Lamina of pinnatifid fronds at most 40 cm long, at the basal lobes pinnate; undersurface of lamina without acicular hairs . . . . . **1. M. cinctum**
b. Lamina of pinnatifid fronds at least 45 cm long, at the basal lobes not pinnate; undersurface of lamina with acicular hairs . . . . . **3. M. egregium**

7a (3). Simple fronds present or absent; number of tertiary veins between two adjacent secondary veins at most 3; rhizome in cross section with less than 20 vascular bundles in cylinder, scattered sclerenchyma strands absent . . . . . 8
b. Simple fronds absent; number of tertiary veins between two adjacent secondary veins at least 3; rhizome in cross section with more than 20 vascular bundles in cylinder, scattered sclerenchyma strands present (many) . . . . . 9

8a. Sori restricted to the distal 1/2–2/3 of the lamina or lobes, present in the costal areoles; sheaths of vascular bundles in rhizome sclerenchymatous; central region of rhizome scales glabrous . . . . . **21. C. insignis**
b. Sori not restricted to the distal part of the lamina or lobes, absent in the costal areoles; sheaths of vascular bundles in rhizome collenchymatous; central region of rhizome scales with long hairs . . . . . **22. C. pteropus**

9a. Longest lateral lobe at most 3 cm wide; number of tertiary veins between two adjacent secondary veins at most 5; margin of lamina sinuate-dentate . . . . . **28. Ph. alatus**
b. Longest lateral lobe more than 3 cm wide; number of tertiary veins between two adjacent secondary veins more than 5; margin of lamina entire . . . . **29. Ph. biseriatus**

10a. (1) Venation pattern type 2 (secondary veins seem to be dichotomous near their base, where a prominent basiscopic tertiary vein branches off) . . . . . 11
b. Venation pattern type otherwise (1 or 4) . . . . . 12

11a. Base of lamina truncato-angustate to hastate; sori present in costal areoles; innervation type 2 (sori in max. 2 rows parallel to each secondary vein) . **23. Lc. buergerianus**
b. Base of lamina narrowly angustate; sori absent in costal areoles; innervation type 3 (sori at least in part in more than 2 rows parallel to each secondary vein) **24. Lc. subhemionitideus**

12a. Venation pattern type 4 (one row of larger main areoles parallel to the primary vein and bordered by medium-sized and/or smaller marginal areoles); lamina with or without acicular hairs; central region of rhizome scales glabrous . . . . . 13
b. Venation pattern type 1 (between each pair of adjacent secondary veins 1–10 small and ± equally sized primary areoles, bordered at the margin of the lamina by a few simple smaller areoles); lamina without acicular hairs; central region of rhizome scales glabrous or with long hairs . . . . . 16

13a. Acicular hairs present or, if absent (or very few present), lamina up to 1 cm wide . 14
b. Acicular hairs absent; lamina more than 1 cm wide . . . . . 15

14a. Stipe with 4–6 vascular strands; lamina index 7.5–40, 35–95 by 1–9 cm, thin-herbaceous ..... **10. M. longissimum**

b. Stipe with 3 vascular strands; lamina index 30–65, 25–45 by 0.5–1, firm-herbaceous to coriaceous ..... **17. M. samarense**

15a. Phyllopodia at least 10 mm apart; rhizome scales at least 3.5 mm long, partly clathrate; stipe with at least 5 vascular strands ..... **9. M. linguiforme**

b. Phyllopodia at most 7 mm apart; rhizome scales at most 3 mm long, fully clathrate; stipe with at most 5 vascular strands ..... **16. M. rampans**

16a. (12). Rhizome without any or with less than 25 scattered sclerenchyma strands in cross section ..... 17

b. Rhizome with at least 30 scattered sclerenchyma strands in cross section ..... 24

17a. Innervation type 3 (sori usually in 2 or more rows parallel to each secondary vein); lamina herbaceous to subcoriaceous; phyllopodia at most 5 cm apart; scattered sclerenchyma strands in rhizome, if present, situated dorsally ..... 18

b. Innervation type 1 (sori mostly irregularly scattered on the smallest veins, but some in 2 or more rows parallel to each secondary vein); lamina membranaceous to herbaceous; phyllopodia at most 3.5 cm apart; scattered sclerenchyma strands in rhizome, if present, ± evenly scattered ..... 19

18a. Rhizome scales with dentate margin, index 3–4.5; rhizome with 7–11 vascular bundles in cylinder; stipe up to 10 cm long ..... **25. N. ningpoensis**

b. Rhizome scales with entire to denticulate margin, index 1–3.5; rhizome in cross section with 10–13 vascular bundles; stipe up to 20 cm long ... **26. N. superficialis**

19a. Tertiary veins (mostly) anadromous, at most 3, between two adjacent secondary veins ..... 8

b. Tertiary veins catadromous, at least 3 between two adjacent secondary veins or, if less than 3, the lamina sinuate to irregularly lobed and the stipe with less than 5 vascular strands ..... 20

20a. Stipe absent or very short (at most 0.5 cm) ..... 21

b. Stipe at least 1.5 cm long ..... 22

21a. Lamina at least 4 cm wide, index less than 20; rhizome at least 4 mm wide, with more than 15 vascular bundles in cylinder in cross section .... **2. M. congregatifolium**

b. Lamina at most 3 cm wide, index at least 20; rhizome at most 3 mm wide, with less than 15 vascular bundles in cylinder in cross section ..... **18. M. sopuense**

22a. Lamina at most 3 cm wide (excluding possible irregular lobes); rhizome without scattered sclerenchyma strands ..... **6. M. heterolobum**

b. Lamina at least 3.5 cm wide (never irregularly lobed); rhizome with at least a few scattered sclerenchyma strands ..... 23

23a. Number of tertiary veins between two adjacent secondary veins at least 6; sori present in costal and marginal areoles; sorus density at least 10/cm$^2$ . **5. M. heterocarpum**

b. Number of tertiary veins between two adjacent secondary veins at most 5; sori absent in costal and marginal areoles; sorus density at most 8/cm$^2$ ... **8. M. leandrianum**

24a. (16) Sori absent in the costal areoles ..... 25

b. Sori present in the costal areoles ..... 28

25a. Lamina membranaceous; sorus density less than 10/cm$^2$; rhizome not waxy/glaucous ..... 26

b. Lamina firm-herbaceous to coriaceous; sorus density more than 10/cm$^2$; rhizome waxy/glaucous or not ..... 27

26a. Lamina index at most 4.5, length 10–35 cm, base truncato-angustate; rhizome at most 3 mm wide ..... **7. M. lastii**

b. Lamina index at least 5, length 30–55 cm, base narrowly angustate **8. M. leandrianum**

27a. Rhizome 4–8 mm wide, in cross section with at least 14 vascular bundles in cylinder; stipe with at least 6 vascular strands; lamina longer or shorter than 40 cm; sori present or absent in the marginal areoles; sorus density up to 100/cm$^2$; apical cell of paraphyses not large and curved ..... **15. M. punctatum**

b. Rhizome 3–5 mm wide, in cross section with at most 14 vascular bundles in cylinder; stipe with at most 5 vascular strands; lamina shorter than 40 cm; sori absent in the marginal areoles; sorus density up to 20/cm$^2$; apical cell of paraphyses often large and curved ..... **20. M. steerei**

28a. (24) Lamina index at most 2 *and* phyllopodia at least 3 cm apart; inner layer of thickened cell walls in rhizome scales warty ..... **19. M. spectrum**

b. Lamina index more than 2 or, if 2, the phyllopodia less than 2 cm apart; inner layer of thickened cell walls in rhizome smooth ..... 29

29a. Scales subclathrate or opaque (and reddish brown to black); rhizome waxy (glaucous) or not ..... **4. M. glossophyllum**

b. Scales fully or partly clathrate; rhizome not waxy (glaucous) ..... 30

30a. Rhizome scales fully clathrate; phyllopodia at least 1 cm apart; fronds at most 90 cm long; lamina at most 8 cm wide ..... 31

b. Rhizome scales partly clathrate; phyllopodia at most 1 cm apart; fronds at most 135 cm long; lamina at most 15 cm wide ..... 32

31a. Sorus density at least 15 / cm$^2$; innervation type 1 (sori mostly irregularly scattered, but some in 2 or more rows parallel to each secondary vein); vascular bundles in cylinder in rhizome at most 11 ..... **12. M. monstrosum**

b. Sorus density at most 10/cm$^2$; innervation type 2 (sori almost exclusively in maximal 2 rows parallel to each secondary vein); vascular bundles in cylinder in rhizome at least 11 ..... **27. N. zippelii**

32a. Lamina membranaceous, base narrowly angustate; scales spreading, pseudopeltate, central region with long hairs; sori at least 1 mm in diameter .. **11. M. membranaceum**

b. Lamina firm-herbaceous, base truncate to obtuse; scales appressed, peltate, central region glabrous; sori at most 1 mm in diameter ..... **13. M. musifolium**

## 13. SPECIES DESCRIPTIONS

### 1. Microsorum cinctum Bosman, *spec. nov.* – Fig. 12.

Rhizoma depressum 4,5–7 mm latum, squamis pseudopeltatis partim clathratis plus minusve dense vestitum. Frondes pinnatae apicem versus pinnatifidae, 50–60 cm longae. Lamina 4–5-jugata, lobis maximis 15–25 cm longis, 3,5–6 cm latis. Venatio et innervatio sororum *M. linguiformi* similes. — T y p u s: *Jermy 8111*, New Guinea, West Sepik, Dewan Mts, Kunias (holo L; iso K, BM).

Rhizome long, dorso-ventrally flattened, 4.5–7 mm wide, not waxy; roots sparsely set; phyllopodia distinct, 3–15 or more mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 11–15, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales*

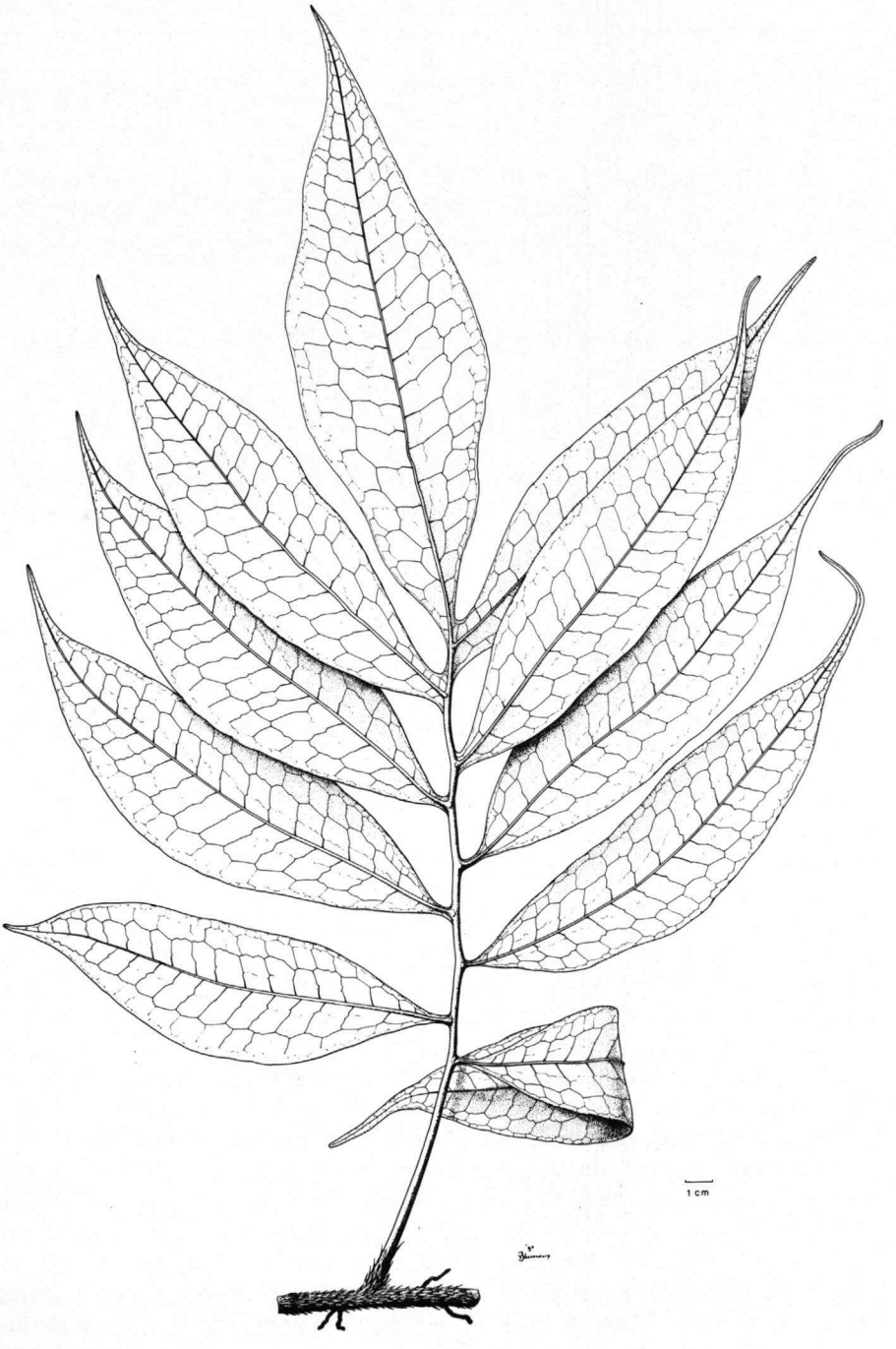


Fig. 12. *Microsorum cinctum* Bosman (*Jermy 8111*, L).

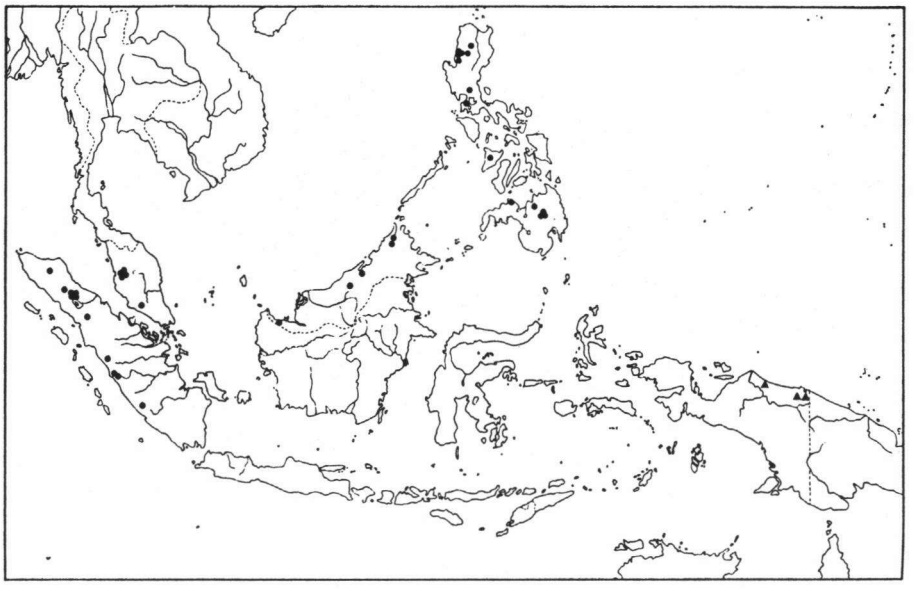

Fig. 13. Distribution of *Microsorum cinctum* Bosman (▲) and *M. congregatifolium* (Alderwerelt) Holttum (●).

more or less densely set, appressed or slightly spreading, pseudopeltate, index 3–4, widest below the middle, 3.5–8 by 1.5–2.5 mm, clathrate except for the marginal region which is hyaline, margin entire, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* pinnate, apically pinnatifid, well proportioned to the rhizome diameter, 50–60 cm long; stipes 10–25 cm long, up to 3 mm in diameter, with a few scales at base, vascular strands 8; lamina index 1–1.5, widest below or about the middle, 35–40 by 30–35 cm, between the lobes c. 2 cm wide, lobes and pinnae 4 or 5 to a side, herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base formed by sessile or shortly petiolulate pinnae, margin entire, apex acuminate; longest pinna at 2nd position from base, index 4–5.5, widest below or about the middle, 15–25 by 3.5–6 cm; apical lobe widest below or about the middle, otherwise ± conform to the upper lateral lobes. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one or more marginal rows of smaller areoles; all veins distinct except the smallest ones; secondary veins 7–13(–17) mm apart, ± straight, dichotomously branched at 1/2 to 2/3 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles; free included veins simple, once- and twice-forked, pointing to all sides. *Sori* superficial, round, diameter unknown (mature sori absent), spreading all over the lamina, present in all areoles, 15–25/cm$^2$, irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate,

3-celled (one observation). Sporangium (one observation): annulus 20-celled, indurated cells 14, hypo- and epistomial cells together 6. *Spores* not found.

Distribution. New Guinea (3): West-Sepik, Bewani Mts (*Croft 1784, Jermy 8111*) and Idenburg R. (*Brass 13390*). Fig. 13.

Habitat. Primary forest. Altitude 300–850 m. Shady places. Epiphytic (low). Sometimes locally common (Idenburg R.).

Notes. 1. The pinnae resemble the simple fronds of *M. rampans*, which may therefore be closely related. In *M. rampans* the pinnatifid fronds are considerably smaller than in *M. cinctum* and not pinnate at base.

2. The description is based on 3 collections.

3. Copeland (1947) 196 based *M. cinctum* on *Polypodium cinctum* Copeland, a name which was never published.

4. Cultivation: a duplicate of the type specimen is cultivated in Bot. Gard. Kew sub no. 214-70.01971.

## 2. Microsorum congregatifolium (Alderwerelt) Holttum

*Microsorum congregatifolium* Holttum (1954) 178. — *Pleopeltis congregatifolia* Alderwerelt (1920) 166. — *Polypodium congregatum* Christensen (1934) 146, nom. nov., non *Polypodium congregatifolium* Alderwerelt (1924) 47 = *Ctenopteris congregatifolia* (Alderwerelt) Copeland. — *Microsorum congregatum* Copeland (1947) 197, nom. illeg. (ICBN art. 63.1). — Type: *Lörzing 5532*, Sumatra, Deli, Sibolangit (lecto, proposed here; holo BO; iso L, UC, US, photo BM); *Lörzing 5565*, Sumatra, Deli, Sibolangit (para BO).

*Polypodium punctatum* subsp. *mindanense* Christ (1906) 994. — *Polypodium punctatum* var. *mindanense* Alderwerelt (1909a) 654. — *Microsorum mindanense* Copeland (1947) 196. — Type: *Copeland 1741*, Philippines, San Ramon, Mindanao (P).

Rhizome short to moderately long, dorso-ventrally flattened, 4–9 mm wide, not waxy; roots very densely set, forming a thick mat; phyllopodia obscure, 2–9 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 16–21, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue occasionally with cavities. *Rhizome scales* apically densely set but otherwise ± sparsely set, slightly spreading, pseudopeltate, index 1–3.5, widest below or about the middle, 1–5 by 0.3–2 mm, clathrate throughout, margin dentate, apex acuminate, central region dorsally with long lax hairs, rarely glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 65–85 cm long; stipes absent or indistinct, up to 7 mm in diameter, with a few scales, vascular strands 3–6; lamina index 11–16, widest about or above the middle, 65–85 by 4–7.5 cm, herbaceous, with short glandular hairs, scales and acicular hairs absent, base cuneate to broadly truncate, margin entire, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct, or the tertiary and smaller veins vague; secondary veins 9–18 mm apart, ± straight or slightly zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 4–7 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple and in part once-forked, pointing to all sides. *Sori* superficial, round, 1–1.5 mm in diameter, re-

stricted to the distal 1/3–1/2 of the lamina, absent in the (narrow) costal and marginal areoles, occasionally present in all areoles, 5–15(–20)/cm$^2$, occasionally in part on tertiary veins, 1 or 2 per quaternary vein, forming 2–4 irregular rows situated parallel to each secondary vein or irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 3–8-celled. Sporangia: annulus 19–21-celled, indurated cells 13–15, hypo- and epistomial cells together 6. *Spores* concavo-convex, hyaline, 50–60 by 30–35 μm, ± smooth.

Distribution. Peninsular Malaysia (5): Perak; Sumatra (15); Borneo (6): Sarawak and Sabah; Philippines (12): Luzon, Panay and Mindanao. Fig. 13.

Habitat. Primary and secondary forests. Altitude 30–1300 m (–1600 m in Sumatra). Near streams in valleys, humid places, usually in dense shade. Epiphytic (usually low), occasionally also epilithic. Sometimes locally abundant.

Notes. 1. The present species can be confused with *M. musifolium,* which has peltate and broader scales with entire margins, a more distinct venation with usually more primary connectives (6–10) between the secondary veins and a much higher sorus density (20–45/cm$^2$).

2. The fronds are reported to be tufted without forming regular nests.

3. No recent collections seen from the Philippines (most recent: 1949).

### 3. Microsorum egregium (Brause) Bosman, *comb. nov.*

*Polypodium egregium* Brause (1920) 199. — Type: *Ledermann 7542,* Papua New Guinea, Kaiserin Augusta-Fluss (BM, S).

Rhizome long, dorso-ventrally flattened, 3–8 mm wide, not waxy; roots sparsely set; phyllopodia distinct, 5–10 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 8–14, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, closely appressed, peltate or occasionally in part (small scales) pseudopeltate, index 1–2, widest below or about the middle, 0.5–2 by 0.5–2 mm, clathrate throughout or except for the marginal region which is hyaline and the central region which is opaque, margin entire or dentate, apex obtuse to rounded, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* pinnatifid, well proportioned to the rhizome diameter, 50–80 cm long; stipes 0.5–22 cm long, up to 4 mm in diameter, with a few scales at base, vascular strands 3–9; lamina index 1.5–2, widest below, about or above the middle, 45–60 by 25–40 cm, between the lobes 0.2–4 cm wide, lobes 1–3 (4) to a side, herbaceous, with glandular hairs and acicular hairs, scales absent, base angustate, margin entire, apex acuminate; longest lobe at 1st or 2nd position from base, index 2.2–4.3, widest about or above the middle, 10–25 by 5–6 cm; apical lobe widest below the middle, longer than the upper lateral lobes. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one or more marginal rows of smaller areoles, all veins distinct; secondary veins 9–13 mm apart, ± straight, dichotomously branched at 2/3–3/4 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles; free included veins simple, once- and in part twice-forked, pointing to

all sides. *Sori* superficial, round, not confluent, 1–1.5 mm in diameter, spreading all over the lamina, present in all areoles, 10–15/cm$^2$, irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 3-celled or occasionally with a 1-celled subapical acicular branch. Sporangia: annulus 19–21-celled, indurated cells 13 or 14, hypo- and epistomial cells together 5–7. *Spores* plano- to concavo-convex, yellowish, 55–80(–85) by (20–)25–35 (–40) µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. Moluccas (2): Batjan, Mt Sibela (*Alston 16930*) and Halmahera (*Nedi 274*); Papua New Guinea (1): Sepik (*Ledermann 7542*). Fig. 14.

Habitat. Primary forest. Altitude 20–40 m (Papua New Guinea), 950 m (Batjan). Epiphytic.

Notes. 1. The description is based on 3 collections.

2. No recent collections seen from Papua New Guinea (most recent: 1912).

## 4. Microsorum glossophyllum (Copeland) Copeland

*Microsorum glossophyllum* Copeland (1947) 196. — *Polypodium glossophyllum* Copeland (1914) 7. — *Pleopeltis glossophylla* Alderwerelt (1917) 391. — Type: *King 388*, Papua New Guinea, Mt Gewagewa (BM, P, SYD).

*Pleopeltis megalosoroides* Alderwerelt (1924) 39. — Type: *Lam 1365*, New Guinea, near Doorman R. (holo L; iso B).

Rhizome short to moderately long, ± cylindrical, 7–8 mm in diameter, often waxy; roots very densely set, forming a thick mat; phyllopodia distinct, up to 6 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 11–18, bundle sheaths collenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* densely set, slightly spreading, pseudopeltate, index 2.5–6.5, widest below the middle, 2.5–6.5 by 0.5–2 mm, opaque, margin denticulate, apex acuminate, central region glabrous, cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 70–125 cm long; stipes up to 2 cm long, up to 7 mm in diameter, with a few scales at base, vascular strands 7–8; lamina index 8–13, widest about or above the middle, 70–125 by 5.5–11 cm, firm-herbaceous, with a few scales, short glandular hairs and acicular hairs absent, base narrowly cuneate, margin entire, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 7–18 mm apart, ± straight or slightly zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 5–7 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple and once-forked, pointing to all sides. *Sori* superficial, round, 1–2.5 mm in diameter, restricted to the distal 1/5–4/5 of the lamina, absent in the marginal areoles, 5–20/cm$^2$, occasionally in part on tertiary veins, 2 per quaternary vein, forming 2–8 irregular rows situated parallel to each secondary vein or irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–4-celled. Sporangia: annulus (19–)20–22-celled, indurated

cells (13) 14 or 15 (16), hypo- and epistomial cells together 6 or 7. *Spores* plano- to concavo-convex, hyaline, 50–80 by 20–45 µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. New Guinea (many); Bougainville (2); Solomon Islands (4). Fig. 14.

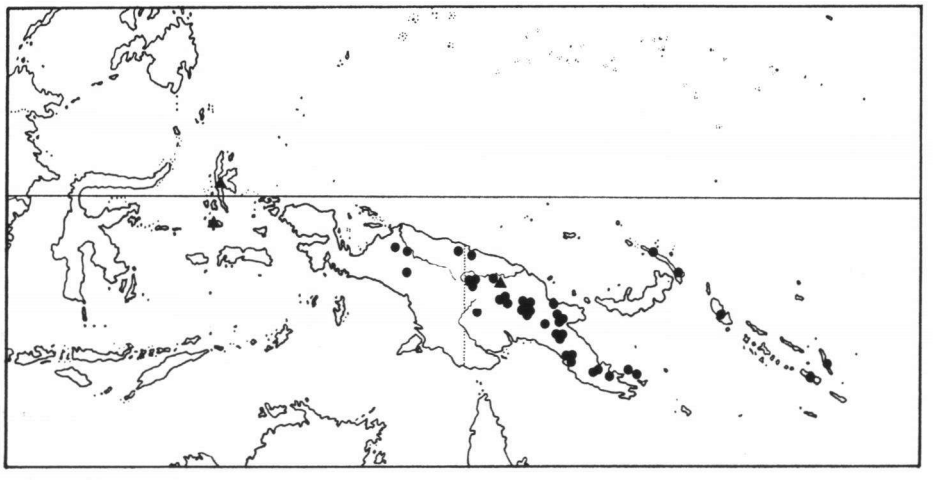

Fig. 14. Distribution of *Microsorum egregium* (Brause) Bosman (▲) and *M. glossophyllum* (Copeland) Copeland (●).

Habitat. Different types of primary or secondary forests (i.a. montane, *Nothofagus*-, *Castanopsis*-), one collection from grassland with *Eucalyptus* stand. Altitude 80–2800 m. Often in exposed, sunny situations (such as forest margins or exposed riverbanks), but also in (half-)shaded places; near rivers or without free water nearby. On various soil-types (limestone, volcanic rocks, brown loam, clay). Once recorded at the base of large reed tussocks and once between stiltroots of pandans. Epiphytic (low) or terrestrial, rarely epilithic, often nest-forming. Often locally common.

Notes. 1. This species is easily recognized by its opaque and blackish rhizome scales (in combination with its otherwise typical microsoroid appearance). Also the often glaucous (or, when dry, greyish or reddish) colour of the fronds is characteristic. In both characters it differs clearly from *M. punctatum*, with which it has often been confused.

2. Vernacular names: Kolkel (Yoowi dial., Hagen-Chimbu), polya (Enga), koiwa (Nauti; also used for *M. linguiforme*), noaturre (Manki).

3. Cultivation: occasionally in botanical gardens.

4. Uses: fresh leaves may be eaten uncooked with salt.

## 5. Microsorum heterocarpum (Blume) Ching

*Microsorum heterocarpum* Ching (1933b) 295. — *Polypodium heterocarpum* Blume (1829) 167, t. 75, non Mettenius (1856b) 37, t. 25, f. 24–25 = *Selliguea heterocarpa* Blume. — *Pleopeltis heterocarpa* Moore (1857) lxxviii. — T y p e: *Blume s.n.*, s.d., Java, Randja Gede (holo L, photo C).

*Polypodium zollingerianum* Kunze (1846) 422. — T y p e: *Zollinger 1499*, Java, Tjipatat (Z, BM).

*Nephrodium pteropodum* Baker (1888) 325. — *Aspidium pteropodum* Diels (1899) 183. — T y p e: *Hose 232*, West Borneo (holo K).

*Polypodium scortechinii* Baker (1891a) 477. — *Pleopeltis scortechini* Beddome (1892) 95. — T y p e: *Scortechini 216*, Perak (holo K).

*Campylogramma lancifolia* Alderwerelt (1916) 7, t. 1. — T y p e: *Rachmat 165*, Capt. van Vuuren's Exploration Exp., Mt Boesoe, Sulawesi (holo BO, not seen).

Rhizome moderately long, ± cylindrical or dorso-ventrally somewhat flattened, 2–6 mm in diameter, not waxy; roots ± densely set; phyllopodia usually distinct, up to 11 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 9–12, bundle sheaths sclerenchymatous, sclerenchyma strands 8–15, scattered, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise more or less sparsely set, appressed, pseudopeltate, index 2.5–4, widest below the middle, 1.5–4 by 0.5–1.5 mm, clathrate throughout, margin dentate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, usually slightly dimorphic. Sterile fronds: 25–80 cm long; stipes 1.5–25 cm long, up to 4 mm in diameter, with a few scales at base, vascular strands 4–8; lamina index 4–8, widest below, about or above the middle, 25–70 by 3.5–15 cm, thin-herbaceous, with short glandular hairs, scales and acicular hairs absent, base long and narrowly angustate, margin entire or slightly sinuate, apex acuminate. Fertile fronds conform to simple fronds except for size and shape: 30–80 cm long; stipes 0.5–45 cm long; lamina index 5–14, widest below, about or above the middle, 20–50 by 2–7 cm. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct or occasionally the smaller veins immersed; secondary veins 6–10 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 6–10 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing: free included veins simple and in part once-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, sometimes (especially in narrow fronds) in part confluent, 1 mm in diameter or 2–5 mm long, spreading all over the lamina, present in all areoles, 10–30/cm$^2$, occasionally in part on tertiary veins, 2 per quaternary vein, forming 4(–8) irregular rows situated parallel to each secondary vein or irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus (18-) 19- or 20- (21-) celled, indurated cells (12) 13 or 14, hypo- and epistomial cells together 6 (7). *Spores* concavo-convex, hyaline, 45–60 by 20–25 µm, ± smooth.

Distribution. Thailand (2); Peninsular Malaysia (19); Sumatra (22); Java (11); Lesser Sunda Islands (1): Flores; Borneo (30); Philippines (4): Luzon and Mindanao; Sulawesi (7); Moluccas (2): Seram. Fig. 15.

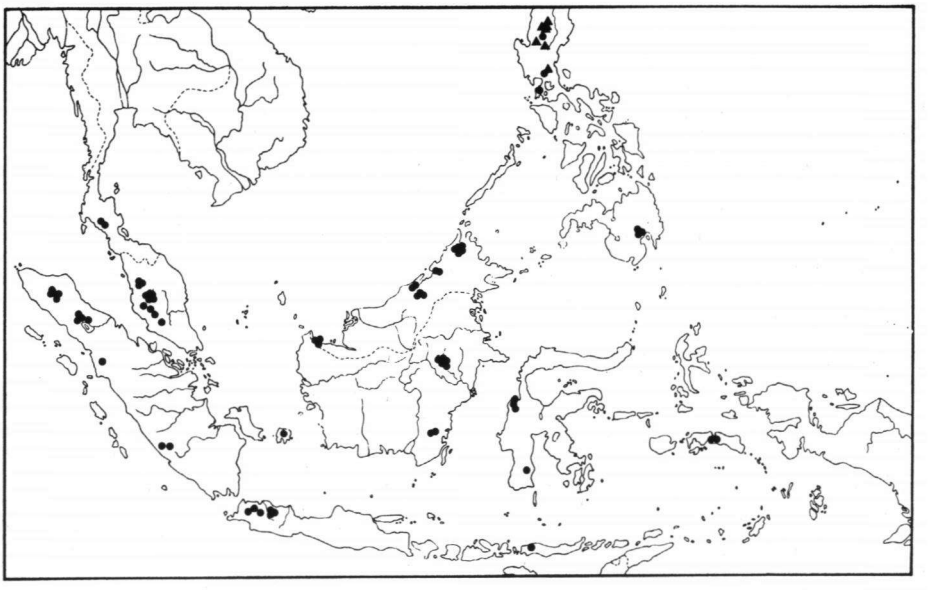

Fig. 15. Distribution of *Microsorum heterocarpum* (Blume) Ching (●) and *M. heterolobum* (Christensen) Copeland (▲).

Habitat. Primary rain forest, often on slopes. Altitude 50–2200 m. Shady and wet places, near streams or waterfalls, sometimes also in drier places. Epilithic, terrestrial or epiphythic. Often locally common.

Notes. 1. The fronds and especially the primary vein of this species are often dark coloured when dry. It differs from the somewhat similar *M. membranaceum* in for instance texture, shape and colour of the fronds. *Microsorum heterocarpum* is sometimes confused with *Tectaria singaporeana* (Wallich) Ching, although the two show only a superficial resemblance.

2. No recent collections seen from Java (most recent: 1923), Lesser Sunda Islands (1932), Philippines (1912), Moluccas (1937).

3. Cultivation: occasionally cultivated in botanical gardens.

## 6. Microsorum heterolobum (Christensen) Copeland

*Microsorum heterolobum* Copeland (1947) 196. — *Polypodium heterolobum* Christensen (1906) 532. — *Polypodium anomalum* Christ (1898a) 201, t. 3, f. 3, nom. illeg. (ICBN art. 64.1), non Hooker (1856) 360 = *Polystichum aculeatum* (Linnaeus) Schott. — Type: *Loher s.n.*, -3-1897, Philippines, Mt Data (holo P; iso K).

Rhizome long, dorso-ventrally flattened, 1.5–4 mm wide, not waxy; roots sparsely set; phyllopodia distinct, occasionally obscure, 5–35 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 9–10, bundle sheaths scleren-

chymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, distinctly spreading, pseudopeltate, index (2–)2.5–3.5(–4.5), widest below the middle, (2–)2.5–4.5(–5) by 0.5–1(–1.5) mm, clathrate throughout, margin denticulate, base sometimes with narrowly triangular lobes, apex acute to acuminate, central region dorsally with long lax hairs or glabrous, inner layer of thickened cell walls smooth. *Fronds* simple or irregularly lobed, well proportioned to the rhizome diameter, 15–40 cm long; stipes 2–15 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 3; lamina index 6.5–15, widest about or above the middle, 10–30 by 1.5–3 cm (excluding the up to 9 by 1 cm and narrowly triangular lobes), herbaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin irregularly sinuate, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary veins vague, smaller veins immersed; secondary veins 5–12 mm apart, zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 2–4 between adjacent secondary veins, sometimes in part interconnected by a quaternary vein; smaller veins variously anastomosing: free included veins simple and in part once-forked, predominantly recurrent. *Sori* superficial, round or in part slightly elongate, sometimes in part confluent, 1–2 mm in diameter or 2.5–4 mm long, spreading all over the lamina or restricted up to the distal 1/2, absent in the marginal areoles or present in all areoles, 5–20/cm$^2$, in part 2 per tertiary vein, forming 2 irregular rows situated parallel to each secondary vein, in part irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3- (4-)celled. Sporangia (see note 1): annulus 19- or 20-celled, indurated cells 13 or 14, hypo- and epistomial cells together 6–8. *Spores* usually abortive, normal spores plano- to concavo-convex, hyaline, 45–75 by (25–)35–50 µm, colliculate, the elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Philippines (11): Luzon. Fig. 15.

Habitat. Primary forest. Altitude 2250–2700 m. Epiphytic.

Notes. 1. *Loher 954* is aberrant in the following characters: annulus 23–27-celled, indurated cells 16–20, spores not abortive.

2. As the spores are often abortive and the fronds irregularly lobed this species is suspected to be a hybrid. The putative parents should be sought among *M. congregatifolium, M. heterocarpum, M. monstrosum,* and perhaps *N. zippelii* (all occur in the same region and resemble *M. heterolobum* in some way).

3. Takeda (1915) 288 interpreted this species as a monstrosity (*'anomalum'*) of his *P. hymenodes* var. *sparsisorum,* which is *Lc. subhemionitideus,* a very different species.

## 7. Microsorum lastii (Baker) Tardieu-Blot

*Microsorum lastii* Tardieu-Blot (1960) 116. — *Polypodium lastii* Baker (1891b) 5. — *Neocheiropteris lastii* Ching (1933a) 111. — Type: *Last s.n.*, s.d., north-western Madagascar, Bé Kilus Mts (holo K, sketch BM, photo P).

Rhizome moderately long, dorso-ventrally slightly flattened, 1.5–3 mm wide, not waxy; roots ± densely set; phyllopodia distinct, 5–15 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 13, bundle sheaths not differentiated, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise ± sparsely set, appressed, pseudopeltate, index 1.5–2, widest below the middle, 2–3 by 1–1.5 mm, clathrate except for the marginal region which is hyaline, the central region which is opaque, margin entire, apex obtuse to acute, central region dorsally with long stiff hairs or occasionally long lax hairs or glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, (15–)20–55 cm long; stipes 5–20 cm long, up to 3 mm in diameter, scales absent, vascular strands 8; lamina index 2.5–4(–4.5), widest below the middle, (10–)15–35 by (3–)5–10 cm, membranaceous, with short glandular hairs, scales and acicular hairs absent, base truncato-angustate, margin entire or occasionally undulate, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 10–17 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 4–6 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, not confluent, 1 mm in diameter or 2–3 mm long, spreading all over the lamina or restricted up to the distal 3/4, absent in the costal and marginal areoles, 3–6/cm$^2$, not on tertiary veins, in part 2 per quaternary vein, forming 2 irregular rows situated parallel to each secondary vein, in part irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–4-celled. Sporangia: annulus 19–21-celled, indurated cells 12–14, hypo- and epistomial cells together 6 or 7. *Spores* plano- to concavo-convex, yellow, (40–)45–50 by 25–30 µm, verrucate-gemmate.

Distribution. Madagascar (6). Fig. 16.

Habitat. Once reported 'among rocks in forest'. Altitude 1000 m (one record). Terrestrial.

Notes. 1. This species resembles *M. leandrianum* very much and may in fact prove to be conspecific, but as of both species only few collections were available, they are kept separate. Both species are also very similar to *M. membranaceum*.

2. The fronds are deciduous in dry seasons.

3. The description is based on 6 collections.

4. No recent collections seen from Madagascar (most recent 1922).

## 8. Microsorum leandrianum Tardieu-Blot

*Microsorum leandrianum* Tardieu-Blot (1959) 444. — Type: *Léandri et al. 1900*, Madagascar, south of Tsiandro (holo P).

Rhizome moderately long, dorso-ventrally slightly flattened, 3–5 mm wide, not waxy; roots ± densely set; phyllopodia more or less distinct, 5–20 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 13, bundle sheaths

not differentiated, sclerenchyma strands 29, scattered, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise more or less sparsely set, appressed or slightly spreading, pseudopeltate, index 2–2.5, widest below the middle, 2–4 by 1–2 mm, clathrate except for the marginal region which is hyaline, the central region which is opaque, margin entire, apex obtuse to acute, central region dorsally with long stiff hairs or long lax hairs or glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 35–65 cm long; stipes 5–10 cm long, up to 4 mm in diameter, scales absent, vascular strands 8; lamina index 5–7, widest below or about the middle, 30–55 by 4.5–8 cm, membranaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire or undulate, apex acute. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 8–14 mm apart, more or less straight, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 4 or 5 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and twice-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, not confluent, 1 mm in diameter or 2–5 mm long, spreading all over the lamina or restricted up to the distal 1/2, absent in the costal and marginal areoles, 4–8/cm$^2$, not on tertiary veins, in part 2 per quaternary vein, forming 2 irregular rows situated parallel to each secondary vein, in part irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–4-celled or occasionally with a 1-celled subapical glandular branch. Sporangia: annulus 17–20-celled, indurated cells (11–)13 or 14, hypo- and epistomial cells together 6 or 7. *Spores* plano- to concavo-convex, yellow, 45–55 by 25–35 µm, verrucate-gemmate.

Fig. 16. Distribution of *Microsorum lastii* (Baker) Tardieu-Blot (▲) and *M. leandrianum* Tardieu-Blot (●).

Distribution. Madagascar (3). Fig. 16.

Habitat. Deciduous forest. Altitude 400–600 m. Shady places, on limestone. Terrestrial.

Notes. 1. See note 1 under *M. lastii*.

2. The description is based on 3 collections.

## 9. Microsorum linguiforme (Mettenius) Copeland

*Microsorum linguiforme* ('*linguaeforme*') Copeland (1929a) 116. — *Polypodium linguiforme* Mettenius (1866) 228. — *Pleopeltis linguiformis* Alderwerelt (1909b) 6. — T y p e s: *Zippelius s.n.*, s.d., New Guinea (lecto, proposed here; holo L); *De la Billardière s.n.*, -9/10-1792, Ambon (para L?; not seen).

*Pleopeltis xiphias* Moore (1881) 331. — T y p e: a plant introduced from the South Pacific by Mr. W. Bull of Chelsea: probably the specimen marked "Hort. Bull., -11-1882", South Pacific Islands (holo K).

*Polypodium annabellae* Forbes (1888) 33, t. 280. — *Pleopeltis annabellae* Alderwerelt (1909b) 5. — *Dendroconche annabellae* Copeland (1911) 91. — T y p e: *Forbes s.n.*, s.d., New Guinea, Murray R. (BM, not seen; type species of *Dendroconche* Copel.).

*Polypodium cyclobasis* Baker (1896) 42. — T y p e s: *Kennedy s.n.*, 1894, NE New Guinea (syn K, not seen); *Micholitz s.n.*, s.d., New Guinea, Stirling Range (syn K, not seen).

*Polypodium schumannianum* Diels (1900) 139, t. 3C, D. — *Pleopeltis musifolia* var. *schumanniana* Rosenstock (1912) 729. — *Microsorum schumannianum* Copeland (1947) 196. — T y p e: *Hellwig 238*, Papua New Guinea, Kaiser Wilhelmsland, Sattelberg (B, not seen).

*Pleopeltis dendroconchoides* Alderwerelt (1920) 165. — T y p e: *Jacobson s.n.*, 16-6-1918, Sumatra, Bt. Batoe, Banting (BO, L, photo BM).

*Dendroconche kingii* Copeland (1931) 407. — T y p e: *King 387*, New Guinea (SYD).

Rhizome long, dorso-ventrally flattened, 1–9 mm wide, not waxy; roots very densely set, forming a thick mat; phyllopodia obscure or distinct, 10–45(–75) mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–15, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue occasionally with cavities. *Rhizome scales* apically ± densely set, otherwise ± sparsely set, appressed or slightly spreading, peltate or pseudopeltate, index 2–5.5, widest below the middle, 3.5–10 by 1–2.5 mm, clathrate except for the basal and sometimes marginal region which is hyaline, margin entire to denticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, occasionally dimorphic (in Papua New Guinea, see note 1), (3–)7.5–50(–70) cm long; stipes up to 12 cm long, up to 5 mm in diameter, sometimes with a few scales at base, vascular strands 5(–7); lamina index (0.8–) 2–5.5(–7.5), widest (below) about or above the middle, (3–)7.5–50(–70) by 2–15 (–17) cm, herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base varying from imbricate, auriculate or cordate to narrowly angustate, margin entire, apex varying from rotundate to acuminate. *Venation pattern:* irregular (in orbicular fronds) or (in other fronds) veins forming one row of main areoles situated parallel to the primary vein and bordered by one or more marginal rows of smaller areoles, all veins distinct; secondary veins 7–30 mm apart, ± straight, dichotomously branched at (1/4–)1/2–2/3 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round or occasionally in part slightly elongate, sometimes in part confluent, 1.5–3 mm in diameter or 3–5 mm long, spreading all over the lamina or restricted up to the distal 1/3, present in all areoles or occasionally absent in the marginal areoles, (2–)5–15/cm$^2$, irregularly scattered, occasionally in part on the smaller anastomosing veins but usually on the free in-

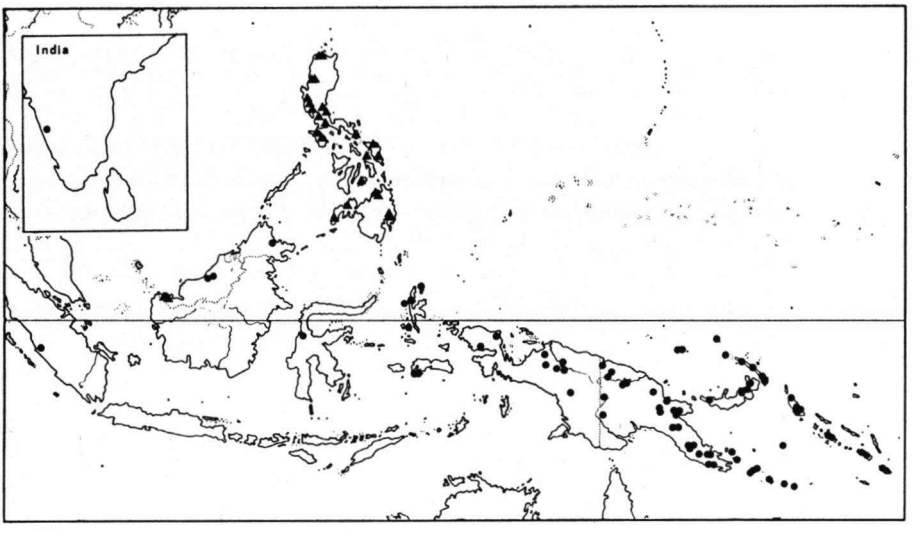


Fig. 17. Distribution of *Microsorum linguiforme* (Mettenius) Copeland (●) (Fiji Islands not on this map) and *M. longissimum* Fée (▲).

cluded veins. Paraphyses uniseriate, 1–3-celled. Sporangia: annulus 20–30(–37)-celled, indurated cells 14–21(–25), hypo- and epistomial cells together 6–9(–12). *Spores* concavo-convex, hyaline to yellow, 45–105 by 30–60 µm, ± smooth.

Distribution. India (2), introduced?: Kerala; Sumatra (3); Borneo (3): Sabah and Sarawak; Sulawesi (1); Moluccas (9); New Guinea (many); Solomon Islands (9); Fiji Islands (8). Fig. 17.

Habitat. Various types of primary and secondary forests (i.a. flood plain, lowland, montane, Dipterocarp-, Castanopsis-, Fagaceous-). Altitude 10–1650 m. Shady and moist places, sometimes near streams. Sandy soil, red clay, limestone. Usually a low epiphyte, sometimes higher ('middle spaces', '10–20 m above the ground'), rarely epilithic or terrestrial. Common in many localities.

Notes. 1. In New Guinea a form with the fertile apical part of the fronds much narrowed, forming a ribbon-like part of c. 20–40 by 1–1.5 cm, was formerly given generic rank (the monotypic genus *Dendroconche*), but as all transitions to 'normal' fronds occur and as there are no other characters by which this form can be distinguished, its formal distinction is not maintained.

2. The rhizome is reported to be creeping and ascending, with the fronds erect or drooping and clustered or at intervals. One collector noted alternating sterile and fertile fronds. The broad frond bases are often closely appressed to the tree (and thus probably humus-collecting).

3. No recent collections seen from the Moluccas (most recent: 1954).

4. Vernacular names: Koiwa (Nauti; also used for *M. glossophyllum*), gwau-utu (Daga).

5. Cultivation: successful in many botanical gardens.

6. Uses: uncooked, salted fronds are eaten locally in New Guinea.

7. Nayar & Madhusoodanan (1977) gave an elaborate description of this species, including details on anatomy and gametophyte. They concluded that *M. linguiforme* shows close resemblance to *Leptochilus* and may be parental to it. Their arguments are not supported here because: a long-creeping dorsoventral rhizome is also found in, e.g., *M. heterocarpum* and *M. spectrum*; rhizomes devoid of scattered sclerenchyma strands are also found (besides species of the *M. longissimum* group) in *M. heterolobum* and *M. congregatifolium*; a relatively large pith is found in many microsoroids (cf. fig. 1 in chapter 5). Moreover, as they stated themselves, the ribbon-like prothallus is not of "the typical narrow and elongated form found in [...] *Leptochilus* and *Paraleptochilus*" but "broad, comparatively short and profusely branched." It may therefore have arisen along a different line of evolution.

## 10. Microsorum longissimum Fée

*Microsorum longissimum* J. Smith ex Fée (1852) 268, t. 20B, f. 2. — *Polypodium myriocarpum* Presl ex Mettenius (1856b) 105, non *Polypodium longissimum* Blume (1828) 127 = *Phymatosorus longissimus* (Blume) Pichi Sermolli. — *Pleopeltis myriocarpa* Alderwerelt (1913) 19, non *Pleopeltis longissima* Moore (1857) lxxviii = *Phymatosorus longissimus* (Blume) Pichi Sermolli. — *Microsorum myriocarpum* Itô (1935) 97, nom. illeg. (ICBN art. 63.1). — T y p e: (see Morton, 1973: 231) *Cuming 66*, Philippines, Luzon, prov. Laguna (B, BM, G, K, L, LE, P, PC, US, Z).

*Drynaria longifolia* Brackenridge (1854) 45. — T y p e: *Brackenridge, U.S. Expl. Exped. 7*, Philippines, Luzon, Mts near Los Baños (holo US).

*Polypodium sablanianum* Christ (1907) 177. — *Pleopeltis sablaniana* Alderwerelt (1909b) 6. — *Microsorum sablanianum* Copeland (1947) 196. — T y p e: *Elmer 6142*, Philippines, Luzon, Benguet, Sablan (holo P; iso G, K, US).

*Phymatodes myriocarpa* Presl [(1836) 196, t. 8, f. 12, nom. nud.]. — *Drynaria longissima* J. Smith [(1841) 397, nom. nud.]. — Based on type of *Microsorum longissimum* Fée.

Rhizome moderately long to long, dorso-ventrally flattened, 2.5–8 mm wide, not waxy; roots sparsely or densely set; phyllopodia distinct, up to 20 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 6–16, bundle sheaths sclerenchymatous, sclerenchyma strands absent, cavity sometimes present. *Rhizome scales* ± densely set, appressed or slightly spreading, pseudopeltate, index 1.5–5.5, widest below the middle, 1–4.5 by 0.5–1.2 mm, clathrate throughout, margin denticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 35–95 cm long; stipes up to 7.5 cm long, up to 5 mm in diam., sometimes with a few scales at base, vascular strands 4–6; lamina index 7.5–40, widest about or above the middle, 35–95 by 1–9 cm, thin-herbaceous, with short glandular hairs, acicular hairs, occasionally some glandular-acicular hairs and a few scales, base narrowly angustate, margin entire, apex acuminate. *Venation pattern:* veins forming one row of main areoles situated parallel to primary vein and bordered by one or more marginal rows of smaller areoles, all veins distinct or sometimes smaller veins vague; secondary veins 5–18 mm apart, ± straight, dichotomously branched at 1/2–2/3 of the lamina width;

tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within main and marginal areoles; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, sometimes in part confluent, 0.5–1.5 mm in diameter or 1–3 mm long, spreading all over the lamina, present in all areoles, (10–)20–65/cm$^2$, irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–4-celled, or occasionally with a 1-celled subapical acicular branch. Sporangia: annulus 18–23-celled, indurated cells 12–16, hypo- and epistomial cells together 6 or 7. *Spores* plano- to concavo-convex, hyaline, 50–105 by 20–50 µm, colliculate, elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Borneo (4): Sarawak; Philippines (many). Fig. 17.

Habitat. Primary or secondary forest; once reported from seasonally dry forest and once from forested limestone ridge. Altitude 30–1200 m. Shady places, once reported near stream. Sometimes (especially Borneo) on limestone. Low epiphytic, with the roots "creeping down vertically to ground level", rarely epilithic. Sometimes locally common.

Notes. 1. This species resembles *M. rampans*, especially in its often light-coloured primary vein, but differs in its shorter stipe, its higher sorus density, its scales and the absence of pinnatifid fronds.

3. The narrow forms of this species have often been identified as *M. tenuilore* (= *M. samarense*), which differs for instance in narrower fronds, thicker texture, sorus position, and size of sporangia and spores.

4. The broader forms of this species were formerly placed under *M. sablanianum*, but as many intermediate sizes are present, the latter is reduced to synonymy.

5. Cultivation: occasionally cultivated in botanical gardens.

## 11. Microsorum membranaceum (Don) Ching

*Microsorum membranaceum* Ching (1933b) 309. — *Polypodium membranaceum* Don (1825) 2. — *Colysis membranacea* J. Smith (1857) 11, nom. illeg. (ICBN art. 64.1), non Presl (1851) 147. — Type: *Wallich s.n.*, s.d., Nepal (holo K; iso B).

*Polypodium transparens* Presl ex Ettingshausen (1864) 95, t. 18, f. 16. — Type: *Hügel 269*, Himalaya (holo W, not seen, photo BM).

*Polypodium grandifolium* Wallich [(1829) 282, nom. nud.; Beddome (1864) 59, pl. 177, nom. inval. (ICBN art. 34.1d)] ex Christ (1898b) 874. — *Polypodium membranaceum* var. *grandifolium* Alderwerelt (1909a) 649. — Type: *Wallich 282*, Nepal (holo K; iso BM, M, UC, US).

*Polypodium hymenodes* Kunze (1850) 279/319, non Wallich [(1829) 283, nom. nud.] = *Leptochilus axillaris* (Cavanilles) Kaulfuss. — Type: *Kunze s.n.*, s.d., cult. Leipzig (holo B).

*Phymatodes grandifolia* Presl [(1836) 198, nom. nud.]. — *Pleopeltis grandifolia* Moore [(1857) LXXVIII, nom. nud.]. — Based on type specimen of *Polypodium grandifolium* Christ.

*Pleopeltis membranacea* Moore [(1860) 191, nom. inval. (ICBN art. 34.1d)]. — Based on type specimen of *Polypodium membranaceum* Don.

*Polypodium hymenodes* var. *sparsisorum* Takeda [(1915) 287, nom. inval. (ICBN art. 26.1 & 32.1b)], q.n.s. (see *Leptochilus subhemionitideus*). — Based on type specimen of *Polypodium hymenodes* Kunze.

Rhizome moderately long, ± cylindrical or dorso-ventrally flattened, 3–10 mm in diameter or wide, not waxy; roots ± densely set; phyllopodia distinct, up to 9 mm

apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 18–23, bundle sheaths not differentiated, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise ± sparsely set, slightly spreading, pseudopeltate, index 1.5–3.5, widest below the middle, 1.5–9 by 1–3 mm, clathrate except for the marginal region which is hyaline and the central region which is opaque, margin entire, apex acute to acuminate, central region dorsally with long stiff hairs, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, (5–)25–110 cm long; stipes up to 15 cm long, up to 5 mm in diameter, with a few scales at base, vascular strands 6–9; lamina index 2–11, widest below or about the middle, (5–)25–110 by (1–)5–15 cm, membranaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire, sinuate or undulate, apex acuminate. *Venation pattern:* veins forming a more or less regular or irregular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 5–15 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 4–8 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and twice-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, sometimes in part confluent, 1–2 mm in diameter or 2.5 mm long, spreading all over the lamina or restricted up to the distal 1/2, absent in marginal areoles, 3–25/cm$^2$, not on tertiary veins, 1 or 2 per quaternary vein, forming 2 irregular rows situated parallel to each secondary vein or in part irregularly scattered on the smaller anastomosing veins. Paraphyses uniseriate, 3-celled. Sporangia: annulus 16–21-celled, indurated cells 12–14, hypo- and epistomial cells together 4–7. *Spores* concavo-convex, yellow, 45–70 by 25–50 µm, sometimes with small spines, verrucate-gemmate.

Distribution. Nepal (19); Sikkim (9); Bhutan (4); India (many), Sri Lanka (6); Burma (5); China (many from Yunnan, few from Kweichow, Kwangtung, Kwangsi and Szechuan); Taiwan (17); northern Thailand (20); Laos (1); North Vietnam (5); Philippines (17): northern Luzon. Fig. 18.

Habitat. Evergreen or deciduous broad-leaved (sub)tropical forests, often in valleys or ravines, once reported from thickets on open grassy hillside. Altitude 600–2600(–4000) m. Usually wet and shady places, often found along streams. In Thailand often on limestone. Epiphytic, epilithic or terrestrial. Locally common or rare.

Notes. 1. This species is easily recognized by its membranaceous, often large and undulate fronds which are light green or yellow when dried. It resembles *M heterocarpum* but differs in, for instance, texture of the fronds and distribution of the sori.

2. Monstrosities occasionally occur in which the apex of the fronds is irregularly lobed.

3. The fronds are shed seasonally, also in cultivation.

4. No recent collections seen from Bhutan (most recent: 1949), Burma (1939), China (1939), Laos (1929), North Vietnam (1936), Philippines (1946).

5. Cultivation: sometimes cultivated in botanical gardens.

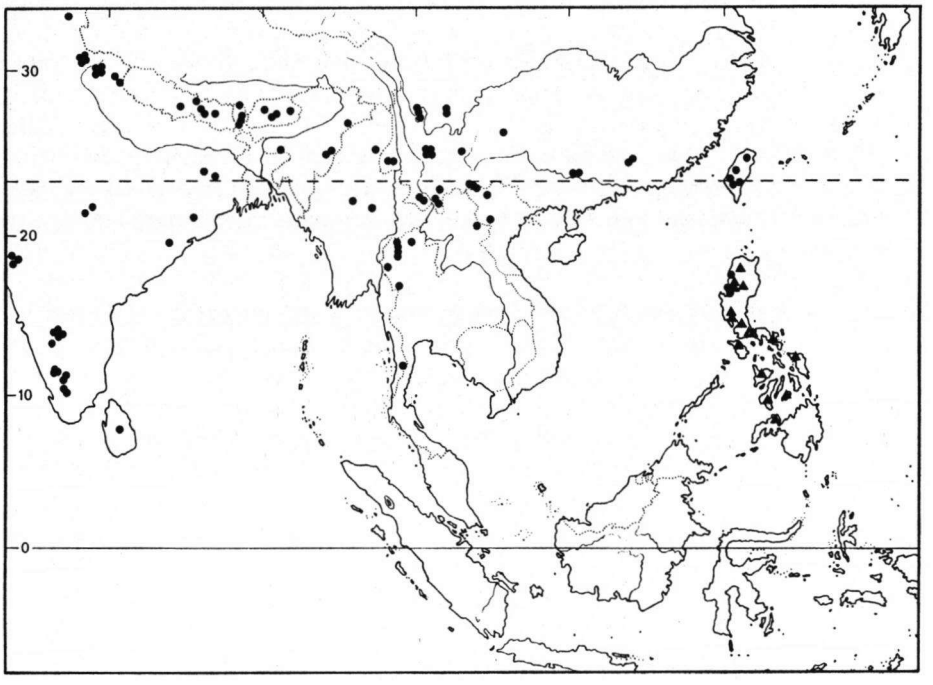


Fig. 18. Distribution of *Microsorum membranaceum* (Don) Ching (●) and *M. monstrosum* (Copeland) Copeland (▲)

## 12. Microsorum monstrosum (Copeland) Copeland

*Microsorum monstrosum* Copeland (1947) 196. — *Polypodium monstrosum* Copeland (1906b) 78. — *Pleopeltis monstrosa* Alderwerelt (1909b) 8. — T y p e: *Elmer 7174*, Philippines, Luzon, Mt Banahao (G, S).

*Polypodium monstrosum* var. *leucophlebium* Copeland (1906b) 78. — T y p e: *Copeland 2069*, Philippines, Luzon, Laguna, Pagsanjan (P, SING).

*Polypodium monstrosum* var. *integriore* Copeland (1906b) 78. — T y p e: *Copeland 1964*, Philippines, Luzon, Lepanto, Bagnen (P).

*Polypodium subopposition* Christ (1906) 995. — *Pleopeltis subopposita* Alderwerelt (1909b) 8. — *Microsorum subopposition* Ching (1933b) 295. — T y p e: *Loher s.n.*, -2-1906, Philippines, Zambales, Pinatubo (holo P).

*Drynaria undulata* J. Smith [(1841) 397, nom. nud.]. — *Bathmium ? undulatum* Fée [(1852) 287, nom. inval.]. — Based on *Cuming 250*, Philippines, Luzon (B, BM, K, P, US).

Rhizome long, ± cylindrical, 1.5–3(–5) mm in diameter, not waxy; roots ± densely set; phyllopodia often obscure, sometimes distinct, 15–60 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–11, bundle sheaths at cortex side sclerenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* more or less densely set, slightly or distinctly spreading, pseudopeltate, index 3.5–5.5, widest below the middle, 3–7 by 1–1.5 mm,

clathrate throughout, margin entire or denticulate, apex acuminate, central region dorsally with long lax hairs or glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, large in proportion to the rhizome diameter, 25–90 cm long; stipes 0.5–15(–25) cm long, up to 3(–3.5) mm in diameter, with a few scales at base, vascular strands 3–5; lamina index (5.5–)7.5–11(–15.5), widest about the middle, 25–70(–90) by 3–8 cm, herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base narrowly angustate, margin entire or sinuate to irregularly lobed, apex acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary veins distinct, smaller veins immersed or vague; secondary veins 7–11 mm apart, ± straight, or slightly zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 4 or 5 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple and in part once-forked, pointing to all sides. *Sori* part slightly elongate, sometimes in part confluent, 1–2 mm in diameter or 1.5–3 mm long, spreading all over the lamina or restricted up to the distal 1/2, absent in the marginal areoles, occasionally present in all areoles, 15–30/cm$^2$, not on tertiary veins, 1 or 2 per quaternary vein, forming 4 or 5 irregular rows situated parallel to each secondary vein or in part irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus 19–23-celled, indurated cells 13–17, hypo- and epistomial cells together 6 or 7. *Spores* concavo-convex, hyaline, 55–70 by 35–40 µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. Philippines (many). Fig. 18.

Habitat. Evergreen forests. Shady and mossy places. Altitude 600–1700 m. Low epiphytic or epilithic.

Notes. 1. This species resembles *M. heterocarpum* but has usually smaller and narrower fronds, shorter stipes, and the venation is less distinct.

2. Hovenkamp & De Joncheere (1988) cited *Hennipman 5099* as the first record of this species for Sulawesi, but this specimen is now identified as *M. sopuense*.

### 13. Microsorum musifolium (Blume) Copeland

*Microsorum musifolium* Copeland (1929a) 112. — *Polypodium musifolium* Blume (1828) 134. — *Pleopeltis musifolia* Moore (1857) lxxviii. — *Drynaria musifolia* J. Smith (1857) 14. — Type: *Blume s.n.*, s.d., Java, near Buitenzorg (holo L, photo C).

Rhizome short to moderately long, ± cylindrical or dorso-ventrally slightly flattened, 5–8 mm in diameter, not waxy; roots densely set forming a thick mat; phyllopodia obscure, up to 10 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 17–21, bundle sheaths collenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* apically ± densely set, otherwise ± sparsely set, appressed, peltate, index 1–2.5, widest below or about the middle, 1.5–5.5 by 1.5–2.5 mm, clathrate except for the marginal region which is hyaline, margin entire, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diam-

eter, 35–135 cm long; stipes absent or indistinct, up to 6 mm in diameter, with a few scales, vascular strands 9–14; lamina index (4.5–)7–11, widest about or above the middle, 35–135 by 5–15 cm, (firm-)herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base truncate to obtuse, margin entire, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins very distinct; secondary veins 7–15 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 6–10 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round, sometimes in part confluent, 0.5–1 mm in diameter, spreading all over the lamina or restricted up to the distal 1/2, absent in the marginal areoles, occasionally present in all areoles, 20–45/cm$^2$, not on tertiary veins, occasionally in part on quaternary veins, irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus (18-) 19- or 20-celled, indurated cells (12) 13 or 14, hypo- and epistomial cells together 6 or 7. *Spores* concavo-convex, hyaline, 45–55 by 25–40 µm, colliculate, the elevations not very prominent, rounded, c. 5 µm wide.

Distribution. Southern Burma (1); Peninsular Malaysia (13); Sumatra (3); Java (5); Borneo (6); Philippines (9): Luzon, Catanduanes and Mindanao; New Guinea (5). Fig. 19.

Habitat. Primary rain forest. Altitude 100–900 m. Wet places: in streambeds or near streams. Low epiphytic or epilithic. Sometimes locally common.

Notes. 1. Characteristic for this species are the large fronds with a truncate to obtuse base, the very regular and distinct venation with 6–10 primary connectives between each pair of secondary veins, and the very small sori that are scattered in high density on only the smallest tertiary veins and are rare in the outer areoles.

2. No recent collections seen from: Java (most recent: 1906), Philippines (1933) and New Guinea (1912).

3. Cultivation: often cultivated in botanical gardens.

## 14. Microsorum pentaphyllum (Baker) Copeland

*Microsorum pentaphyllum* Copeland (1947) 196. — *Polypodium pentaphyllum* Baker (1891a) 478. — *Pleopeltis pentaphylla* Alderwerelt (1909b) 9. — Type: *Wallis s.n.*, 1870/71, Philippines (holo MICH, not seen; iso K).

*Polypodium curranii* Copeland (1909) 114. — *Pleopeltis curranii* Alderwerelt (1917) 398. — *Microsorum curranii* Copeland (1947) 196. — Type: *Curran FB 15728* (= *BS 954*), -12-1908, Philippines, Benguet, Mosquito Creek (G, M, P, PC, U, UC, US, Z).

Rhizome moderately long to long, dorso-ventrally slightly flattened, 2–4 mm wide, not waxy; roots sparsely set; phyllopodia obscure or distinct, up to 15 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–8, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, appressed, pseudopeltate, index (2–)3–5.5, widest below the middle, (1–)2–5 by 0.5–1 mm, clathrate throughout, margin den-

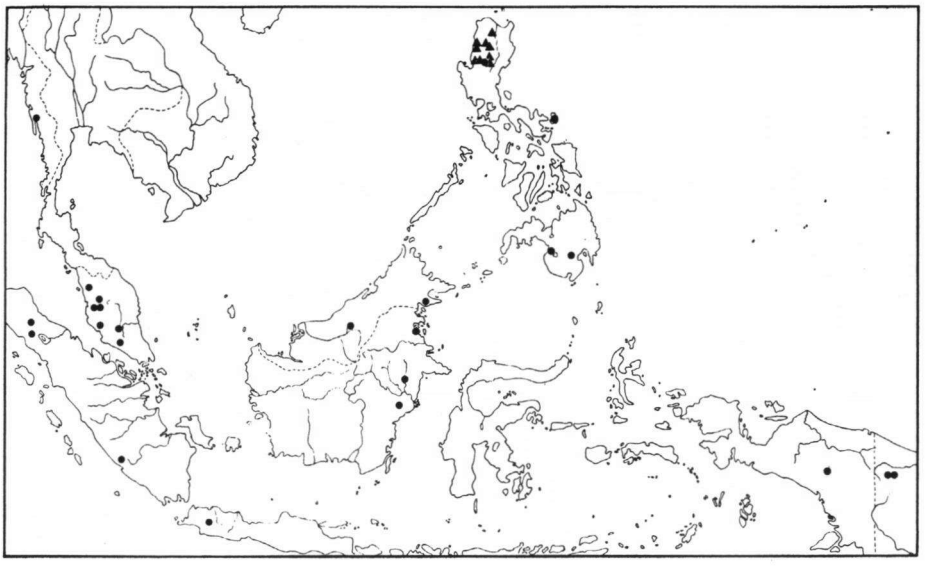

Fig. 19. Distribution of *Microsorum musifolium* (Blume) Copeland (●) and *M. pentaphyllum* (Baker) Copeland (▲).

ticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* pinnatifid, occasionally bipinnatifid or more copiously (almost dichotomously) branched, well proportioned to the rhizome diameter, 25–55 cm long; stipes 1.5–8 cm long, up to 2 mm in diameter, with a few scales at base, vascular strands 3; lamina index 1.5–4, widest above the middle, 20–50 by 5–30 cm, between the lobes ± 0.5–2 cm wide, lobes 2–4 to a side, herbaceous to subcoriaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire, apex acuminate; longest lobe at 1st (or 2nd) position from base, index 6–20(–60), widest at base, 5.5–25 by 0.5–1.5 cm; apical lobe shorter or occasionally conform to or longer than the upper lateral lobes. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one marginal row of smaller areoles, secondary and smaller veins vague, sometimes the smaller veins completely immersed; secondary veins 4–13 mm apart, ± straight, dichotomously branched at 1/4–2/3 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles; free included veins simple, once- or and in part twice-forked, predominantly recurrent. *Sori* superficial or slightly sunken, round or occasionally in part slightly elongate, rarely in part confluent, (0.5–)1 mm in diameter or 1.5 mm long, spreading all over the lamina, in all areoles, 20–45/cm$^2$ (the lowest density usually in the marginal areoles), irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus 20–25-celled, indurated cells 14–18, hypo- and epistomial cells together 6 or 7. *Spores* concavo-convex, hyaline, 55–80 by 25–30 µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. Philippines (15): Luzon. Fig. 19.

Habitat. Evergreen forest. Altitude 1000–2000 m. Epiphytic.

Note. 1. This species is easily recognized by its long and narrow (linear-oblong) lobes with parallel margins.

## 15. Microsorum punctatum (Linnaeus) Copeland

*Microsorum punctatum* Copeland (1929a) 111. — *Acrostichum punctatum* Linnaeus (1763) 1524. — *Polypodium punctatum* Swartz (1801) 21, nom. illeg. (ICBN art. 64.1), non Thunberg (1784) 337 = *Hypolepis punctata* (Thunberg) Mettenius. — *Polypodium lingulatum* Swartz (1806) 30. — *Phymatodes lingulata* Presl (1836) 198. — *Pleopeltis punctata* Beddome (1876) 22. — Type: *Fothergill s.n.*, s.d., China (not found in LINN).

*Polypodium polycarpon* Cavanilles (1801) 246, non Swartz (1801) 21 (see note 4). — *Niphobolus polycarpus* Sprengel (1827) 45. — *Phymatodes polycarpa* Presl (1836) 198, t. 8, f. 19. — *Pleopeltis polycarpa* Moore (1857) lxxviii. — *Microsorum polycarpon* Tardieu (1960) 114. — Type: *Née s.n.*, s.d., probably from the Philippines or Marianas, but reported erroneously by Cavanilles from "San Antonio, Quito" (Ecuador) [see Christensen (1937) 12] (MA).

*Polypodium polycarpon* Swartz (1801) 21, nom. illeg., non Cavanilles (1801) 246 (see note 4). — *Drynaria polycarpa* Brackenridge (1854) 44, nom. nov. (see note 5). — Type [see Morton (1974) 347]: *Thunberg s.n.*, s.d., Java (syn UPS); *Groendal s.n.*, s.d., Mauritius (syn S?, n.v.).

*Polypodium irioides* Poiret (1804) 513. — *Phymatodes irioides* Presl (1836) 196. — *Drynaria irioides* J. Smith (1841) 398 (excl. *Cuming 21*). — *Microsorum irioides* Fée (1852) 268, t. 20B, f. 1. — *Pleopeltis irioides* Moore (1857) lxxviii. — *Colysis irioides* J. Smith (1875) 101. — Type [see Morton (1974) 347]: ?*Commerson s.n.*, s.d., Mauritius (holo P Herb. Lamarck, photo B, BM and C).

*Polypodium crassinerve* Schumacher (1827) 227. — Type: *Schumacher herb. no. 87* (or *86*?), Africa, Guinea (holo C, photo BM).

*Polypodium ambiguum* Blume (1828) add. 125. — Type: ?*Blume s.n.*, s.d., Moluccas, Banda (L) or *Anonymus s.n.*, s.d., HBL 908.296-49: "*Aspidium Microcarpum* Reinw." (L).

*Microsorum irregulare* Link (1833) 110. — Type: *Anonymus s.n.*, s.d., cult. in Hort. Berol. (holo B, iso PC; type species of *Microsorum* Link).

*Polypodium glabrum* Wallich [(1829) 281, nom. nud.] ex Roxburgh (1844) 482, nom. illeg. (ICBN art. 64.1), non Burman (1768) 235 = ?. — Type: *Wallich 281*, near Calcutta (lecto, proposed by Morton (1974) 348; holo BR, Herb. Roxburgh; iso BM, K).

*Polypodium sessile* Kaulfuss ex Kunze (1848) 116. — *Phymatodes sessilis* Presl (1836) 198. — *Microsorum sessile* Fée (1852) 268. — *Pleopeltis sessilis* Moore (1857) lxxviii. — Type: *Sieber, Syn. Fil. no. 31*, Mauritius (B, BM, K, PC, PR, S).

*Polypodium millisorum* Baker (1877) 109. — *Pleopeltis millisora* Alderwerelt (1909b) 8. — Type: *Moseley et al. s.n.*, Challenger Exp., 24/25-9-1874, Polynesia, Little Kei Is. (BM, K).

*Polypodium superficiale* var. *australiense* Bailey (1891) 21, t. 4. — *Microsorum superficiale* var. *australiense* Andrews (1977) 12. — Type: *Wild s.n.*, s.d., Australia, Atherton near Herberton (not seen).

*Polypodium validum* Copeland (1905) 191. — *Pleopeltis valida* Alderwerelt (1909b) 8. — *Microsorum validum* Ching (1933b) 295. — Type: *Copeland 973*, Mindanao, Davao, Sibulan R. (not seen).

*Polypodium punctatum* subsp. *subdrynariaceum* Christ (1906) 994. — *Polypodium punctatum* var. *subdrynariaceum* Alderwerelt (1909a) 654. — Type: *Ridley 8935*, Serangoon, near Singapore (holo P).

*Polypodium punctatum* subsp. *subirideum* Christ (1906) 994. — *Polypodium punctatum* var. *subirideum* Alderwerelt (1909a) 654. — *Microsorum subirideum* Copeland (1947) 197. — Type: *Elmer 5884*, Castilla, Baguio, Benguet (holo P).

*Polypodium neoguineense* Copeland (1911) 89. — *Pleopeltis neoguineensis* Alderwerelt (1917) 390. — *Microsorum neoguineense* Copeland (1947) 196. — T y p e: *King 335*, Papua New Guinea, Lakekamu (holo SYD, photo BM).

*Polypodium irioides* var. *lobatum* f. *cristatum* Bailey (1911) 199, pl. 21. — T y p e: *Turner s.n.*, 1895, near Mackay (holo SYD, not seen).

*Polypodium aspidistrifrons* Hayata (1915) 308, f. 103. — T y p e: *Sôhma s.n.*, -7-1912, Taiwan, Akôchô, Daitetsu (TI).

*Aspidium microcarpon* Blume [(1828) 142, nom. inval. (ICBN art. 34, 1a)]. — Based on type specimen of *Polypodium ambiguum* Blume.

*Polypodium polycephalum* Wallich [(1829) 273, nom. nud.]. — Based on *Wallich 273*, Sylhet (BM, K).

Rhizome short, ± cylindrical, 4–8 mm in diameter, often waxy; roots very densely set, forming a thick mat; phyllopodia more or less distinct, 2–15(–30) mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 14–17, bundle sheaths not differentiated, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise ± sparsely set, slightly spreading, pseudopeltate, or occasionally peltate, index 2–5.5, widest below the middle, 2–8 by 1–2(–2.5) mm, clathrate or subclathrate (i.e. the superficial cell-walls more or less opaque, brownish), margin dentate to denticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 10–100(–175) cm long; stipes up to 12 cm long, up to 8 mm in diameter, with a few scales at base, vascular strands 6–8(–9); lamina index 4–20(–25), widest about or occasionally above the middle, 10–100(–175) by 1.5–10(–15) cm, firm-herbaceous to subcoriacous or occasionally coriaceous, with short glandular hairs and a few scales, acicular hairs absent, base varying from cordate to narrowly angustate, margin entire or occasionally undulate or irregularly lobed, apex varying from rotundate to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and smaller veins immersed or secondary veins distinct; secondary veins 6–25 mm apart, slightly zigzag, dichotomously branched at 4/5 or more of the lamina width; tertiary veins catadromous, (3) 4–6 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round, usually in part confluent, 1–1.5 mm in diameter, restricted to the distal 1/10–2/3 of the lamina, usually absent in the costal and occasionally absent in the marginal areoles, (5–)10–55 (–100)/cm$^2$, not on tertiary veins, irregularly scattered on the quaternary and smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus 19–21(–25)-celled, indurated cells 13–15(–19), hypo- and epistomial cells together 6 or 7. *Spores* plano-convex, hyaline or yellowish, 45–55(–75) by 25–35(–45) µm, ± smooth.

Distribution. Paleotropics and subtropics. Fig. 20.

Habitat. Various types of primary and secondary, evergreen and deciduous forests (i.a. Dipterocarp-, Castanopsis-, mangrove, montane, coastal, riverine), plantations (coconut, rubber), occasionally also in savanna vegetations. Altitude up to 2200 m. Shady or more exposed places, often along streams but also in drier

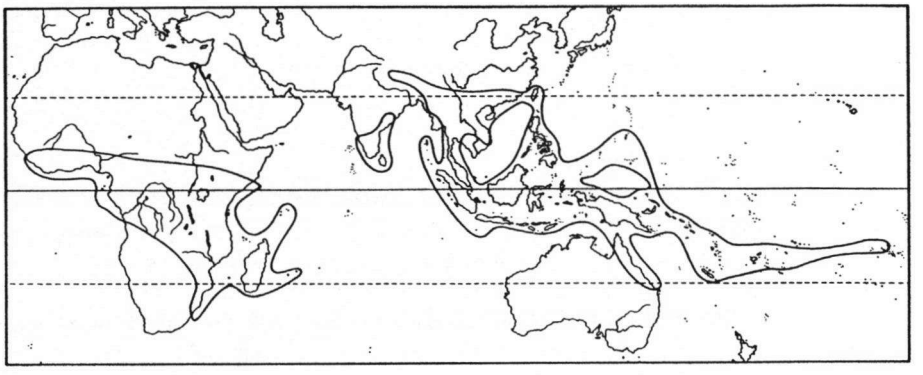

Fig. 20. Distribution of *Microsorum punctatum* (L.) Copeland.

areas. Usually epiphytic (high or low) but quite often also epilithic or terrestrial. Common in most places.

Notes. 1. Often, especially in cultivated plants, irregularly lobed (cristate, bifurcate, etc.) fronds occur. Some of these forms have been described as cultivars: *M. punctatum* 'Craig's monstrosum' Hughes (1985) and *M. punctatum* cv. *grandiceps* Piggott (1988), or as formae (see synonymy). These 'monstrosities' are usually not very stable and similar fronds may arise from 'normal' plants. Plants with such deviating fronds are also found in quite a number of other microsoroids and do not deserve any formal taxonomic recognition.

2. The rhizome is climbing or creeping with the fronds in erect tufts, which are often compared with the 'nests' of *Asplenium nidus*, but are less regular.

3. As this species is very common, recent collections from most parts of the distribution area have been seen.

4. Both *Polypodium polycarpon* Swartz and *Polypodium polycarpon* Cavanilles were published in 1801 (Stafleu & Cowan, 1976–1988). Morton (1974: 347) assumed for convenience that *P. polycarpon* Swartz was published later (in 1802). Christensen (1906: 555), on the other hand, considered Swartz' name to be from 1801 and that of Cavanilles from 1802 and thus cited: "*P. polycarpon* Cav. ex Swartz." Following the ICBN (art. 64.4), the first who of two simultaneously published names rejected one and adopted the other must be followed. Swartz (1806: 30) cited Cavanilles under *P. polycarpon* but on page 227 he put a question mark after this synonym. As far as I could trace, Gaudichaud-Beaupré (1827: 347) was the first to adopt *P. polycarpon* Cavanilles and to reject *P. polycarpon* Swartz, by treating it as a synonym of the former.

5. Brackenridge based *Drynaria polycarpa* on the illegitimate *P. polycarpon* Swartz, and it should therefore be treated as a nom. nov. (ICBN art. 72.2, ex. 2).

6. Vernacular names: Téké (Timor), wassanke (Alor), saugtikel (Manggarai; Flores), theng oewa la or thê wâ lâ (Karieng; Thailand), hâng sing (Thailand), dege (Kishambo; Tanzania), pahat (Loyalty Is.), bucibuci kau (Fiji), bukel belu (Palau

Is.), eawawan (Igorat; Luzon), o toto fufungu (Tobelorese; Halmahera), tutuwungu (Tobaro; Halmahera), baluk (Kurte Plestok; New Guinea), kopeh-kopeh (Matapaili; New Guinea), vata-vata (Kulumo; New Guinea).

7. Cultivation: cultivated in many botanical gardens (see also note 1). Also easy to grow as a house-plant (A small specimen that I treated badly in a usually unheated room for several years still thrives).

8. Uses: warmed with alcohol and applied on arms and legs it is used for rheumatism in some areas of North Vietnam.

9. Chemistry: According to Swain & Cooper-Driver (1973) 100% of the triterpenes in this species can be classified as Fern-9(11)-ene. Soeder (1985), who gave a survey of the literature on fern constituents for 1966–1984, found among all species here described only one record for *M. punctatum*: it contains triterpenoids and alkanes.

10. Pal & Pal (1962) described and illustrated the development and structure of the gametophyte of this species.

11. According to Benl (1976) *M. punctatum* is a colonizer of lava flows in Africa.

## 16. Microsorum rampans (Baker) Parris

*Microsorum rampans* Parris (1986) 69. — *Polypodium rampans* Baker (1876) 109. — T y p e: *Moseley et al. s.n.*, Challenger Exp. -3-1875, Papua New Guinea, Admiralty Is. (holo K, sketch BM).

*Polypodium bamlerianum* Rosenstock (1910) 163. — *Pleopeltis bamleriana* Alderwerelt (1917) 381. — *Microsorum bamlerianum* Copeland (1947) 196. — T y p e: *Bamler s.n.*, -2-1909, New Guinea, Logaueng (S not seen, photo BM).

*Polypodium kingii* Copeland (1911) 89. — *Pleopeltis kingii* Alderwerelt (1917) 396. — *Microsorum kingii* Copeland (1947) 196. — T y p e: *C. King 122*, Papua New Guinea (SYD, photo BM).

*Polypodium wobbense* Brause (1912) 51. — *Pleopeltis wobbensis* Alderwerelt (1917) 382. — *Microsorum wobbense* Copeland (1947) 197. — T y p e s: *Schlechter 16364*, Papua New Guinea, Kaiser Wilhelmsland, Wälder von Wobbe (syn; BISH, K, P, S, UC, US); *Schlechter 17369*, New Guinea, Kaiser Wilhelmsland, Wälder am Minjem-Thor (syn; BM, K, P, UC, US).

*Pleopeltis myriocarpa* var. *schlechteriana* Alderwerelt (1913) 19. — T y p e: *Schlechter 13920*, New Guinea, Bismarck Mts (K, P).

*Polypodium tuanense* Copeland (1914) 8. — *Pleopeltis tuanensis* Alderwerelt (1917) 398. — *Microsorum tuanense* Copeland (1947) 196. — T y p e: *C. King 384*, Papua New Guinea, Mt Tuan (BM).

Rhizome long, dorso-ventrally flattened, 1–4 mm wide, not waxy; roots sparsely set; phyllopodia distinct, up to 7 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–9, bundle sheaths sclerenchymatous, sclerenchyma strands absent, cavity occasionally present. *Rhizome scales* (see note 3) more or less densely set, closely appressed, usually peltate, occasionally some larger scales pseudopeltate, index 1–4, widest below or about the middle, 0.5–3 by 0.3–1.5 mm, clathrate throughout, margin entire or dentate, apex acuminate or obtuse to rounded, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple or pinnatifid, well proportioned to the rhizome diameter. Simple fronds: 15–45 cm long; stipes 0.5–15 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 3–5; lamina index 4–15, widest below or about the middle, 15–40 by 1.5–

5.5 cm, thin-herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base narrowly angustate to obtuso-angustate, margin entire, apex acute or acuminate. Pinnatifid fronds conform to simple fronds except for size and shape: 25–60 cm long; stipes 5–20 cm long, up to 1.5 mm in diameter; lamina index 1–1.5, widest below the middle, 20–40 by 15–35 cm, between the lobes c. 1–3 cm wide, lobes 1–3 (4) to a side; longest lobe at 1st (2nd) position from base, index 3.5–12, widest below the middle or at base, 7.5–20 by 1.3–2.5 cm; apical lobe widest just above or at base, longer than the upper lateral lobes. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one or two marginal rows of smaller areoles, secondary veins distinct, smaller veins more or less vague; secondary veins 5–15 mm apart, ± straight, dichotomously branched at 1/2–2/3 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles: free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round or in part slightly (occasionally much, ± pteridoid, see note 2) elongate, sometimes in part confluent, 1–2.5 mm in diameter or 2–3 (–35) mm long, spreading all over the lamina, present in all areoles, 1–20/cm$^2$ (the highest concentration in the marginal areoles), irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–4- (5)-celled. Sporangia: annulus (17–)18–22(–23)-celled, indurated cells (12) 13–15 (16), hypo- and epistomial cells together 5–7. *Spores* concavo-convex, hyaline, 50–95 by 25–45 µm, colliculate, elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. New Guinea (many). Fig. 21.

Habitat. Various types of primary and secondary forests (i.a. swamp forest, transition oak-rain forest, lowland, hill, montane, flood-plain). Altitude 5–950 (–1250) m. Shady places, near streams or not near free water. Occasionally reported from limestone areas. Low epiphytes, up to 6 m high on the base of trunks or on small trees; rarely terrestrial. Sometimes locally common.

Notes. 1. See note 1 under *M. cinctum* and note 1 under *M. longissimum*.

2. Occasionally (e.g., *Craven & Schodde 1034*) most sporangia are arranged in long elongated sori along the margin of the lamina on the marginal tertiary vein, while only a few sori are scattered over the rest of the lamina surface.

3. In *M. rampans* two ecologically correlated types of rhizome scales occur. In the first type (found in almost one-third of the total number of specimens), the scales are ovate to orbicular with a rounded or obtuse apex and many 2-celled marginal hairs on an entire margin. The cell walls are very thick and reddish brown. In the second type the scales are narrowly ovate with a caudate apex and very few 1-celled hairs on a dentate margin. These scales have thinner, brown cell walls. The two scale types seem to be slightly correlated with the frond type and habitat of the plants. The scales with the rounded or obtuse apex occur usually on plants with simple as well as pinnatifid fronds or pinnatifid fronds only. Most of these plants (60%) have been collected at altitudes of 500 m or more, although they also occur at lower altitudes. The scales with the caudate apex are only found on plants with exclusively entire fronds. These plants grow usually (90%) at altitudes of 500 m or less and are rare in hill and montane forests.

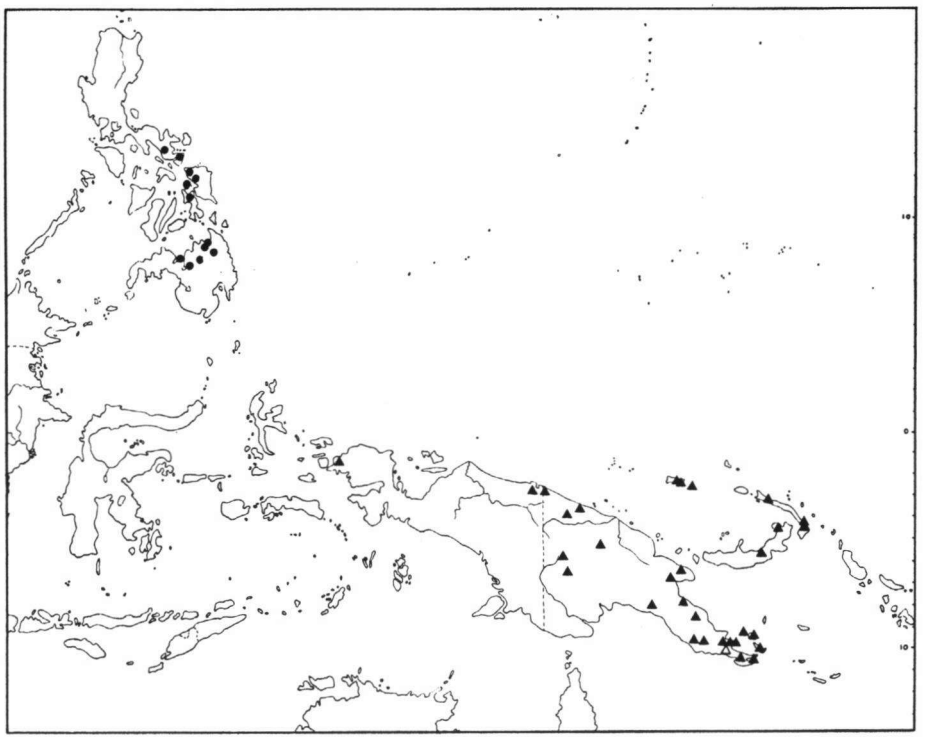

Fig. 21. Distribution of *Microsorum rampans* (Baker) Parris (▲) and *M. samarense* (J. Smith) Bosman (●).

4. The rhizome is reported to be climbing with the juvenile fronds on the lowest parts (thereby occasionally covering the forest floor) and the fertile fronds on the upper parts.

5. Vernacular names: La lumu (W Nakanai), gabi (Yebora; Morobe).

6. Cultivation: occasionally cultivated in botanical gardens.

7. Uses: once reported as "not used by the natives."

## 17. Microsorum samarense (J. Smith) Bosman, *comb. nov.*

*Diblemma samarense* J. Smith (1841) 399. — *Taenitis samarensis* Mettenius (1856a) 27. — *Colysis samarensis* J. Smith (1875) 101. — T y p e: *Cuming 332*, Philippines, Samar (holo K; iso L, P, PC, Z; type species of *Diblemma* J. Smith).

*Polypodium tenuilore* J. Smith ex Mettenius (1856b) 86. — *Colysis tenuiloris* J. Smith (1875) 101. — *Microsorum tenuilore* Copeland (1929a) 113. — *Diblemma tenuilore* Ching (1940) 260. — T y p e: *Cuming 287*, Philippines, Mindanao (BM, K, L, P, PC, Z; not MICH, which is *Microsorum longissimum* Fée).

*Drynaria tenuiloris* J. Smith [(1841) 397, nom. nud.]. — *Pleopeltis tenuiloris* Moore [(1857) lxxviii, nom. nud.]. — Based on type specimen of *Polypodium tenuilore* Mett.

Rhizome moderately long to long, dorso-ventrally flattened, 1–4 mm wide, not waxy; roots sparsely set; phyllopodia obscure, up to 11 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 5–10, bundle sheaths sclerenchymatous, sclerenchyma strands absent, cavity occasionally present. *Rhizome scales* more or less densely set, appressed or slightly spreading, pseudopeltate, index (1–)2–5, widest below the middle, (0.5–)1–3 by 0.5–1 mm, clathrate throughout, margin denticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 25–50 cm long; stipes 0.5–4.5 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 3; lamina index 30–65, widest below or about the middle, 25–45 by 0.5–1 cm, firm-herbaceous to coriaceous, with short glandular hairs, a few scales, and (a few) acicular hairs, base narrowly angustate, margin entire, apex acuminate. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one or two marginal rows of smaller areoles, secondary and smaller veins immersed, occasionally the secondary veins vague; secondary veins 5–13 mm apart, ± straight, dichotomously branched at 1/4–2/3 of the lamina width; tertiary veins bordering the main areoles catadromous; smaller veins variously anastomosing within the main and marginal areoles; free included veins simple, once- and twice-forked, predominantly recurrent. *Sori* sunken, round or in part elongate, sometimes in part confluent, 0.5–1.5 mm in diameter or 1.5–40 mm long, spreading all over the lamina, absent in the costal areoles or present in all areoles, 10–60/cm$^2$, irregularly scattered on the smaller anastomosing veins, the marginal veins and on the free included veins. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus (15–)19–21-celled, indurated cells (9–)12–15, hypo- and epistomial cells together 6 or 7. *Spores* concavo-convex, hyaline, 50–70 by 20–30 µm, colliculate, the elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Philippines (21). Fig. 21.

Habitat. Primary forest. Altitude 150–400 m. Limestone. Epiphytic or epilithic. Common in western Samar.

Notes. 1. This species is characterized by its linear lanceolate fronds with light coloured primary vein, its rather thick texture leaving the veins (almost) completely immersed, and its often elongated sori, which in some fronds are almost all concentrated on the marginal vein (cf. note 2 under *M. rampans*). It resembles the narrow forms of *M. longissimum* but these differ in usually broader fronds, thinner texture and thus more distinct venation, and larger sporangia and spores.

### 18. Microsorum sopuense Bosman, *spec. nov.* — Fig. 22.

Rhizoma depressum 1–3 mm latum, squamis peltatis clathratis sparse vestitum. Frondes simplices, 60–75 cm longae, stipitibus usque 0,5 cm longis. Lamina 60–75 cm longa, 2–3 cm lata. Venatio et innervatio sororum *M. heterocarpo* similes. — Typus: *Hennipman 5619*, Sulawesi, Sopu Valley, south of Palu (holo L).

Rhizome long, dorso-ventrally flattened, 1–3 mm wide, not waxy; roots ± densely set; phyllopodia distinct, up to 25 mm apart. Rhizome anatomy (in cross section):

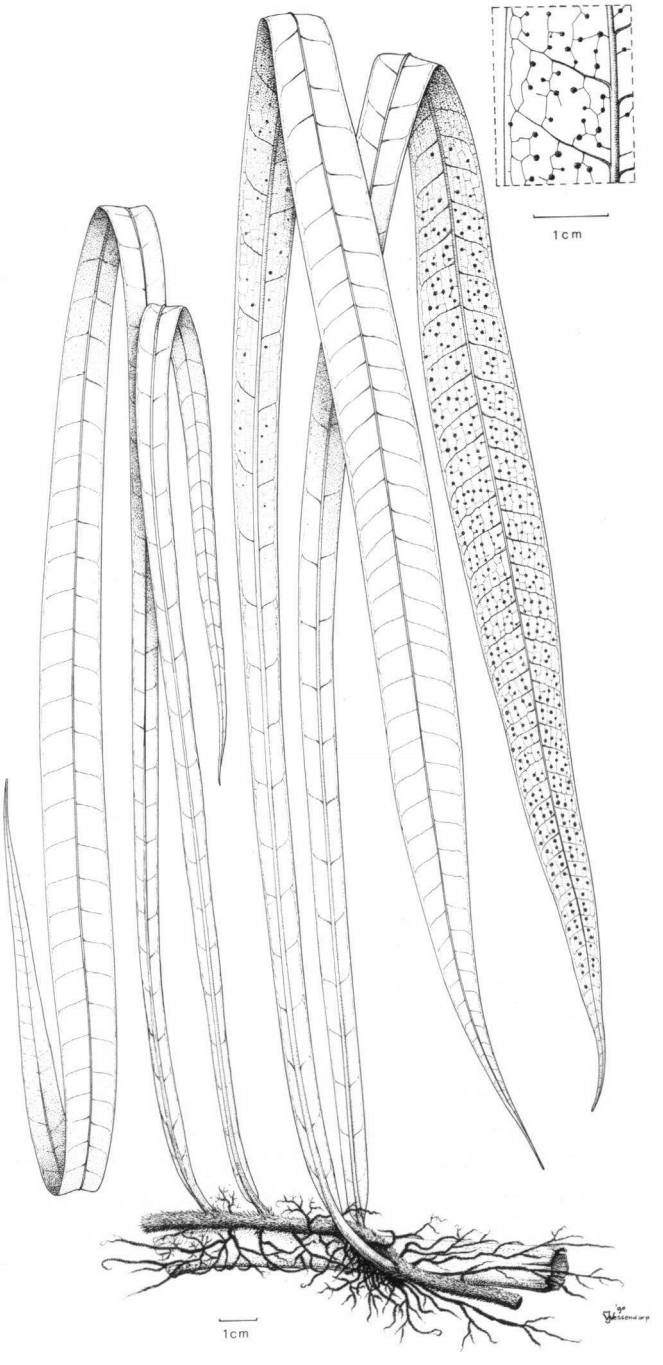


Fig. 22. *Microsorum sopuense* Bosman (*Hennipman 5619*, L).

vascular bundles in cylinder 8–12, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise ± sparsely set, appressed or slightly spreading, peltate, index (2.5–)5–7.5, widest below the middle, (2–)3.5–6 by 0.5–1 mm, clathrate throughout, margin denticulate, base with a distinct undulation, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 60–75 cm long; stipes up to 0.5 cm long, up to 2.5 mm in diameter, with a few scales at base, vascular strands 3–5; lamina index 20–40, widest about or above the middle, 60–75 by 2–3 cm, thin-herbaceous, with short glandular hairs, scales and acicular hairs absent, base cuneato-angustate, margin entire, apex acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and tertiary veins distinct, smaller veins vague; secondary veins 6–10 mm apart, zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 3 or 4 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, pointing to all sides. *Sori* superficial, round, not confluent, 1 mm in diameter, restricted to the distal 1/3–2/3 of the lamina, present in all areoles, 15–20(–30)/cm$^2$, occasionally in part on tertiary veins, 2 per quaternary vein, forming 2 irregular rows situated parallel to each secondary vein, in the costal areoles on the free included veins. Paraphyses uniseri-

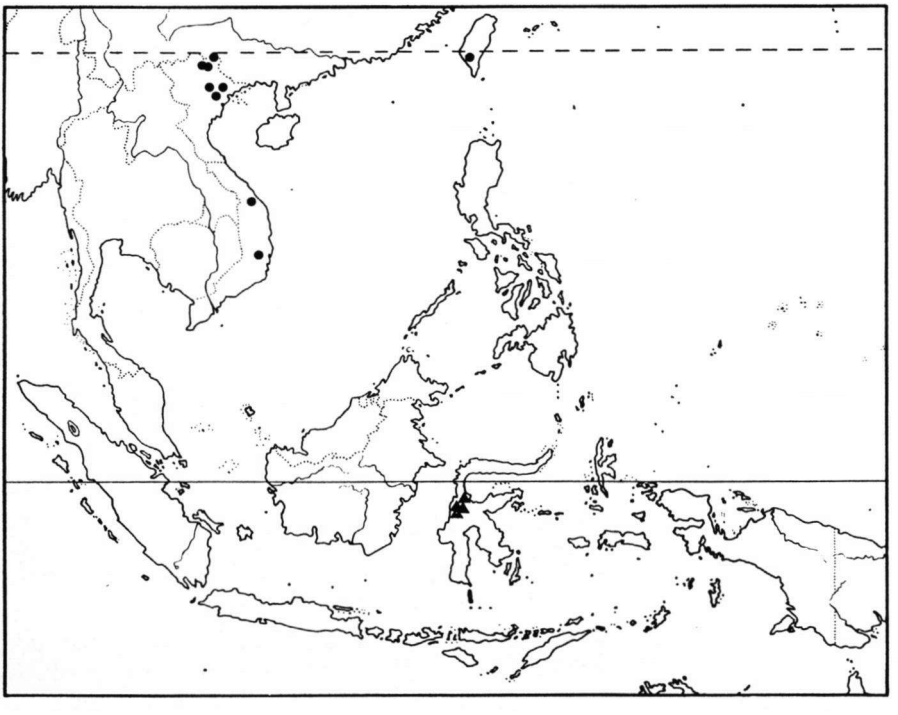

Fig. 23. Distribution of *Microsorum sopuense* Bosman (▲) and *M. steerei* (Harrington) Ching (●).

ate, 2- or 3-celled. Sporangia: annulus 18- or 19-celled, indurated cells 12 or 13, hypo- and epistomial cells together 6. *Spores* concavo-convex, hyaline, 35–40 by 20–25 µm, ± smooth (LM).

Distribution. Central Sulawesi (4). Fig. 23.

Habitat. Primary rainforest. Altitude 1000–1200 m. Near stream. Epiphytic (low). Very common in Sopu Valley.

Notes. 1. The description is based on 4 collections.

2. As good spores were very rare in the available collections, no SEM observations were made.

## 19. **Microsorum spectrum** (Kaulfuss) Copeland

*Microsorum spectrum* Copeland (1947) 197. — *Polypodium spectrum* Kaulfuss (1824) 94. — *Phymatodes spectrum* Presl (1836) 197. — *Drynaria spectrum* J. Smith (1842) 61. — *Pleopeltis spectrum* Moore (1862) 348. — *Colysis spectrum* J. Smith (1866) 98. — Type: *de Chamisso s.n.* s.d., Hawaii, Owahu (PC).

*Polypodium thouinianum* Gaudichaud (1827) 348, t. 5, f. 1. — *Drynaria thouiniana* Fée (1852) 270. — Type: *Gaudichaud-Beaupré s.n.*, s.d., Hawaii, Owahu (holo FI, not seen, photo US).

*Polypodium spectrum* var. *ovatum* Hillebrand (1888) 560. — Type not indicated.

*Polypodium spectrum* var. *pentadactylum* Hillebrand (1888) 560. — Type not indicated.

Rhizome long, dorso-ventrally flattened, 1.5–6 mm wide, often with short accessory branches (bearing one frond) opposite the phyllopodia, not waxy; roots ± densely set; phyllopodia distinct, 30–80 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 14–15, bundle sheaths collenchymatous or occasionally slightly sclerenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* densely set, closely appressed, pseudopeltate, index 1.5–2.5, widest below the middle, 3–5 by 2 mm, clathrate except for the marginal region which is hyaline and the central region where some cells are opaque and some anticlinal cell-walls not thickened, margin entire and often eroded, apex obtuse, central region glabrous, inner layer of thickened cell walls warty. *Fronds* simple or pinnatifid, well proportioned to the rhizome diameter. Simple fronds: 10–20 cm long; stipes 5–10 cm long, up to 1 mm in diameter, with a few scales at base, vascular strands 6 or 7; lamina index 1.3–2, widest below the middle or at base, 8–15 by 4–7.5 cm, thin-herbaceous to herbaceous, with short glandular hairs, scales and acicular hairs absent, base auriculato- or cordato-angustate, margin entire or rarely sinuate, apex acute to acuminate. Pinnatifid fronds conform to simple fronds except for size and shape: 20–55 cm long; stipes 5–30 cm long, up to 3.5 mm in diameter; lamina index 0.7–1, widest below the middle or at base, 15–30 by 15–35 cm, between the lobes ± 5–20 cm wide, lobes 1 or 2 to one side, the 1st lobe basiscopically sometimes with a small lobe (see note 2); the longest lobe at 2nd (or 1st in case of 1 pair of lobes) position from base, index 0.7–2(–3), widest at base, 5–15 by 3.5–10 cm; apical lobe widest at base, longer than the upper lateral lobes. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 6–14(–20) mm apart, slightly zigzag, dichotomously branched near

the margin of the lamina; tertiary veins catadromous, 4–6 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and twice-forked, pointing to all sides. *Sori* superficial, round or rarely in part slightly elongate, not confluent, 1–2 mm in diameter, spreading all over the lamina, present in all areoles, 5–15/cm$^2$, not on tertiary veins, occasionally in part on quaternary veins, irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2–5(–7)-celled, or occasionally in part the apex biseriate and clathrate. Sporangia: annulus 21–24(–28)-celled, indurated cells 14–16(–19), hypo- and epistomial cells together 6–10. *Spores* concavo-convex, hyaline, 50–70 by 30–45 µm, more or less smooth.

Distribution. Hawaii Is. (many): Hawaii, Maui, Molokai, Oahu, Kauai.

Habitat. Primary and secondary forests. Altitude 180–1050 m. Along trails, on wooded or exposed ridges or streambanks. Sometimes in (deep) shade. Epiphytic on (mossy) tree trunks, occasionally terrestrial or epilithic. Sometimes locally common.

Notes. 1. The shape of the fronds is characteristic for this species: the pinnatifid fronds are hastate or sometimes almost triangular with one pair of lateral lobes (which have occasionally a smaller basiscopic lobe). The pustulated cell walls of the clathrate part of the rhizome scales are a unique character.

2. The smaller lobes on the basiscopical side of the lateral lobes originate from the costa of the lateral lobe, from the point where this costa meets the main rachis or rarely (as a normal lateral lobe) from a point lower down the main rachis.

3. This species may grow as ground cover with some parts ascending tree trunks.

4. Vernacular names: Peahi (Oahu), potato fern (Hawaii).

5. Phillips & White (1967) induced wound tissue in the stipe of this species which proved to be anatomically similar to that at the sites of disarticulation.

## 20. Microsorum steerei (Harrington) Ching

*Microsorum steerei* Ching (1933b) 306. — *Polypodium steerei* Harrington (1878) 32. — Type: *Steere s.n.*, -10-1873, Taiwan, Ape's Hill, Takow (= Kaohsiung) (lecto, proposed by Price (1982) 202; holo MICH; iso K).

*Polypodium tonkinense* Baker (1890) 266. — Type: *Balansa 148*, Tonkin, Takeuin, near Quang Yen (holo K; iso P).

*Polypodium playfairii* Baker (1891a) 474. — Type: *Playfair 383*, Taiwan, Ape's Hill (holo K).

Rhizome short; ± cylindrical, 3–5 mm in diameter, often waxy; roots densely set, often forming a thick mat; phyllopodia distinct, 1–10 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 11–14, bundle sheaths not differentiated, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. Rhizome scales apically densely set, otherwise ± sparsely set, slightly spreading, pseudopeltate, index (2–)3.5–7, widest below the middle, (2.5–)4–8 by 0.5–1.5 mm, clathrate throughout, margin denticulate, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 10–35(–45) cm long; stipes up to 7 cm long, up to

1.5 mm in diameter, scales absent, vascular strands 4–5; lamina index 6–10(–17), widest about or above the middle, 10–35(–40) by 1.5–4.5(–5) cm, coriaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire, apex acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and smaller veins immersed or secondary veins vague; secondary veins 7–15 mm apart, slightly zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 3–6 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial or slightly sunken, round, not confluent, 1–2 mm in diameter, spreading all over the lamina or restricted up to the distal 1/2, absent in the costal and marginal areoles, 10–20/ $cm^2$, not on tertiary veins, in part 2 per quaternary vein, forming 2–4 irregular rows situated parallel to each secondary vein, in part irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate with the apical cell often large and curved, (1-) 2- or 3-celled. Sporangia: annulus 19–22 (–26)-celled, indurated cells (11–)15(–19), hypo- and epistomial cells together 6–8. *Spores* plano- to concavo-convex, hyaline, 50–60 by 30–35(–40) µm, colliculate, the elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Taiwan (2); China: Kwangsi (3); North and South Vietnam (15). Fig. 23.

Habitat. Few reports: "in cave near entrance" and "by slope, under woods". Altitude 100–200 m. Four times reported from limestone.

Notes. 1. This species resembles very much some of the smaller and more coriaceous specimens of *M. punctatum*, but the apex of the fronds is usually more acuminate and the typical apical cell of the paraphyses has never been found in *M. punctatum*.

2. Chemistry: Lee et al. (1961) found flavanones in this species.

## 21. Colysis insignis (Blume) J. Smith

*Colysis insignis* J. Smith (1875) 101. — *Polypodium insigne* Blume (1828) 127. — *Pleopeltis insignis* Beddome (1866) t. 214. — *Microsorum insigne* Copeland (1929a) 112. — Types: *Zippelius s.n.*, s.d., Java (lecto, proposed here; holo L, photo C); *Blume s.n.*, s.d., Java (para; L).

*Polypodium diffundens* Kunze (1846) 422. — Type: *Zollinger 1299* Java (P, Z).

*Drynaria decurrens* Brackenridge (1854) 48. — *Pleopeltis decurrens* Moore (1862) 345. — *Microsorum decurrens* Copeland (1960) 481. — Type: *Brackenridge 11*, U. S. Expl. Exped., Philippines, Luzon, mountains near Los Baños (holo US; iso K).

*Polypodium dilatatum* Wallich [(1829) 295, nom. nud.] ex Hooker (1864) 85, nom. illeg., (ICBN art. 64.1), non Hoffmann (1795) 7 = *?Dryopteris spinulosa* (Müller) Kuntze, nec Liebmann (1849) 208 = *?Ctenitis effusa* (Swartz) Copeland. — *Pleopeltis dilatata* Beddome (1866) t. 122. — *Colysis dilatata* J. Smith (1875) 101. — *Polypodium euryphyllum* emend. Christensen (1906) 525: excl. *Polynesia* [= *Phymatosorus commutatus* (Blume) Pichi Sermolli]. — *Microsorum dilatatum* Sledge (1960) 143. — *Kaulinia dilatata* Nayar & Kaur (1974) 89. — Type: *Wallich 295*, Nepal (holo K; iso US).

*Polypodium hancockii* Baker (1885) 106. — *Microsorum hancockii* Ching (1933b) 309. — *Kaulinia hancockii* Nayar (1964) 67. — T y p e: *Hancock 100*, Taiwan, Tamsui District (BM, K).

*Selliguea anceps* Christ (1898b) 879. — *Polypodium anceps* Christensen (1906) 509. — T y p e: *Henry 10089a*, China, Yunnan, Mengtze (B, K, US).

*Polypodium dolichopterum* Copeland (1906a) 162. — *Pleopeltis dolichoptera* Alderwerelt (1909b) 9. — T y p e: *Copeland 1717*, Philippines, Mindanao, San Ramon (BM, P, S, photo UC).

*Polypodium rivulare* Copeland (1906a) 163, nom. illeg. (ICBN art. 64.1), non Vahl (1807) 51 = *Nephrolepis rivularis* (Vahl) Mettenius. — *Pleopeltis rivularis* Alderwerelt (1909b) 9. — T y p e: *Copeland 1998*, Philippines, Laguna, Los Baños (syn; B, BM, P); *Copeland 2021*, Philippines, Batangas, Mt Malarayat (syn; B).

*Pleopeltis insignis* f. *aperta* Alderwerelt (1914) 29. — T y p e: *Matthew 670*, Sumatra, Padang Pandjang (holo K).

*Microsorum ? palmatum* Fée [(1852) 269, nom. inval. (ICBN art. 34.1 a)], excl. *Cuming 126* and *Drynaria palmata* J. Smith (1841) 397, which is based on *Polypodium palmatum* Blume (1828) 131 = *Crypsinus taeniatus* var. *palmatus* (Blume) Christensen, incl. *Cuming 52*, (BM, K, L).

Rhizome moderately long, dorso-ventrally flattened or ± cylindrical, 0.5–10 mm wide, not waxy; root densely set; phyllopodia more or less distinct, 2.5–11 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–16, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* apically densely set, otherwise ± sparsely set, appressed or slightly spreading, pseudopeltate, index 2–5.5, widest below the middle, (2–)2.5–7.5 by 0.5–2.5(–3) mm, clathrate throughout, margin entire to denticulate and occasionally with small triangular lobes, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple or pinnatifid, well proportioned to the rhizome diameter. Simple fronds: 2.5–65 cm long; stipes 1–10 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 5–7; lamina index 4–11, widest below, about or above the middle, 2–65 by 0.5–6.5 cm, thin-herbaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire or rarely sinuate, apex acute to acuminate. Pinnatifid fronds conform to simple fronds except for size and shape: 10–195 cm long; stipes 1–85 cm long, up to 10 mm in diameter; lamina index 1–3, widest below or about the middle, 8–110 by 3–55 cm, between the lobes c. 0.5–5 cm wide, lobes 1–12(–14) to one side; longest lobe at 1st–3rd(–5th) position from base, index 3–8.5, widest below or about the middle or at base, 2–27 by 0.3–5.5 cm; apical lobe conform to or shorter or longer than the upper lateral lobes. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, sometimes each of these rows forming main areoles in a row situated parallel to the primary vein and bordered by one or more marginal rows of smaller areoles, secondary and smaller veins immersed or vague; secondary veins 4–13 mm apart, ± straight or zigzag, dichotomously branched near the margin of the lamina but immersed at 3/4–4/5 of the lamina width; tertiary veins mostly anadromous, sometimes catadromous, 1–3 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple and in part once-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate, sometimes in part confluent, 0.5–1.5 mm in

diameter or 1.5–5 mm long, restricted to the distal 1/2–2/3 of the lamina, present in all areoles or absent in the marginal areoles, 5–20(–30)/cm$^2$, 2 per tertiary vein, forming 2 irregular rows situated parallel to each secondary vein or irregularly scattered on the smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, 2- or 3- (4-)celled. Sporangia: annulus 15–23(–25)-celled, indurated cells 9–15(–17), hypo- and epistomial cells together 6–8. *Spores* plano- to concavo-convex, hyaline to yellowish, 40–70 by 25–35 µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. Nepal (3); Sikkim (16); Bhutan (1); India: Assam (11); Burma (2); Japan: Ryu-Kyu Is. (many); Taiwan (7); China (many): Yunnan, Szechwan, Kweichow, Kwangsi, Kwangtung, Kiangsi, Fukien; Thailand (15); North and South Vietnam (17); Peninsular Malaysia (8); Sumatra (4); Java (many); Lesser Sunda Islands: Flores (1); Borneo (5); Philippines (many). Fig. 24.

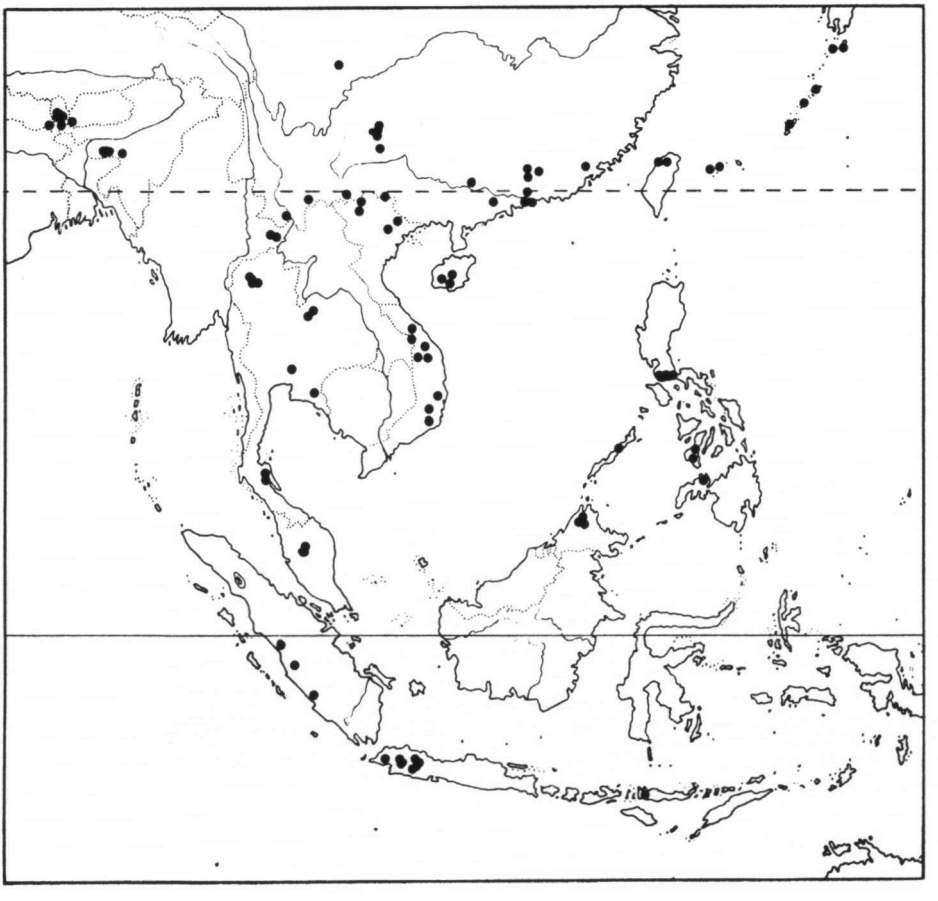

Fig. 24. Distribution of *Colysis insignis* (Blume) J. Smith.

Habitat. Primary and secondary forests, often in wooded ravines, sometimes in thickets. Altitude 50–2300 m. In or along streams or falls, in undergrowth of shrubs, twice reported from caves. Shady, mossy, muddy and wet places. Granite, limestone, sandstone, sandy soil or loam. Usually epilithic, occasionally epiphytic or terrestrial. Locally common and abundant or rare and scattered.

Notes. 1. This species is very variable in size, but typical features are its simple or pinnatifid and thin-herbaceous fronds with usually very long and narrow bases, its rather irregular venation with usually only the basal part of the secondary veins distinct, and its irregularly scattered sori, which are often slightly elongated.

2. Formerly this species was described under four different species of *Microsorum,* which were mainly recognized for the following areas: *M. insigne:* Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands, and Borneo; *M. hancockii:* Japan, Taiwan, Eastern China, Thailand, North and South Vietnam; *M. dilatatum:* northern India and northeastern Himalayan states, western China, Burma; and *M. decurrens:* Philippines. They agree essentially in most characters and represent only a gradual difference in the size of the fronds and the number of lateral lobes: larger fronds with often more lobes in the northwestern areas and smaller fronds with fewer lobes in the southern and especially eastern areas (see table 8). This may be the result of complex hybridization processes or simple local variation along a morphocline, but as the morphological variation shows overlap in most areas it is not possible to keep the species separate. Further studies of other characters (e.g., chromosomes) may reveal more about the causes of variability in this species.

Table 8. Number of pairs of lateral lobes.

| Area | Number | Area | Number |
|---|---|---|---|
| Northern India & Himalaya | (0–)4–12(–14) | Sumatra | 2–4 |
| Thailand | 0–11 | Borneo | 2–4 |
| Peninsular Malaysia | 5–8 | North & South Vietnam | 0–4 |
| China & Burma | 0–8 | Taiwan | 0–2(–4) |
| Java | (0–)2–5(–8) | Japan | 0–2(–3) |
| Philippines | 0–5 | Lesser Sunda Islands | 2 |

3. Larger specimens of *C. insignis* are often confused with *Tectaria grandidentata* (Cesati) Holttum, but the latter differs for instance in its erect rhizome with tectarioid scales and its fronds with undulate-dentate margin and reduced lower lobes.

4. Luzon specimens are usually very small, but as there is a gradual transition to larger specimens in other parts of the Philippines this local form is not formally recognized.

5. No recent collections seen from: Bhutan (most recent: 1879), Assam (1959), Burma (1922), Vietnam (1947), Sumatra (1923), Java (1953), Philippines (1958).

6. Vernacular names: Hokozaki-uraboshi (Japan).

7. Cultivation: rarely cultivated in botanical gardens.

## 22. Colysis pteropus (Blume) Bosman, *comb. nov.*

*Polypodium pteropus* Blume (1828) 125, Add. 3. — *Pleopeltis pteropus* Moore (1857) lxxviii. — *Microsorum pteropus* Copeland (1929a) 112. — *Kaulinia pteropus* Nayar (1964) 67. — T y p e: *Blume s.n.*, s.d., Java, G. Toembal (lecto, proposed here; holo L, photo C and UC; type species of *Kaulinia* Nayar).

*Polypodium tridactylum* Wallich [(1829) 315, nom. nud.] ex Hooker & Greville (1831) t. 209. — *Phymatodes tridactyla* Presl (1836) 196. — *Drynaria tridactyla* Fée (1852) 271. — *Pleopeltis tridactyla* Moore (1857) lxxviii. — *Colysis tridactyla* J. Smith (1875) 101. — T y p e: *Wallich 315*, Mt Sylhet Dehlus (holo K; iso BM, C, K, UC, US).

*Polypodium zosteriforme* Wallich [(1829) 280, nom. nud.] ex Mettenius (1856b) 86, t. 1, f. 26–27. — *Pleopeltis zosteriformis* Beddome (1866) t. 123. — *Colysis zosteriformis* J. Smith (1875) 100. — *Pleopeltis pteropus* var. *zosteriformis* Beddome (1883) 362. — *Microsorum zosteriforme* Ching (1933b) 311. — *Kaulinia zosteriformis* Nayar & Kaur (1974) 87. — T y p e: *Wallich 280*, Tenasserim, Nepal and Mt Chappedang (holo K; iso BM, PC, S).

*Pleopeltis pteropus-minor* Beddome (1876) 23. — *Pleopeltis pteropus* var. *minor* Beddome (1883) 361. — *Polypodium pteropus* var. *minor* Wu et al. (1932) 298, pl. 140. — *Microsorum pteropus* f. *minor* Ching (1933b) 312. — *Microsorum pteropus* var. *minor* Christensen & Tardieu-Blot (1939) 194. — *Kaulinia pteropus* var. *minor* Nayar & Kaur (1974) 87. — T y p e: *Beddome s.n.*, specimen corresponding with Beddome, Ferns South. India (1863) 60, t. 179, S India or Sri Lanka (holo MH, not seen).

*Microsorum brassii* Copeland (1929b) 181. — T y p e: *Brass 1153*, New Guinea, Upoia, Vailala R. (holo A, not seen, photo BM, photo K).

*Polypodium aquaticum* Christ (1909) 153. — T y p e: *Versteeg 1203*, Dutch New Guinea (K, L, sketch BM).

*Polypodium micropteris* Baker (1906) 14. — T y p e: *Henry 12630*, China, Yunnan, mountains. east of Szemao (BM, K, P).

*Polypodium udum* Christ (1910) 140. — T y p e: *Cavalerie 3388*, China, Kweichow, Lofou (BM, K, P).

*Phymatodes zosteriformis* Presl [(1836) 196, nom. nud.]. — Based on type specimen of *Polypodium zosteriforme* Mettenius.

*Drynaria dubia* J. Smith [(1841) 397, nom. nud.]. — Based on *Cuming 324*, Philippines, Samar (BM, L, LE, P, PC).

Rhizome moderately long, dorso-ventrally flattened, 0.5–5 mm wide, not waxy; roots ± densely set; phyllopodia obscure or distinct, 1.5–20 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 10–14, bundle sheaths collenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, appressed, pseudopeltate or basifixed with small non-overlapping auricles, index 3–5, widest below the middle, 1.5–5 by 0.5–1 mm, clathrate except for the central region which is opaque, margin entire, apex acuminate, central region usually dorsally with long lax hairs, occasionally glabrous, inner layer of thickened cell walls smooth. *Fronds* simple or pinnatifid, well proportioned to the rhizome diameter. Simple fronds: 5.5–40 cm long; stipes up to 12 cm long, up to 2 mm in diameter, with usually many scales at base, vascular strands 7; lamina index 5–35, widest below or about the middle, 3.5–30 by 0.2–5.5 cm, thin-herbaceous to membranaceous, with short glandular hairs and quite a few scales (see note 2), acicular hairs absent, base narrowly angustate, margin entire, apex acute to acuminate. Pinnatifid fronds conform to simple fronds except for size and shape: 15–55 cm long; stipes up to 20 cm long, up to 2 mm in diameter; lamina

index 1.5–2.5, widest about or above the middle, 15–45 by 5–25 cm, between the lobes c. 0.5–3 cm wide, lobes 1 (or 2) to one side (or 1–5 in very small fronds); longest lobe rarely with a small basiscopic lobe, at 1st position from base, index 3.5–8, widest below or about the middle or at base, 4.5–17 by 0.3–5 cm; apical lobe widest below the middle or just above base, longer than the upper lateral lobes. *Venation pattern:* veins forming one row of main areoles situated parallel to the primary vein and bordered by one (or two) marginal rows of smaller areoles, each main areole usually including an indistinct more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins bordering the main and marginal areoles distinct, the smaller veins more or less vague; secondary veins 3–7 mm apart, straight or slightly zigzag, dichotomously branched at 1/2 or more of the lamina width; tertiary veins anadromous, up to 3 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and twice-forked, predominantly excurrent and recurrent. *Sori* superficial, round or in part slightly elongate, sometimes in part confluent, 1–2.5 mm in diameter or 2–7 mm long, spreading all over the lamina, absent in the costal and marginal areoles, 0–20/cm$^2$, rarely in part on the costal tertiary vein, usually on quaternary veins or on the smaller anastomosing veins, but not on the free included veins, irregularly scattered or sometimes forming an almost circular pattern within each main areole. Paraphyses uniseriate, 2- or 3-celled. Sporangia: annulus 18–23-celled, indurated cells 12–17, hypo- and epistomial cells together (4) 5 or 6. *Spores* concavo-convex, hyaline to yellowish, 40–50 by 20–30 µm, sometimes with small spines, colliculate, the elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Nepal (1); Sikkim (4); northern and southern India (many);

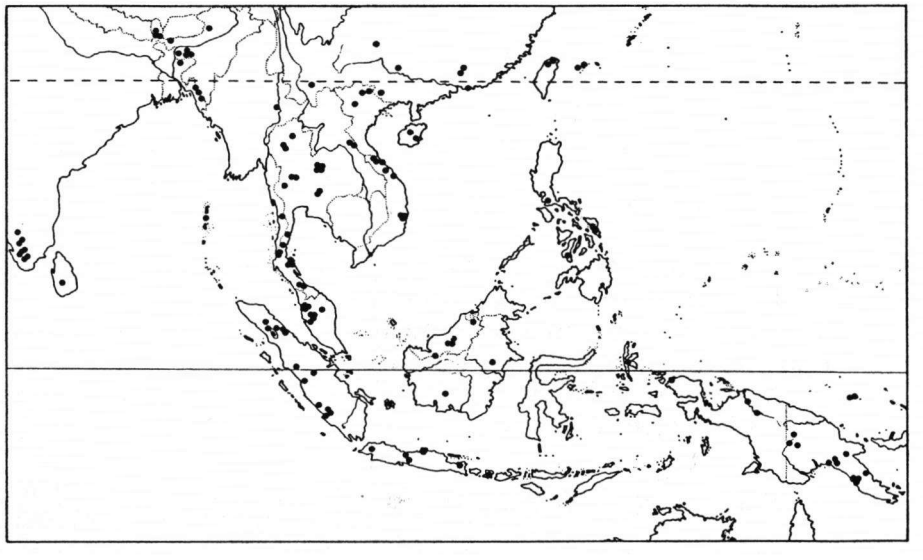

Fig. 25. Distribution of *Colysis pteropus* (Blume) Bosman.

Burma (4); Andamans (1); Japan: Iriomote I. & Ishigaki I. (7); Taiwan (2); China (many): Yunnan, Kweichow, Kwangsi, Kwangtung; Thailand (many); Laos (2); North and South Vietnam (15); Peninsular Malaysia (14); Sumatra (12); Java (9); Lesser Sunda Islands: Lombok (1); Borneo (7); Philippines (8); Moluccas: Halmahera (1); New Guinea (24). Fig. 25.

Habitat. Primary or secondary evergreen forests, mixed deciduous forests, once reported from an *Areca* plantation and once from a stream-side forest in open savanna area. Altitude 10–1000(–2000) m. Usually in wet or damp places, on shaded banks or in riverbeds, waterfalls and stagnant pools, sometimes partially or completely submerged for long periods (i.e., sometimes rheophytic), occasionally also in drier and more open places. On sandstone, schist, granite, silica, and limestone rocks and on sand, loam and limestone soils. Epilithic or rarely epiphytic or terrestrial. Locally rare (but often gregarious) or common.

Notes. 1. *Colysis pteropus* resembles *C. insignis* but is easily distinguished by a higher density of scales on stipes and larger veins, a more distinct venation (especially the main areoles), usually narrower main areoles, and the sori wanting in the outer areoles.

2. The laminal scales, too, may have long lax hairs in its central area. It seems likely, this species being a facultative rheophyte, that these hairs function as root-hairs.

3. This species may reproduce vegetatively by small plants borne in the same places where sori are usually innervated.

4. No recent collections seen from Nepal (most recent: 1827), Sikkim (1879), Burma (1945), Laos (1930), North and South Vietnam (1940), Java (1939), Lombok (1906) and Halmahera (1859/60).

5. With the inclusion of *Kaulinia pteropus* in the present species, the genus *Kaulinia* Nayar (1964) 67 is here reduced to a synonym of *Colysis*.

6. Cultivation: often in botanical gardens and commercially as an aquarium plant.

7. Van Steenis (1981, 1987) marked this species as a strict rheophyte, but noted that Posthumus told him that he also found it once in a stagnant pool (which makes it a facultative rheophyte). He further remarked that *M. pteropus* is also able to attain the fertile state in submerged conditions. His *M. leptopus*, both on page 83 and in the index (1981), grown as a waterplant for aquaria, is obviously a misprint for *M. pteropus*.

8. Leach & Osborne (1985) in their survey of freshwater plants of Papua New Guinea treated the small simple forms (*'M. brassii'*) as distinct from the larger and mostly pinnatifid forms (*'M. pteropus'*), although they remarked that *M. brassii* is closely related to and possibly a very reduced form of *M. pteropus*.

9. Ernst (1908) extensively studied the morphology and anatomy of *M. pteropus* in relation to its aquatic habitat preference.

### 23. **Leptochilus buergerianus** (Miquel) Bosman, *comb. nov.*

*Polypodium buergerianum* Miquel (1867) 170. — *Microsorum buergerianum* Ching (1933b) 302. — Type: *Buerger s.n.*, s.d., Japan (holo L, photo BM).

*Polypodium subhastatum* Baker (1889) 177. — *Microsorum subhastatum* Ching (1933b) 298. — *Neocheiropteris subhastata* Tagawa (1952a) 217. — *Lepidomicrosorum subhastatum* Ching ex Ching & Shing (1983) 12, pl. 2. — T y p e: *Henry 5450*, Hupeh (holo K; type species of *Lepidomicrosorum* Ching & Shing).

*Polypodium hederaceum* Christ (1902) 215. — *Lepidomicrosorum hederaceum* Ching ex Ching & Shing (1983) 11, pl. 1. — T y p e s: *Bodinier (& Chaffanjon) 2087*, Kweichow, nr Kouy Yang, Mont du Collège (syn; P); *Bodinier (& Laborde) 2087*, Kweichow, Tsin-gay, nr Kao Po (syn; P).

*Polypodium superficiale* var. *chinense* Rosenstock (1914) 134. — T y p e: *Cavalerie s.n.* (not *1472*, see note 3), -12-1912, Kweichow, Gan chuen (B, L, P, S, UC, US).

*Polypodium subhastatum* var. *longifrons* Takeda (1915) 292. — *Microsorum subhastatum* var. *longifrons* Ching (1933b) 298. — T y p e s: *Anonymus s.n.*, s.d., Japan (syn; K); *Takeda s.n.*, 4-4-1906, Japan, Mt Higanesan (syn; E).

*Lepidomicrosorum latibasis* Ching & Shing (1983) 6, pl. 3, f. 3. — T y p e: *H.J. Li 6337*, Hubei, He-Feng (holo PE).

*Lepidomicrosorum lanceolatum* Ching & Wang ex Ching & Shing (1983) 8. — T y p e: *P.S. Wang 75804*, Guizhou, An Shun (holo PE).

*Lepidomicrosorum asarifolium* Ching & Shing (1983) 11. — T y p e: *J.-F. Chen 730107*, Jiangxi, Jing-Gang-shan (holo PE).

*Lepidomicrosorum brevipes* Ching & Shing (1983) 13. — T y p e: *Sichuan-Guizhou Exp. 1528*, Guizhou, Zhen-yi (holo PE).

*Lepidomicrosorum suijiangense* Ching & Chu ex Ching & Shing (1983) 13. — T y p e: *W.M. Chu 4791*, Yunnan, Suijiang (holo PE).

*Polypodium buergerianum* var. *stipitatum* Takeda [(1915) 290, nom. inval. (ICBN art. 26.1 & 32.1b)]. — Based on type specimen of *Polypodium buergerianum* Miquel.

*Polypodium subhastatum* var. *hederaceum* Takeda [(1915) 292, nom. inval. (ICBN art. 26.1 & 32.1b)]. — Based on type specimen of *Polypodium subhastatum* Baker.

Rhizome long, dorso-ventrally flattened, 1.5–2.5 mm wide, not waxy; roots sparsely set; phyllopodia distinct, 3–25 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 8–9, bundle sheaths sclerenchymatous, sclerenchyma strands absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, distinctly spreading, pseudopeltate, index 2–4, widest below the middle, 1.5–4.5 by 0.5–1 mm, clathrate throughout, margin dentate to denticulate, sometimes with small triangular lobes, apex acuminate, central region dorsally with long lax hairs or glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to rhizome diameter, 2–40 cm long; stipes up to 12 cm long, up to 1 mm in diameter, with a few scales at base, vascular strands 3; lamina index 2–7(–20), widest below or about the middle, 2–30 by 0.5–4.5 cm, thin-herbaceous to herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base truncato-angustate to hastate, occasionally narrowly angustate or with some irregular triangular lobes, margin entire or occasionally slightly undulate, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct to vague; secondary veins 3–6 mm apart, slightly zigzag, dichotomously branched near the margin of the lamina (but with prominent tertiary vein basiscopically branching off near the primary vein); tertiary veins catadromous, (3 or) 4–6 between adjacent secondary veins, interconnected by some quaternary veins, which in part form a prominent vein situated parallel to each secondary vein; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all

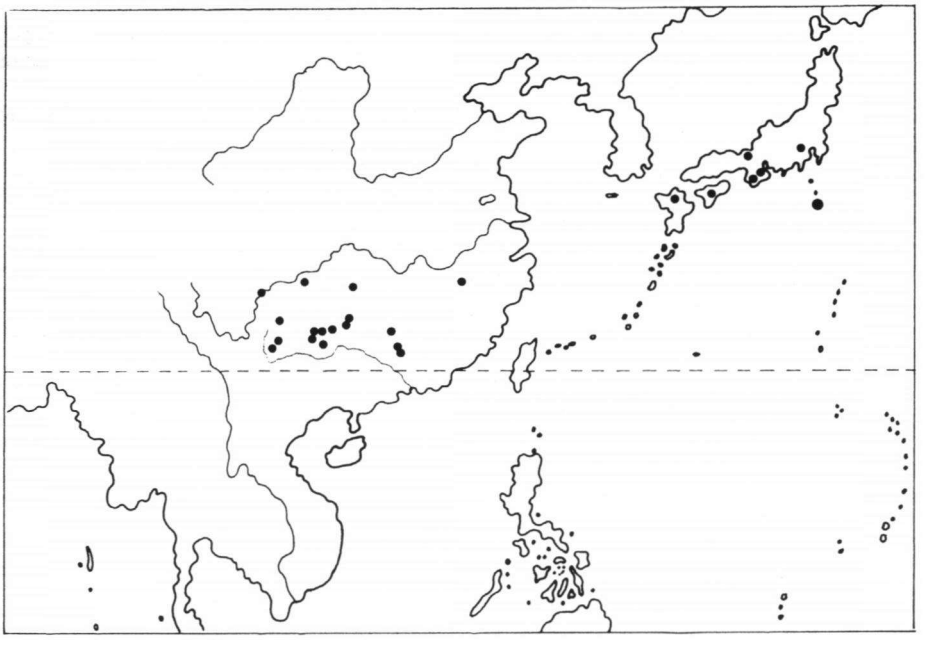

Fig. 26. Distribution of *Leptochilus buergerianus* (Miquel) Bosman.

sides. *Sori* superficial, round or in part slightly elongate (running parallel to the primary vein), occasionally in part confluent, 1–1.5 mm in diameter or 2–2.5 mm long, spreading all over the lamina or restricted up to the distal 1/4, absent in the marginal areoles, 3–15/cm$^2$, 2 per tertiary vein, not on quaternary veins, forming 2 irregular rows situated parallel to each secondary vein. Paraphyses uniseriate, (3-) 4- or 5-celled or in part peltate (especially in young sori). Sporangia: annulus 18–21-celled, indurated cells 12–15, hypo- and epistomial cells together 6 or 7. *Spores* plano- to concavo-convex, hyaline to yellowish, 40–60(–70) by 25–45(–60) µm, colliculate, the elevations tapering, c. 1.5–2 µm wide.

Distribution. Japan (11); China (24): Yunnan, Szechwan, Kweichow, Hupeh, Hunan, Kiangsi. Fig. 26.

Habitat. (Evergreen) forests. Altitude (100–)500–1500 m. Moist and (lightly) shaded places. Epilithic or epiphytic, rarely terrestrial.

Notes. 1. Many specimens identified as *M. buergerianum* (now a synonym of the present species) lack the typical small hastate fronds and belong to *N. ningpoensis*. Specimens of the present species are usually identified as *M. subhastatum*.

2. No recent collections seen from North Vietnam (most recent: 1922).

3. Rosenstock (1914: 134) cited *Cavalerie 1472*, but this specimen (BM, P) differs in date, locality, and identification from the original description: 10-9-1903, Kweichow, Pin Fa, *Polypodium superficiale*. As the Cavalerie collections are sometimes not or not correctly numbered, the type cited here seems most likely the correct one.

4. With the inclusion of *Polypodium subhastatum* in the present species, the genus *Lepidomicrosorum* Ching & Shin (1983: 1), with type species *Lc. subhastatum* (Baker) Ching, is here reduced to the synonymy of *Leptochilus*.

5. Vernacular name: Yanone-shida (Japan).

## 24. Leptochilus subhemionitideus (Christ) Bosman, *comb. nov.*

*Polypodium subhemionitideum* Christ (1899) 5. — T y p e: *Henry 9265B*, Yunnan, Mengtze, eastern mountains (holo P; iso B, K).

*Polypodium superficiale* var. *attenuatum* Rosenstock (1914) 134. — T y p e: *Cavalerie 4009*, China, Kuy-tcheu, Gan chuen (BM, K, P).

*Polypodium hymenodes* var. *marginale* Takeda (1915) 288. — *Microsorum hymenodes* var. *marginale* Ching (1933b) 301. — T y p e s: *Henry 9265A*, Yunnan, Mengtze (syn; K, P); *Henry 13340*, China, Yung-Chang (Yuan-Chang) (syn; K, P).

*Microsorum rubripes* Ching & Liu (1983) 11. — S y n t y p e s: *Z.Y. Liu 1171 & 1200*, Sichuan, Nanchuan, Jingfoshan (SZ?, not seen).

*Lepidomicrosorum huanense* Ching & Shing (1983) 6, pl. 3, f. 1. — T y p e: *L.H. Liu 15053*, Hunan, Xin-Ning (holo PE).

*Lepidomicrosorum emeicola* Ching & Shing (1983) 7. — T y p e: *R.C. Ching s.n.*, -3-1956, Sichuan, Mt Emei (holo, PE).

*Lepidomicrosorum sichuanense* Ching & Shing (1983) 8, pl. 4, f. 1. — T y p e: *S.Y. Chang & Y.S. Ren 7596*, Sichuan, Bao-Xin (holo PE).

*Lepidomicrosorum hongchunpingense* Ching & Shing (1983) 9, pl. 4, f. 3. — T y p e: *K.H. Shing & K.Y. Lang 932*, Sichuan, Mt Emei (holo PE).

*Lepidomicrosorum hongchunpingense* var. *laceratum* Ching & Shing (1983) 9. — T y p e: *K.H. Shing & K.Y. Lang 1084*, Sichuan, Mt Emei (holo PE).

*Lepidomicrosorum laojunense* Ching & Shing (1983) 10, pl. 4, f. 4. — T y p e: *S.K. Wu 61380*, Yunnan, Wen-Shan, Lao-jun Shan (holo PE).

*Lepidomicrosorum emeiense* Ching & Shing (1983) 10. — T y p e: *K.H. Shing & K.Y. Lang 1005*, Sichuan, Mt Emei (holo PE).

*Lepidomicrosorum caudifrons* Ching & Chu ex Ching & Shing (1983) 10. — T y p e: *W.M. Chu 4973*, Yunnan, Suijiang (holo, PE).

*Lepidomicrosorum undulatum* Ching & Chiu ex Ching & Shing (1983) 11. — T y p e: *P.S. Chiu 4657*, Guangxi, Long-sheng (holo PE).

*Polypodium hymenodes* auct. non Kunze (1850) 279/319 = *Microsorum membranaceum* Ching, nec Wallich [(1829) 283, nom. nud.] = *Leptochilus axillaris* (Cavanilles) Kaulfuss: Takeda (1915) 287 (excl. *Schlechter 13920* = *M. rampans*, *Henry 1489* = *N. ningpoensis* and monstr. *anomalum* = *M. heterolobum*) and Ching (1933b) 295 (sub '*M. hymenodes* (Kunze) Ching').

Rhizome moderately long to long, dorso-ventrally flattened, 1–4 mm wide, not waxy; roots sparsely set; phyllopodia obscure or distinct, 3–40 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 10–13, bundle sheaths sclerenchymatous, sclerenchyma strands 4–7, situated dorsally of the vascular cylinder, ground-tissue without cavities. *Rhizome scales* densely set, distinctly spreading, pseudopeltate, index (1.5–)2–5, widest below the middle, 1.5–5 by 0.5–1.5 mm, clathrate throughout, margin denticulate to dentate, apex acuminate, central region dorsally with long lax hairs or occasionally glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 6.5–45 (–60) cm long; stipes up to 11 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 3; lamina index 4.5–30, widest about the middle, 3–45 by

0.5–4(–5) cm, membranaceous to herbaceous or occasionally firm-herbaceous, with short glandular hairs and a few scales, acicular hairs absent, base narrowly angustate to cuneato-angustate, margin entire or sinuate, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and smaller veins more or less distinct or immersed; secondary veins 3–10 mm apart, zigzag, dichotomously branched near the margin of the lamina (but with a prominent tertiary vein basiscopically branching off near the primary vein); tertiary veins catadromous, 1–3 between adjacent secondary veins, usually interconnected by some quaternary veins, which in part sometimes form a prominent vein situated parallel to each secondary vein; smaller veins variously anastomosing; free included veins simple and once-forked, pointing to all sides. *Sori* superficial, round or in part slightly elongate (parallel to the primary vein), sometimes in part confluent, 1–2 mm in diameter or 2.5 mm long, spreading all over the lamina, absent in the costal or marginal areoles, 3–15/cm$^2$, in part 2 per tertiary vein, forming 2 irregular rows situated parallel to each secondary vein, in part irregularly scattered on quaternary and smaller anastomosing veins and on the free included veins. Paraphyses uniseriate, (4-) 5- or 6-celled, occasionally in part peltate (especially in young sori). Sporangia: annulus 18–21- (22-)celled, indurated cells (12) 13–15 (16), hypo- and epistomial cells together 5–7. *Spores* plano- to concavo-convex, hyaline to yellowish, (45–)50–75 by 25–45(–50) µm, colliculate, the elevations tapering, c. 1.5–2 µm wide.

Distribution. Nepal (2); Burma (1); Taiwan (2); China (many): Yunnan, Kweichow, Szechwan, Hunan, Kiangsi; N Vietnam (9); S Vietnam (1). Fig. 27.

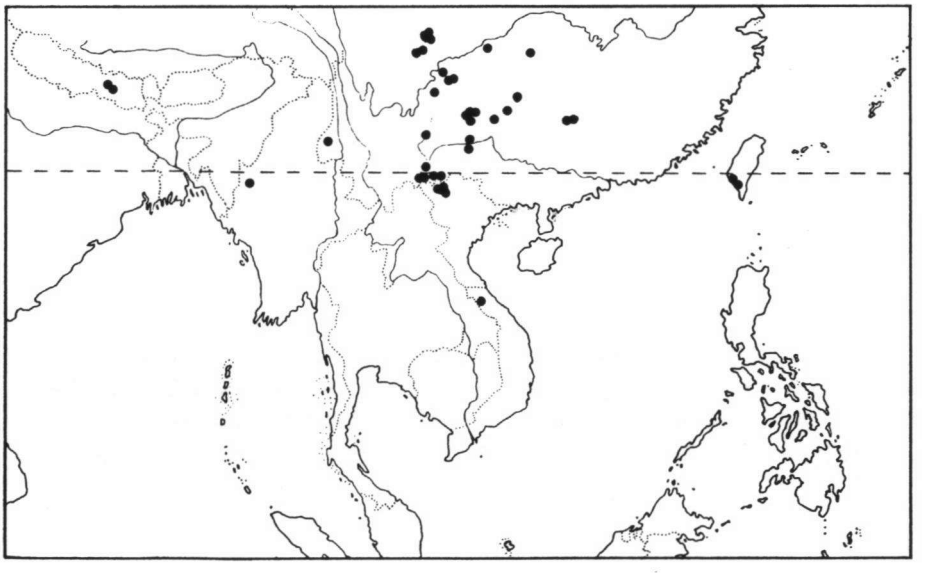

Fig. 27. Distribution of *Leptochilus subhemionitideus* (Christ) Bosman.

H a b i t a t. Various types of forest (*Cryptomeria-*, *Metasequoia-*), wooded ravines and cliffs, thickets. Altitude: 600–2600 m. Wet and shady places. Epiphytic or epilithic, rarely terrestrial. Locally often rare.

N o t e s. 1.The fronds of this species are rather variable in size, shape, and texture. Smaller fronds may resemble those of *Lc. buergerianus*, but do not have the truncato-angustate to hastate base typical of that species. Specimens with larger fronds have often been confused with *N. ningpoensis* or even *N. superficialis* but both differ from the present species in their venation pattern, which does not have a prominent tertiary vein branching off the secondary vein near the primary vein (as if the secondary vein were dichotomous at its base).

2. The rhizome of this species is reported to be 'scandent'.

3. No recent collections seen from Burma (most recent 1938) and North and South Vietnam (1936).

4. From the short descriptions the following species appear also to be synonymous with *Leptochilus subhemionitideus*:

*Lepidomicrosorum crenatum* Ching & Shing (1983) 11. — T y p e: *R.C. Ching 88*, China, Mt Emei, Qing-Yin-Ge (holo PE, not seen).

*Lepidomicrosorum lineare* Ching & Shing (1983) 5. — T y p e: *P.S. Chiu 4824*, Guangxi: Longsheng, Hua-ping Forest Reserve (holo PE, not seen).

*Lepidomicrosorum longshengense* Ching & Shing (1983) 9. — T y p e: *F.N. Wei 284*, Guangxi: Long-sheng, Hua-ping Forest Reserve (holo PE, not seen).

*Lepidomicrosorum microsorioides* Ching & Shing (1983) 7. — *Neolepisorus microsorioides* Zhu (1979) 96, pl. 3. — T y p e: *W.M. Zhu 4985*, Yunnan: Suijang Xian, Ershisigang, Jianchangwan (HGUY, not seen).

*Lepidomicrosorum nanchuanense* Ching & Liu (1984) 27. — T y p e: *Z.Y. Liu 4004* (holo Med. Plants Res. Inst. of Sichuan, Chongqing, Sichuan, not seen; not in SZ).

5. Vernacular names: Thapre (Nepal).

## 25. Neocheiropteris ningpoensis (Baker) Bosman, *comb. nov.*

*Polypodium ningpoense* Baker (1891a) 474. — *Polypodium buergerianum* var. *ningpoense* Takeda (1915) 291. — T y p e: *Hancock 24*, China, Chekiang, Ningpo Mts (holo K).

*Polypodium superficiale* var. *anguinum* Christ (1905) 16. — T y p e: *Faber s.n.*, 1885/86, Hongkong (holo P).

*Microsorum buergerianum* forma *laciniatum* Ching (1933b) 303. — T y p e: *Faurie 208*, Taiwan, Bankinsing (holo P; iso L).

*Lepidomicrosorum subsessile* Ching & Shing (1983) 6. — T y p e: *K.H. Shing & K.Y. Lang 793*, Sichuan, Mt Emei (holo PE).

*Lepidomicrosorum angustifolium* Ching & Shing (1983) 8. — T y p e: *K.C. Kuan & W.T. Wang 2439*, Sichuan, Mt Emei (holo PE).

Rhizome long, dorso-ventrally flattened, 1.5–4 mm wide, not waxy; roots sparsely set; phyllopodia obscure or distinct, up to 50 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 7–11, bundle sheaths sclerenchymatous, sclerenchyma strands 2–15, situated dorsally of the vascular cylinder, ground-tissue without cavities. *Rhizome scales* more or less densely set, slightly spreading, pseudo-

peltate, index 3–4.5, widest below the middle, 3–6.5 by 1–2 mm, clathrate throughout, margin dentate and often with small triangular lobes, apex acuminate, central region dorsally with long lax hairs, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 5–50(–80) cm long; stipes up to 10 cm long, up to 1.5 mm in diameter, with a few scales at base, vascular strands 3–4; lamina index 4–16, widest below or about the middle, 5–40(–65) by 1–5 cm, herbaceous to subcoriaceous, with short glandular hairs and a few scales, acicular hairs absent, base angustate, margin entire or sinuate to undulate, apex acute to acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and smaller veins immersed or secondary veins vague; secondary veins 5–10 mm apart, ± zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 3 or 4 between adjacent secondary veins, interconnected by some quaternary veins, which in part sometimes form a prominent vein situated parallel to each secondary vein; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, predominantly excurrent and recurrent. *Sori* superficial, round or in part slightly elongate, occasionally in part confluent, 1.5–2 mm in diameter or 2.5 mm long, spreading all over the lamina or restricted up to the distal 1/2, absent in the marginal areoles or present in all areoles, 5–15/cm$^2$, 2(–4) per tertiary vein, forming 2(–4) irregular rows situated parallel to each secondary vein. Paraphyses uniseriate, 3–5-celled. Sporangia: annulus 18–21-celled, indurated cells 12–15, hypo- and epistomial cells together 6. *Spores* concavo-convex, hyaline, 45–55 by 25–35 µm, colliculate, the elevations tapering, c. 1.5–2 µm wide.

Distribution. Japan (many); Taiwan (many); China (many): Kweichow, Szechwan, Hupeh, Kwangsi, Kwangtung, Kiangsi, Fukien, Chekiang; Laos (1); North Vietnam (12); South Vietnam (13). Fig. 28.

Habitat. Evergreen primary forest, broad-leaved temperate forests, (swampy) thickets. Altitude (10–)500–1500(–1950) m. Shaded and wet places, sometimes near streams. On silt, loam or clay. Epiphytic (low, usually not above 3 m) or (less often) epilithic. Locally rare or fairly common.

Notes. 1. This species is characterized by its small to medium-sized, simple fronds, usually of firm texture with immersed venation and with sori in two (or four near the margin of the lamina) rows parallel to the secondary veins. It has often been confused with *N. superficialis*, which it indeed strongly resembles, but from which it differs for instance in the distinctly dentate scales.

2. Specimens of *N. ningpoensis* are usually identified as *M. buergerianum*. The type specimen of the latter, however, has small hastate fronds and peltate paraphyses in the young sori and belongs to a different species, viz. *Leptochilus buergerianus*, usually identified as *M. subhastatum* (Baker) Ching.

3. Specimens with sinuate fronds and the sori mainly concentrated in the marginal area have been frequently collected especially from Taiwan.

4. The rhizome is reported to be climbing and closely appressed, with the fronds often pendent.

5. No recent collections seen from Laos (most recent: 1920), North Vietnam (1936) and South Vietnam (1947).

6. Vernacular name: Nukaboshi-kuriha-ran (Japan), which is also used for *N. superficialis*.

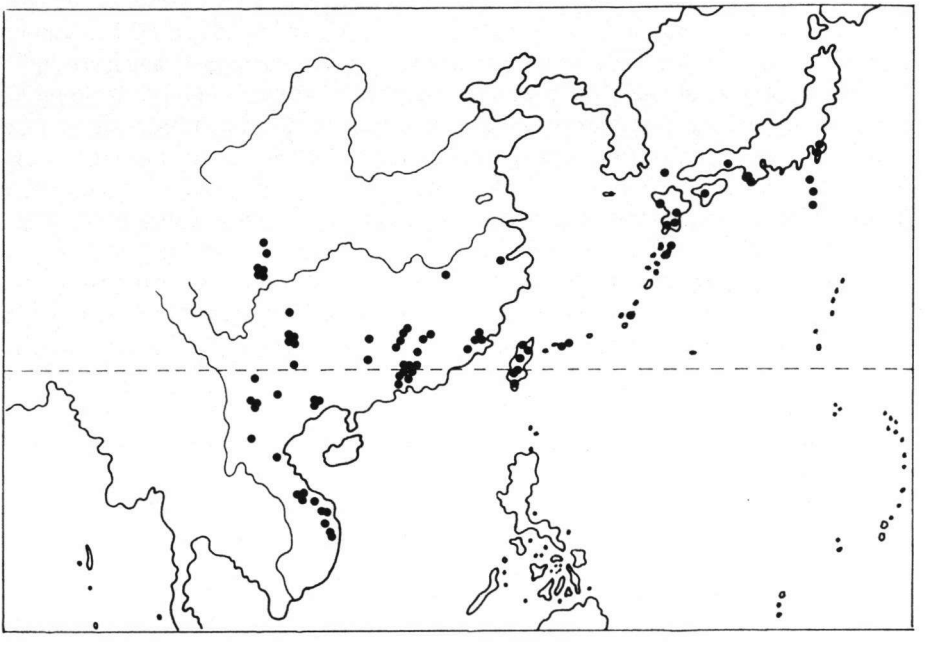

Fig. 28. Distribution of *Neocheiropteris ningpoensis* (Baker) Bosman.

## 26. Neocheiropteris superficialis (Blume) Bosman, *comb. nov.*

*Polypodium superficiale* Blume (1828) 123. — *Pleopeltis superficialis* Beddome (1865) t. 75. — *Colysis superficialis* J. Smith (1875) 101. — *Microsorum superficiale* Ching (1933b) 299. — T y p e: *Blume s.n.*, s.d., Java (holo L).

*Polypodium brachylepis* Baker (1880) 494. — *Microsorum brachylepis* Nakaike (1981) 492. — T y p e: *Maries s.n.*, s.d., China, Kiu Kiang (holo K, sketch BM).

*Polypodium nigrocinctum* Christ (1898b) 874. — T y p e s: *Henry 9264*, China, Yunnan, Mengtze, Ti-cho-shan (syn; BM, K, NY, P, US); *Henry 11454*, China, Yunnan, Mengtze (syn; K, P).

Rhizome long, dorso-ventrally flattened, 2–5 mm wide, not waxy; roots sparsely set; phyllopodia distinct, up to 50 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 10–13, bundle sheaths sclerenchymatous, sclerenchyma strands 11, situated dorsally of the vascular cylinder, occasionally absent, ground-tissue without cavities. *Rhizome scales* more or less densely set, occasionally appressed, usually slightly spreading, pseudopeltate, index 1–3.5, widest below the middle, 2–6 by 1–2.5 mm, clathrate throughout or except for the marginal region which is hyaline, margin entire or occasionally denticulate, apex obtuse to acuminate,

central region dorsally with long lax hairs or occasionally glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, well proportioned to the rhizome diameter, 15–60 cm long; stipes 3–20 cm long, up to 2 mm in diameter, with a few scales at base, vascular strands 3–4; lamina index 4.5–11, widest below the middle, 10–40 by 2–6 cm, herbaceous to subcoriaceous, with short glandular hairs and a few scales, acicular hairs absent, base narrowly angustate to cuneato-angustate, margin entire, apex acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, secondary and smaller veins immersed, occasionally more or less distinct; secondary veins 6–10 mm apart, slightly zigzag, dichotomously branched at 3/4 or more of the lamina width; tertiary veins catadromous, 3–5 between adjacent secondary veins, interconnected by some quaternary veins, which in part often form a prominent vein situated parallel to each secondary vein; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, predominantly excurrent and recurrent. *Sori* superficial, round, sometimes in part confluent, 1–2.5 mm in diameter, spreading all over the lamina or restricted up to the distal 1/2, absent marginal areoles or present in all areoles, 5–15/cm$^2$, 2–4 per tertiary vein, occasionally in part on quaternary veins, forming 2–4 irregular rows situated parallel to each secondary vein. Paraphyses uniseriate, 3–8-celled. Sporangia: annulus 18–22-celled, indurated cells 12–16, hypo- and epistomial cells together 6 or 7. *Spores* concavo-convex, hyaline to yellowish, 45–75 by 25–45 µm, colliculate, the elevations not very prominent, rounded, 0.5–2(–3) µm wide.

Distribution. Tibet (1); India: Assam, Manipur (16); Burma (3); Japan (5); China (35): Yunnan, Szechwan, Kwangsi, Kwangtung, Kiangsi, Chekiang; Thailand (13); North Vietnam (10); Peninsular Malaysia (3); Sumatra (16); Java (24). Fig. 29.

Habitat. Primary or secondary forests, once reported from low brushwoods and once from an exposed ridge. Altitude 400–2600 m. Usually shady and wet places, sometimes near a stream, but twice reported from fully exposed situations. Sometimes on limestone soils. Usually low (not above 3 m) epiphytic, occasionally epilithic or terrestrial. Locally rare or common.

Notes. 1. The specimens with relatively narrow fronds resemble those of *N. ningpoensis* (often identified as *M. buergerianum,* see note 2 under *N. ningpoensis*). However, the large entire or at most denticulate rhizome scales of *N. superficialis* are unmistakable. From *Lc. subhemionitideus,* which has also been confused with it, this species differs both in morphology of the scales and in texture of the fronds.

2. No recent collections seen from Tibet (most recent: 1950), Burma (1938), and North Vietnam (1937).

3. Both Alderwerelt and Beddome suggested affinity of *Polypodium peltatum* Alderwerelt with *M. superficiale* (= *N. superficialis*). The description of the former is not elaborate enough to confirm this. [*Polypodium peltatum* Alderwerelt (1909a) 632. — *Pleopeltis superficialis* var. *latifrons* Beddome (1893) 226. — Type: *Scortechini s.n.,* s.d., Peninsular Malaysia, Perak (holo K, not seen)].

4. Vernacular name: Nukaboshi-kuriha-ran (Japan), also used for *N. ningpoensis.*

5. Chemistry: Masuda et al. (1989) isolated fernenoic and adianeoic acids from the rhizome of this species.

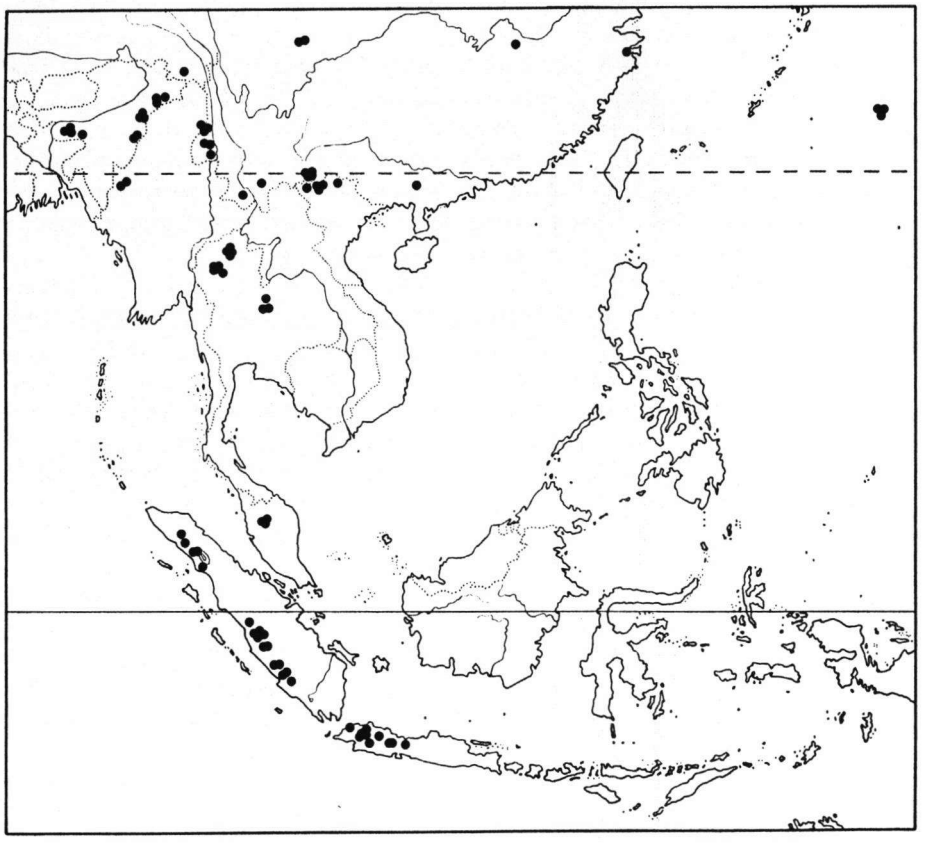

Fig. 29. Distribution of *Neocheiropteris superficialis* (Blume) Bosman.

## 27. Neocheiropteris zippelii (Blume) Bosman, *comb. nov.*

*Polypodium zippelii* Blume (1829) 172, t. 80. — *Pleopeltis zippelii* Moore (1862) 348. — *Polypodium heterocarpum* var. *zippelii* Baker (1868) 360. — *Colysis zippelii* J. Smith (1875) 100. — *Microsorum zippelii* Ching (1933b) 308. — T y p e: *Zippelius s.n.*, s.d., Java (holo L, photo B, BM).

*Polypodium oxyphyllum* Kunze (1848) 116. — T y p e: *Zollinger 2029*, Java (syn; L); *Zollinger 2332*, Java (syn; BM, LE, P, PR).

*Polypodium luzonicum* Copeland (1906a) 162, t. 23. — *Pleopeltis luzonica* Alderwerelt (1909b) 7. — *Microsorum luzonicum* Tagawa (1955) 51. — T y p e: *Copeland 1918*, Phillipines, Luzon, Bagnen, Lepanto (P, S, SING, US).

*Drynaria subfalcata* J. Smith [(1841) 397, nom, nud.] — *Bathmium? subfalcatum* Fée [(1852) 287, nom, nud.] — Based on *Cuming 113*, Philippines, Luzon (A, BM, K, L, LE, P, PC, US).

Rhizome long, ± cylindrical, occasionally dorso-ventrally slightly flattened, 1–3 (–4) mm in diameter, not waxy; roots ± densely set, not forming a thick mat; phyllo-

podia distinct, 10–70 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 11–17, bundle sheaths collenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* more or less densely set, distinctly spreading, pseudopeltate, index 1.5–4.5, widest below the middle, 2.5–6.5 by 1–2 mm, clathrate throughout, margin denticulate or dentate, base sometimes with narrowly triangular lobes, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* simple, large in proportion to the rhizome diameter, 6.5–75 cm long; stipes up to 12 cm long, up to 2.5 mm in diam., with a few scales at base, vascular strands 7; lamina index 5.5–14, widest about or above the middle, 6.5–65 by 1–8 cm, herbaceous to firm-herbaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire or occasionally sinuate, apex acuminate. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct or the smaller veins vague; secondary veins 4–13 mm apart, ± straight or slightly zigzag, dichotomously branched near the margin of the lamina; tertiary veins catadromous, 3–7 between adjacent secondary veins, interconnected by some quaternary veins, which in part sometimes form a distinct vein situated parallel to each secondary vein; smaller veins variously anastomosing; free included veins simple, once- and in part twice-forked, pointing to all sides. *Sori* superficial, round or sometimes those on the costal tertiary vein slightly elongate, occasionally in part confluent, 1.5–2 mm in diameter or 2–4 mm long, spreading all over the lamina, absent in the marginal areoles, 2–10/cm$^2$, (1) 2 per tertiary vein, not on quaternary veins, forming (1) 2 ± regular rows situated parallel to each secondary vein and 1–5 to the primary vein. Paraphyses uniseriate, 3- or 4-celled. Sporangia: annulus 20–24-celled, indurated cells 14–18, hypo- and epistomial cells together 6–8. *Spores* plano- to concavo-convex, hyaline to yellow, 45–55 by 25–35 μm, colliculate, the elevations tapering, c. 1.5–2 μm wide.

Distribution. Sikkim (7); Burma (2); China (8): Yunnan, Kwangsi, Hainan; Thailand (6); Laos (4); Cambodia (1); N & S Vietnam (3); Peninsular Malaysia (7); Sumatra (19); Java (22); Lesser Sunda Islands (8); Borneo (11); Philippines: Luzon & Mindanao (12); Sulawesi (11); New Guinea (1: *Hoogland 9142*). Fig. 30.

Habitat. Primary and secondary forest (i.a. evergreen rain, monsoon, and oak forest). Altitude 400–1900 m, once reported from 2500 m and from 4000 m. Shady and wet places, often near streams. Once reported from limestone. Epiphytic, sometimes epilithic, rarely terrestrial. Locally often rare, sometimes common.

Notes. 1. This species is characterized by the distinct venation and the two rather regular rows of sori situated between adjacent secondary veins (two sori per primary connective). The sori are sometimes confined to the costal area, ultimately leaving only one row of sori parallel to the primary vein. The relation between the diameter of the rhizome and the diameter of the stipes (and size of the fronds) is in this species different from that found in most other species of microsoroids: the rhizome is rather thin for the stipes and fronds that are borne on it.

2. The fronds are reported to be 'drooping'.

3. No recent collections seen from Sikkim (most recent: 1957), Burma (1922), China (1938), Laos (1938), Cambodia (1939), Vietnam (1925) and Java (1956).

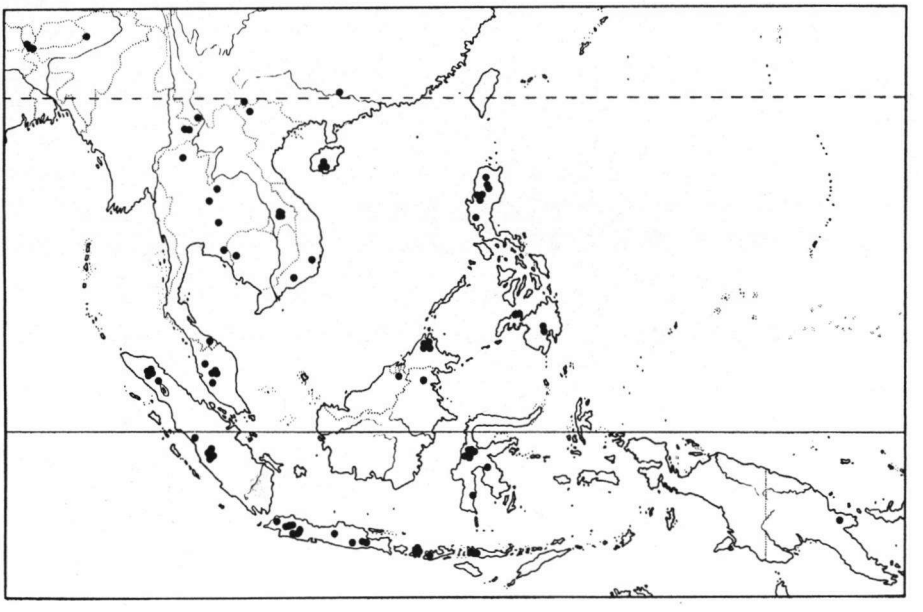

Fig. 30. Distribution of *Neocheiropteris zippelii* (Blume) Bosman.

## 28. Phymatosorus alatus (Brackenridge) Bosman, *comb. nov.*

*Drynaria alata* Brackenridge (1854) 48, t. 6, f. 1. — *Phymatodes alata* Seeman (1861) 261. — *Pleopeltis alata* Moore (1862) 344. — *Polypodium alatum* Hooker (1864) 85, nom. illeg. (ICBN art. 64.1), non Linnaeus (1753) 1086 = *?Dryopteris scolopendrioides* (Linnaeus) Kuntze. — *Polypodium wilkesii* Christensen (1906) 247, 574. — *Microsorum wilkesii* Ching (1941) 239, nom. illeg. (ICBN art. 63.1). — *Microsorum alatum* Copeland (1947) 196. — T y p e: *Brackenridge 12*, U. S. Expl. Exp., Fiji Is., Ovalau (holo US).

Rhizome short, ± cylindrical, 6–10 mm in diameter, not waxy; roots ± densely set; phyllopodia distinct, 3–16 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 21–34, bundle sheaths collenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* densely set, appressed, pseudopeltate, index 1.5–2.5, widest below the middle, (1.5–)3–5 by (1–)2–3 mm, clathrate except for the marginal region which is hyaline and the central region which is opaque, margin entire, apex acuminate, central region glabrous, inner layer of thickened cell walls smooth. *Fronds* pinnatifid, well proportioned to the rhizome diameter, 75–120 cm long; stipes (10–)30–55 cm long, up to 6 mm in diameter, with a few scales at base, vascular strands 12–14; lamina index 1–1.5, widest below the middle, 40–70 by 30–50 cm, between the lobes c. 0.5–3 cm wide, lobes (2–)5–8(–11) to a side, thin-herbaceous to membranaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin sinuate-dentate, apex acuminate; longest lobe at 2nd position from base, index 3.5–11, widest below or about the middle, 16–27 by 1.5–3 cm; apical lobe widest

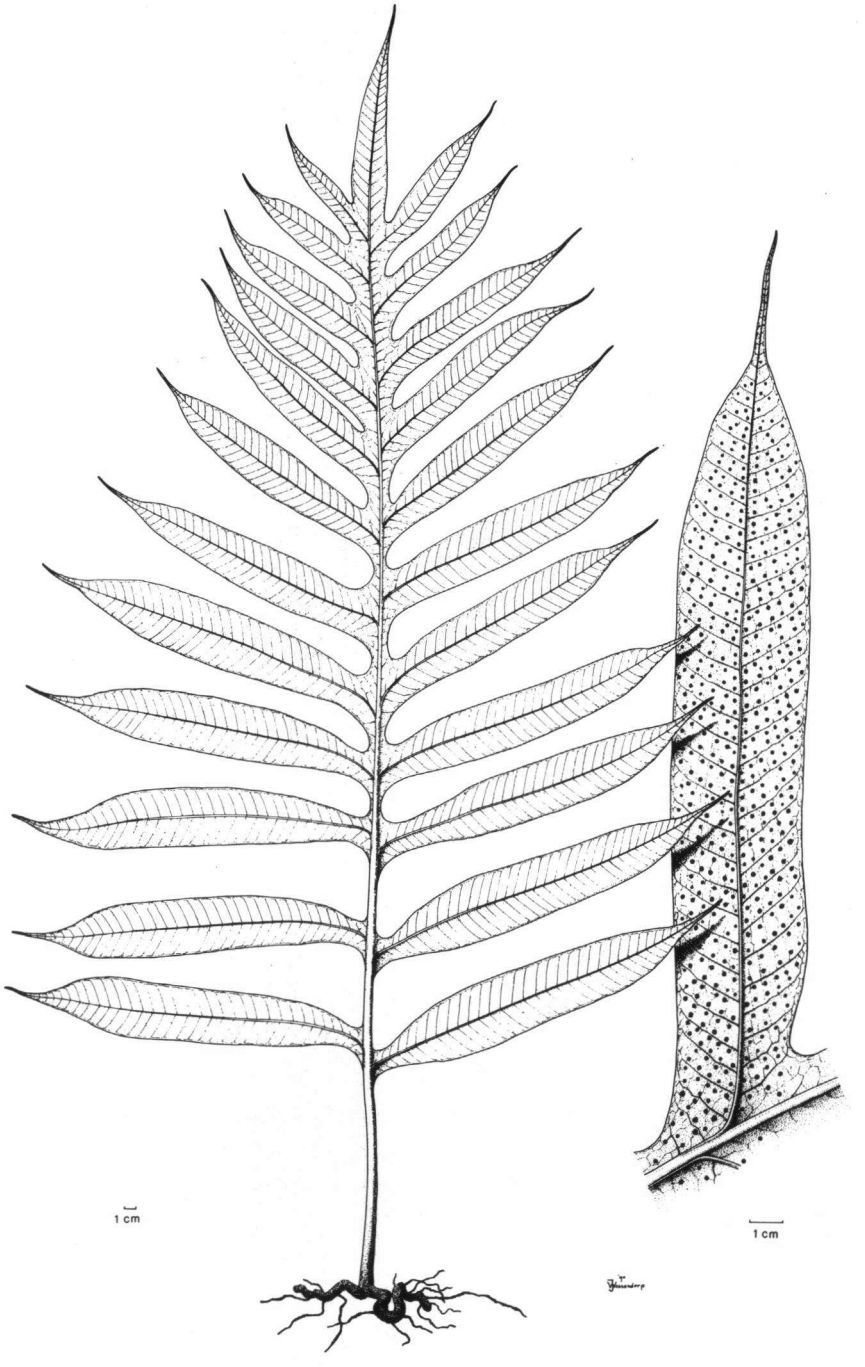


Fig. 31. *Phymatosorus biseriatus* Bosman (*Croft 1870*, L).

below the middle, otherwise conform to or shorter than the upper lateral lobes. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles between each pair of adjacent secondary veins, all veins distinct; secondary veins 5–6 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins anadromous, 3–5 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple, once- and twice-forked, pointing to all sides. *Sori*
confluent, 0.5–1.5 mm in diameter, spreading all over the lamina or restricted up to the distal 1/3, absent in the marginal areoles, 5–15/cm$^2$, occasionally in part on tertiary veins, 2 per quaternary vein, forming c. 2 regular rows situated parallel to each secondary vein. Paraphyses uniseriate, (2-) 3- or 4-celled. Sporangia: annulus (18-) 19- or 20-celled, indurated cells 12–14, hypo- and epistomial cells together 5–7. *Spores* concavo-convex, hyaline, 45–60 by 25–30(–40) µm, more or less smooth.

Distribution. Fiji Islands (14): Viti Levu, Ovalau.

Habitat. Dense forests, forested ridges. Altitude 100–1200 m. Shady places. Epiphytic.

Notes. 1. This species is characterized by its pinnatifid and thin-herbaceous or membranaceous fronds with sinuate-dentate margin and pale coloured veins bearing the sori in two regular rows parallel to each secondary vein. It is phenetically
*Ph. biseriatus* (see note 1 under that species).

2. No recent collections seen from Fiji (most recent: 1953).

## 29. **Phymatosorus biseriatus** Bosman, *spec. nov.* — **Fig. 31.**

Rhizoma plus minusve teres, diametro 7–8 mm, squamis pseudopeltatis partim clathratis dense vestitum. Frondes pinnatifidae, 120 cm longae, stipitibus usque 30 cm longis. Lamina lobis 11–12-jugatis, lobis maximis 30 cm longis, 5 cm latis, tenuiter herbacea, margine integro. Venatio *Ph. alato* similis. Sori 1 in venulis quaternariis, venulis tertiariis approximatis, regulariter inter venulas secundarias biseriales. — Typus: *Croft 1870*, New Ireland, Mt Tumbumpo (holo L).

Rhizome moderately long, ± cylindrical, 7–8 mm in diameter, not waxy; roots ± densely set; phyllopodia distinct, more than 25 mm apart. Rhizome anatomy (in cross section): vascular bundles in cylinder 24, bundle sheaths collenchymatous, sclerenchyma strands at least 50, scattered, ground-tissue without cavities. *Rhizome scales* densely set, appressed, pseudopeltate, index 1.2–1.5, widest below the middle, 3.5–5.5 by 3–4 mm, clathrate except for the marginal region which is hyaline, margin entire, apex rounded, central region glabrous, inner layer of thickened cell walls smooth. *Frond* pinnatifid, well proportioned to the rhizome diameter, 120 cm long; stipe 30 cm long, 9 mm in diameter, with a few scales at base, vascular strands 22; lamina index 1.3, widest below the middle, 90 by 70 cm, between the lobes c. 2 cm wide, lobes 11 or 12 to a side; thin-herbaceous, with short glandular hairs, scales and acicular hairs absent, base narrowly angustate, margin entire, apex acuminate; longest lobe at 3rd position from base, index 6, widest below the middle, 30 by 5 cm; apical lobe widest just above base, longer than the upper lateral lobes. *Venation pattern:* veins forming a more or less regular row of ± equally sized areoles be-

tween each pair of adjacent secondary veins, all veins distinct; secondary veins 7–10 mm apart, ± straight, dichotomously branched near the margin of the lamina; tertiary veins anadromous, 7 between adjacent secondary veins, interconnected by some quaternary veins; smaller veins variously anastomosing; free included veins simple and once-forked, pointing to all sides. *Sori* superficial, round, not confluent, 1 mm in diameter, restricted to the distal 1/3 of the lamina, absent in the costal and marginal areoles, 5–8/cm$^2$, close to the tertiary veins, 1 per quaternary vein, forming 2 ± regular rows situated parallel to each secondary vein. Paraphyses uniseriate, 3- or 4- (5-)celled. Sporangia: annulus 18- or 19-celled, indurated cells 12 or 13, hypo- and epistomial cells together 6. *Spores* plano to concavo-convex, hyaline, 40 by 25–30 µm, colliculate, the elevations not very prominent, rounded, c. 0.5–2(–3) µm wide.

Distribution. New Guinea, Bismarck Arch.: New Ireland, western slopes of Mt Tumbumpo, Central Lelet Plateau, 160 km SE of Kavieng and 40 km SE of Konos (1; type collection).

Habitat. Stunted forest on ridges and upper slopes. Altitude 1000 m. No free water. Terrestrial. Moderately common, scattered plants.

Notes. 1. This species is phenetically closest to *Ph. alatus*. These two species differ remarkably from other *Phymatosorus* species in sorus innervation: two more or less regular rows of sori parallel to each secondary vein, on quaternary veins. The most prominent differences between the present species and *Ph. alatus* are listed below in table 9.

Table 9. Differences between *Phymatosorus biseriatus* and *Ph. alatus*.

| Feature | *Ph. biseriatus* | *Ph. alatus* |
|---|---|---|
| Distribution | New Ireland | Fiji |
| Habitat | terrestrial | epiphytic |
| Rhizome scales: index | 1.2–1.5 | 1.5–2.5 |
| Rhizome scales: apex | rounded | acuminate |
| Margin of lamina | entire | sinuate-dentate |
| Lateral lobes: width | up to 5 cm | up to 3 cm |
| Sori: noumber of quaternary veins | 1 | 2 |
| Spore surface | colliculate | ± smooth |

2. The description is based on one collection (with one frond).

3. This species is reported to be an "erect ground fern with creeping fleshy underground rhizome."

## 14. DOUBTFUL SPECIES

D 1. *Polypodium altum* Bojer

*Polypodium altum* Bojer (1837) 417. — T y p e: not indicated, "Ile de Maurice, dans les forêts de la Rivière Noire, aux Trois Brais."

According to Christensen (1906) 508 this species is synonymous with *Polypodium punctatum* (= *M. punctatum*). Bojer's description is too short to confirm this.

D 2. *Microsorum glossipes* (Baker) Copeland

*Microsorum glossipes* Copeland (1947) 197. — *Polypodium glossipes* Baker (1891a) 476. — *Pleopeltis glossipes* Alderwerelt (1909b) 6. — T y p e: *Beccari s.n.*, s.d., 'Mountains of New Guinea' (holo FI, not found; sketch BM and K).

The short description and sketches suggest similarity with *M. rampans*.

D 3. *Microsorum ohwianum* Tagawa

*Microsorum ohwianum* Tagawa (1936) 752. — T y p e: *Ohwi 1774*, Taiwan, Mt Daibu, Takao Prov. (holo KYO, not seen).

The description suggests similarity with *N. ningpoensis*.

## 15. EXCLUDED NAMES

E 1. *Microsorum accedens* (Blume) Copeland (1929a) 12.
Based on *Polypodium accedens* Blume = **Lemmaphyllum accedens** (Blume) Donk.

E 2. *Microsorum acutifolium* (Brause) Copeland (1947) 197.
Based on *Polypodium acutifolium* Brause = **Phymatosorus** spec.

E 3. *Microsorum alatum* (Brackenridge) Copeland.
See 28. **Phymatosorus alatus** (Brackenridge) Bosman.

E 4. *Microsorum alternifolium* (Willdenow) Copeland (1947) 197.
Based on *Polypodium alternifolium* Willdenow = **Phymatosorus nigrescens** (Blume) Pichi Sermolli.

E 5. *Microsorum brachylepis* (Baker) Nakaike.
See 26. **Neocheiropteris superficialis** (Blume) Bosman.

E 6. *Microsorum brassii* Copeland.
See 22. **Colysis pteropus** (Blume) Bosman.

E 7. *Microsorum buergerianum* (Miquel) Ching.
See 23. **Leptochilus buergerianus** (Miq.) Bosman.

E 8. *Microsorum buergerianum* f. *laciniatum* Ching.
See 25. **Neocheiropteris ningpoensis** (Baker) Bosman.

E 9. *Microsorum commutatum* (Blume) Copeland (1947) 196.
Based on *Polypodium commutatum* Blume = **Phymatosorus commutatus** (Blume) Pichi Sermolli.

E 10. *Microsorum cromwellii* (Rosenstock) Copeland (1947) 197.
Based on *Polypodium cromwellii* Rosenstock = **Phymatosorus** spec.

E 11. *Microsorum cuspidatum* (Don) Tagawa (1966) 495.
Based on *Polypodium cuspidatum* Don = **Phymatosorus lucidus** (Roxburgh) Pichi Sermolli.

E 12. *Microsorum decurrens* (Brackenridge) Copeland.
See 21. **Colysis insignis** (Blume) J. Smith.

E 13. *Microsorum dilatatum* (Hooker) Sledge.
See 21. **Colysis insignis** (Blume) J. Smith.

E 14. *Microsorum diversifolium* (Willdenow) Copeland (1929a) 114.
Based on *Polypodium diversifolium* Willdenow = **Phymatosorus diversifolius** (Willdenow) Pichi Sermolli.

E 15. *Microsorum ensato-sessilifrons* (Hayata) Itô (1935) 96.
Based on *Polypodium ensato-sessilifrons* Hayata = **Colysis** spec.

E 16. *Microsorum ensatum* (Thunberg) Itô (1935) 96.
Based on *Polypodium ensatum* Thunberg = **Neocheiropteris ensata** (Thunberg) Ching.

E 17. *Microsorum fortunei* (Moore) Ching (1933b) 304.
Based on *Drynaria fortunei* Moore = **Neocheiropteris** spec.

E 18. *Microsorum griseorhizoma* Gilli (1978) 25.
= **Phymatosorus** spec.

E 18a. *Microsorum grossum* (Langsdorff & Fischer) Andrews (1990) 280.
Based on *Polypodium grossum* Langsdorff & Fischer = **Phymatosorus grossus** (Langsdorff & Fischer) Brownlie.

E 19. *Microsorum hancockii* (Baker) Ching.
See 21. **Colysis insignis** (Blume) J. Smith.

E 20. *Microsorum hemionitideum* (Presl) Copeland (1929a) 112.
= **Colysis hemionitidea** Presl.

E 21. *Microsorum henryi* (Christ) Kuo (1985) 42/67.
Based on *Polypodium henryi* Christ = **Neocheiropteris** spec.

E 22. *Microsorum heterophyllum* (Linnaeus) Hawkes (1951) 52.
Based on *Polypodium heterophyllum* Linnaeus = **Microgramma heterophylla** (Linnaeus) Wherry.

E 23. *Microsorum hymenodes* var. *marginale* (Takeda) Ching.
See 24. **Leptochilus subhemionitideus** (Christ) Bosman.

E 24. *Microsorum insigne* (J. Smith) Copeland.
See 21. **Colysis insignis** (Blume) J. Smith.

E 25. *Microsorum jinfoshanense* Ching & Liu (1983) 12.
Judging from the description this species seems to be very similar to 25. *Neocheiropteris ningpoensis* (Baker) Bosman.

E 26. *Microsorum latilobatum* Hennipman & Hetterscheid (1984) 6.
This species is definitely *microsoroid,* but I could not assign it to any of the genera I recognize. For a full discussion of this species, including synonymy and typification, I refer to Hennipman & Hetterscheid (1984).

E 27. *Microsorum lineare* (Thunberg) Copeland (1929a) 112.
Based on *Polypodium lineare* Thunberg = **Phymatosorus** spec.

E 28. *Microsorum longifolium* (Blume) Copeland (1929a) 112.
Based on *Grammitis longifolia* Blume = **Phymatosorus** spec.

E 29. *Microsorum lucidum* (Roxburgh) Copeland (1947) 196.
Based on *Polypodium lucidum* Roxburgh = **Phymatosorus lucidus** (Roxburgh) Pichi Sermolli.

E 30. *Microsorum luzonicum* (Alderwerelt) Tagawa.
See 27. **Neocheiropteris zippelii** (Blume) Bosman.

E 31. *Microsorum maximum* (Brackenridge) Copeland (1938) 73.
Based on *Drynaria maxima* Brackenridge = **Phymatosorus** spec.

E 32. *Microsorum membranifolium* (Brown) Ching (1941) 239.
Based on *Polypodium membranifolium* Brown = **Phymatosorus** spec.

E 33. *Microsorum multijugatum* (Copeland) Copeland (1947) 196.
Based on *Polypodium multijugatum* Copeland = **Phymatosorus** spec.

E 34. *Microsorum neglectum* (Blume) Copeland (1929a) 112.
Based on *Polypodium neglectum* Blume = **Colysis** spec.

E 35. *Microsorum nigrescens* (Blume) Copeland (1938) 74.
Based on *Polypodium nigrescens* Blume = **Phymatosorus nigrescens** (Blume) Pichi Sermolli.

E 36. *Microsorum normale* (Don) Ching (1933b) 299.
Based on *Polypodium normale* Don = **Leptochilus** spec.

E 37. *Microsorum novae-zealandiae* (Baker) Copeland (1947) 196.
Based on *Polypodium novae-zealandiae* Baker = **Phymatosorus novae-zealandiae** (Baker) Pichi Sermolli.

E 38. *Microsorum ovatum* (Hooker & Greville) Nair & Bennet (1969) 432.
Based on *Polypodium ovatum* Hooker & Greville = **Neocheiropteris** spec.

E 39. *Microsorum pappei* (Kuhn) Tardieu-Blot (1960) 115.
Based on *Polypodium pappei* Kuhn = **Neocheiropteris** spec.

E 40. *Microsorum papuanum* (Baker) Parris (1986) 69.
Based on *Polypodium papuanum* Baker = **Phymatosorus** spec.

E 41. *Microsorum papyraceum* (Copeland) Copeland (1947) 197.
Based on *Polypodium papyraceum* Copeland = **Phymatosorus** spec.

E 42. *Microsorum parksii* (Copeland) Copeland (1947) 196.
Based on *Polypodium parksii* Copeland = **Phymatosorus** spec.

E 43. *Microsorum paucijugum* (Alderwerelt) Iwatsuki & Kato (1981) 123.
Based on *Polypodium paucijugum* Alderwerelt. Judging from the description this species seems to be very similar to small forms of *Colysis insignis* (Blume) J. Smith.

E 44. *Microsorum persicariifolium* (Schrader) Alston (1932) 315.
Based on *Polypodium persicariifolium* Schrader = **Microgramma persicariifolia** (Schrader) Presl.

E 45. *Microsorum phanerophlebium* (Copeland) Copeland (1947) 196.
Based on *Polypodium phanerophlebium* Copeland = **Phymatosorus** spec.

E 46. *Microsorum pitcairnense* Copeland (1938) 74.
= **Phymatosorus** spec.

E 47. *Microsorum powellii* (Baker) Copeland (1947) 196.
Based on *Polypodium powellii* Baker = **Phymatosorus powellii** (Baker) Pichi Sermolli.

E 48. *Microsorum pseudo-acrostichum* (Alderwerelt) Ching (1941) 240.
Based on *Pleopeltis pseudo-acrosticha* Alderwerelt = **Crypsinus** spec.

E 49. *Microsorum pteropus* (Blume) Copeland.
See 22. **Colysis pteropus** (Blume) Bosman.

E 50. *Microsorum pteropus* var. *minor* (Beddome) Christensen & Tardieu-Blot.
See 22. **Colysis pteropus** (Blume) Bosman.

E 51. *Microsorum pteropus* f. *minor* (Beddome) Ching.
See 22. **Colysis pteropus** (Blume) Bosman.

E 52. *Microsorum pustulatum* (Forster) Copeland (1947) 196.
Based on *Polypodium pustulatum* Forster = **Phymatosorus scandens** (Forster) Pichi Sermolli.

E 53. *Microsorum rizalense* Copeland (1952) 42.
= **Neocheiropteris** spec.

E 54. *Microsorum rubidum* (Kunze) Copeland (1947) 197.
Based on *Polypodium rubidum* Kunze = **Phymatosorus nigrescens** (Blume) Pichi Sermolli.

E 55. *Microsorum rubripes* Ching & Liu.
See 24. **Leptochilus subhemionitideus** (Christ) Bosman.

E 56. *Microsorum sarawakense* (Baker) Ching (1933b) 295.
Based on *Polypodium sarawakense* Baker = **Neocheiropteris** spec.

E 57. *Microsorum scandens* (Forster) Tindale (1960) 241.
Based on *Polypodium scandens* Forster = **Phymatosorus scandens** (Forster) Pichi Sermolli.

E 58. *Microsorum schneideri* (Christ) Copeland (1947) 197.
Based on *Polypodium schneideri* Christ = **Phymatosorus** spec.

E 59. *Microsorum scolopendria* (Burman) Copeland (1929a) 112.
Based on *Polypodium scolopendria* Burman = **Phymatosorus scolopendria** (Burman) Pichi Sermolli.

E 60. *Microsorum sibomense* (Rosenstock) Copeland (1947) 196.
Based on *Polypodium sibomense* Rosenstock = **Phymatosorus** spec.

E 61. *Microsorum simulans* Ching & Liu (1984) 26.
From the description this species seems to be synonymous to **Leptochilus buergerianus** (Miquel) Bosman.

E 62. *Microsorum subgeminatum* (Christ) Copeland (1947) 197.
Based on *Polypodium subgeminatum* Christ = **Phymatosorus** spec.

E 63. *Microsorum subhastatum* (Baker) Ching.
See 23. **Leptochilus buergerianus** (Miquel) Bosman.

E 64. *Microsorum subhastatum* var. *longifrons* (Takeda) Ching.
See 23. **Leptochilus buergerianus** (Miquel) Bosman.

E 65. *Microsorum subnormale* (Nakai) Itô (1935) 97.
Based on *Phymatodes subnormalis* Nakai = **Neocheiropteris** spec.

E 66. *Microsorum subtriquetrum* (Christ) Christensen & Tardieu-Blot (1939) 195.
Based on *Polypodium taeniopsis* Christ = **Crypsinus** spec.

E 67. *Microsorum sulawesiense* Ohba (1974) 173.
= **Phymatosorus** spec.

E 68. *Microsorum superficiale* (Blume) Ching.
See 26. **Neocheiropteris superficialis** (Blume) Bosman.

E 69. *Microsorum superficiale* var. *semilinearis* Clarke (1880) 558.
= **Leptochilus** spec.

E 70. *Microsorum surinamense* (Jacquin) Alston (1932) 315.
Based on *Polypodium surinamense* Jacquin = **Microgramma lycopodioides** (L.) Copel.

E 71. *Microsorum sylvaticum* (Brackenridge) Copeland (1947) 196.
Based on *Drynaria sylvatica* Brackenridge = **Phymatosorus commutatus** (Blume) Pichi Sermolli.

E 72. *Microsorum taeniatum* (Swartz) Copeland (1929a) 112.
Based on *Polypodium taeniatum* Swartz = **Crypsinus taeniatus** (Swartz) Copeland.

E 73. *Microsorum takedae* (Nakai) Itô (1935) 97.
Based on *Phymatodes takedae* Nakai = **Neocheiropteris** spec.

E 74. *Microsorum tenuinerve* (Copeland) Copeland (1947) 196.
Based on *Polypodium tenuinerve* Copeland = **Phymatosorus** spec.

E 75. *Microsorum thurnii* (Baker) Alston (1932) 315.
Based on *Polypodium thurnii* Baker = **Microgramma** spec.

E 76. *Microsorum trifidum* Fée (1852) 269.
= **Tectaria trifida** (Fée) Price.

E 77. *Microsorum variabile* (Ching) Tagawa (1952b) 192.
Based on *Phymatodes variabilis* Ching = **Phymatosorus nigrescens** (Blume) Pichi Sermolli.

E 78. *Microsorum varians* (Mettenius) Hennipman & Hetterscheid (1984).
This species is definitely *microsoroid,* but I could not assign it to any of the genera I recognize. For a full discussion of this species, including synonymy and typification, I refer to Hennipman & Hetterscheid (1984).

E 79. *Microsorum vieillardii* (Mettenius) Copeland (1947) 196.
Based on *Polypodium vieillardii* Mettenius = **Phymatosorus** spec.

E 80. *Microsorum vitense* (Baker) Copeland (1938) 73.
Based on *Polypodium vitense* Baker = **Phymatosorus commutatus** (Blume) Pichi Sermolli.

E 81. *Microsorum wallichianum* (Sprengel) Copeland (1929a) 112.
Based on *Polypodium wallichianum* Sprengel = **Crypsinus** spec.

E 82. *Microsorum wilkesii* (Christensen) Ching.
See 28. **Phymatosorus alatus** (Brackenridge) Bosman.

E 83. *Microsorum zippelii* (Blume) Ching.
See 27. **Neocheiropteris zippelii** (Blume) Bosman.

E 84. *Microsorum zosteriforme* (Mettenius) Ching.
See 22. **Colysis pteropus** (Blume) Bosman.

## 16. IDENTIFICATION LIST

*Microsorum*

1. *cinctum*
2. *congregatifolium*
3. *egregium*
4. *glossophyllum*
5. *heterocarpum*
6. *heterolobum*
7. *lastii*
8. *leandrianum*
9. *linguiforme*
10. *longissimum*
11. *membranaceum*
12. *monstrosum*
13. *musifolium*
14. *pentaphyllum*
15. *punctatum*
16. *rampans*
17. *samarense*
18. *sopuense*
19. *spectrum*
20. *steerei*

*Colysis*

21. *insignis*
22. *pteropus*

*Leptochilus*

23. *buergerianus*
24. *subhemionitideus*

*Neocheiropteris*

25. *ningpoensis*
26. *superficialis*
27. *zippelii*

*Phymatosorus*

28. *alatus*
29. *biseriatus*

No cross references to individual collectors are made for collections numbered in the following series: ANU, BKF, BS, BSIP, BW, CCC, FB, HFP, Iwatsuki et al.: B, P, S, and T-series, LAE, NGF, PNH, SAN, S (SAR), SF (SFN), USC.

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## 17. GLOSSARY OF BOTANICAL TERMS

For illustration and analysis of types of venation patterns, innervation of sori, and spore surface sculpture see chapter 5.

**anadromous (veins):** originating consecutively in acro- and basiscopic direction, i. e., the first tertiary branch on a secondary vein points in acroscopic direction.

**catadromous (veins):** originating consecutively in basi- and acroscopic succession, i. e., the first tertiary branch on a secondary vein points in basiscopic direction.

**cavities (rhizome):** intercellular cavities in the ground tissue of the rhizome, sometimes interconnected to form a system of canals, rarely with a gap leading to the dorsal surface of the rhizome.

**central region (scales):** the region above the stalk or above the point of attachment to the rhizome.

**clathrate throughout (scales):** with thickened and lignified (brown) anticlinal walls and translucent superficial walls, giving the scale a web-like appearance.

**colliculate (spores):** with rounded broad closely spaced elevations, covering the surface (Van Uffelen & Hennipman, 1985).

**confluent (sori):** situated very close together, so that fully developed sori cannot be individually recognized unless the sporangia are removed to reveal the actual shape and number of receptacula involved (usually two or a few).

**costal areole:** primary areole formed by the primary vein, two adjacent secondary veins and the first tertiary vein.

**gemmate (spores):** with broad projections of $\geq 1$ µm high and the horizontal axis $\geq$ the vertical axis; trunk constricted (Harris, 1955).

**main areoles:** (in venation types 3 and 4) conspicuous relatively large areoles either including primary areoles or being of primary order themselves.

**marginal areoles:** relatively small (primary or secondary) areoles bordering the main areoles or primary areoles in the marginal part of the lamina.

**paraphyses:** trichomes found either among the sporangia and inserted on the receptacle, or upon the sporangium and showing (inferred) congruence with the indument on the sterile frond (Baayen & Hennipman, 1987).

**partly clathrate (scales):** clathrate, excluding the marginal cells (sometimes only in the basal half of the scales), which have translucent anticlinal walls.

**primary areoles:** areoles of the first order formed by two adjacent secondary veins and tertiary veins (or a tertiary vein and the primary vein in the case of costal areoles).

**primary vein:** the rachis of the lamina in simple fronds or the costa of lateral lobes in pinnatifid fronds.

**proportion to rhizome (fronds):** maximum length of fronds (per specimen): maximum rhizome diameter (per specimen); a value of $> 200$ is called 'large in proportion', while a value of $\leq 200$ is called 'well proportioned'.

**pseudopeltate (scales):** basally attached scales with two basal auricles on either side of the stalk which more or less overlap; when auricles fully overlap, superficially resembling peltate scales.

**quaternary vein:** vein connecting two adjacent tertiary veins in a $\pm$ regular way.

**secondary vein:** main vein springing from the primary vein and running towards the margin of the lamina, usually $\pm$ parallel to other secondary veins.

**soral vein:** tertiary or quaternary vein which is more prominent than other veins of the same order and on which a (usually rather large) sorus is innervated.

**stipe:** the basal part of the rachis from the phyllopodium up to the base of the lamina; if the base of the lamina very gradually attenuates an arbitrarily chosen point where the lamina on both sides is c. 1/2 mm wide marks the apical end of the stipe.

**subclathrate (scales):** as clathrate, but with the superficial walls more or less opaque (brown); intermediates between fully clathrate and subclathrate scales may occur.

**tertiary vein:** vein connecting two adjacent secondary veins in a $\pm$ regular way.

**verrucate (spores):** with broad projections, if more or less isodiametric, larger than granulate; trunk not constricted (Van Uffelen & Hennipman, 1985).

**waxy (rhizome):** covered by a thin waxy layer which turns the surface glaucous; when absent the dried surface varies from green to brown or blackish.

## 18. INDEX TO NAMES OF TAXA

This index pertains only to the taxonomic part (chapters 11, 13–15). Accepted names are in roman type (new names and combinations **bold**), synonyms are in *italics*. The numbers refer to the numbered descriptions of accepted taxa (1–20: *Microsorum*; 21–29: other genera), to the numbers of dubious names (D), and to those of excluded names (E). If names are exclusively mentioned in a note to a description this is indicated by '(note)'. Correct names for earlier homonyms of invalid names are not included in the index.

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**Books:** dates of publication and shortened titles conform those advised by Stafleu & Cowan (1976–1988); if parts/volumes are published in different years, only the parts (years) used are listed; publishers are only given for publications after 1945. **Serials:** abbreviations of names of serials conform to those advised by Brown & Stratton (1963).


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