



The microsoroid ferns: Inferring the relationships of a highly diverse lineage of Paleotropical epiphytic ferns (Polypodiaceae, Polypodiopsida)

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ABSTRACT

The relationships of the microsoroid ferns were studied using a DNA sequence-based phylogenetic approach. Nucleotide sequences for up to four chloroplast genome regions were assembled for 107 samples from 87 species. Microsoroids s.l. include six lineages of which two are species rich. The results indicate that several genera are not monophyletic (e.g. *Microsorium*), several controversial genera are confirmed to be monophyletic (e.g. *Leptochilus*), and some genera new to science should be recognized (*M. membranaceum* clade). Unique insights were gained into the biogeographic history of this highly diverse epiphytic vascular plant lineage that is widespread in continental Asia to Australasia. Evidence was found for splits into lineages diversifying in parallel in continental Asia and Malesia. No evidence was recovered for an African radiation because all African microsoroid species either also are found in Asia or have sister species in continental Asia. In contrast, evidence for independent radiations were discovered for the Australasian region.

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1. Introduction

The Polypodiaceae as defined by Smith et al. (2006b) are likely the most diverse group of extant ferns (Schneider et al., 2004b; Smith et al., 2006b). They are not only the lineage of derived ferns that has the highest number of species but they also display a vast range of morphological variation. Ecologically, by contrast, they appear less variable, because the majority of these ferns grow as epiphytes in tropical to subtropical climates where they are, besides orchids, the most abundant pantropical lineage of epiphytic vascular plants. Only a few species are found in temperate regions in which they usually display life histories, varying between epi-

phytic, saxicolous, and terrestrial growth. A closer look at the ecology of the tropical diversity of the Polypodiaceae reveals variation in life histories that has allowed different polypodiaceous lineages to colonize successfully the various epiphytic habitats found in tropical forests. Some strategies found in Polypodiaceae are unique among ferns, but found in other vascular plant epiphytes. These include mutualistic ant–fern associations in which fern rhizomes are modified such that they provide ants with domiciles (Haufler et al., 2003; Gay, 1993; Gómez, 1974). Other adaptive strategies should also be mentioned briefly in this context: (1) poikilohydry as found in *Pleopeltis polypodioides*, (2) CAM photosynthesis as found in *Pyrrosia piloselloides*, (3) litter collecting as found in *Drynaria* and *Platyserium*, (4) dispersal with chlorophyllous (green) spores as found in the grammitids, and (5) dwarfism of the sporophyte generation as found in some grammitid species. In the light of this diversity, we require a robust phylogenetic hypothesis. It is therefore not surprising that the phylogeny of the Polypodiaceae is the most exten-

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sively studied among the larger fern families. Only the filmy ferns have been studied to a similar extent (e.g., Ebihara et al., 2007; Hennipman et al., 2006).

The earliest attempts to infer the relationships of the Polypodiaceae using DNA sequence data date back to the mid nineties of the last century (Haufler and Ranker, 1995). These years were arguably the beginning of a revolution in pteridology, which resulted in renewal of our understanding of fern evolution (Schneider et al., 2004b; Smith et al., 2006a). In the case of Polypodiaceae, about 20 studies have been published exploring the relationships of these ferns using DNA sequence variation in a phylogenetic framework. These studies have addressed various questions, ranging from the deep relationships among these ferns, to the relationships within some of the most diverse genera (Haufler and Ranker, 1995; Haufler et al., 2000, 2003; Janssen and Schneider, 2005; Janssen et al., 2007; Kreier and Schneider, 2006a,b; Kreier et al., 2007; Lu and Li, 2006; Ranker et al., 2003, 2004; Schneider et al., 2002, 2004a,b,c, 2006a,b, 2008; Smith et al., 2006a). Major questions concerning the deep relationships of the Polypodiaceae, especially the generic classification of *Polypodium* L. and its segregates, have been resolved. Schneider et al. (2004c) has addressed the deep relationships of the polypodiaceous lineages, while most other studies have focused on the relationships within selected lineages. These include the drynarioids (Janssen and Schneider, 2005), loxogrammioids (Kreier and Schneider, 2006b), platycerioids (Kreier and Schneider, 2006b), and various neotropical genera (Kreier et al., 2007; Schneider et al., 2006b; Smith et al., 2006a). Specialized questions such as the relationships of enigmatic genera (Schneider et al., 2004a) or the relationships within putative genera (Haufler et al., 2003; Lu and Li, 2006), biogeographically defined assemblages (Schneider et al., 2006a) have been addressed.

Although the microsoroid clade forms one of the five main lineages in Polypodiaceae and is one of the most species rich fern lineages in the paleotropics, it has received little attention from systematics, and its generic classification is poorly understood. Besides the global study by Schneider et al. (2004c), none of the existing studies have focused on the deeper relationships within this lineage. However, any study including more than one sample of the genus *Microsorium* Link has rejected the genus' monophyly (Schneider et al., 2004a,c, 2006b). This is far from surprising because each author studying this group using morphological evidence has suggested a different classification (Ching, 1978b; Bosman, 1986, 1991; Hennipman et al., 1990; Nootboom, 1997, 1999). At one extreme, Nootboom (1997, 1999) accepted only two genera, whereas several authors (e.g. Lu, 1999; Shi, 1999) argue for more than 10 genera of which many were described by Ching and his students (Ching, 1978a; Ching and Shing, 1983a,b; Ching and Wu, 1980). Furthermore, Schneider et al. (2004c) demonstrated that the most recent classification of the microsoroid ferns by Hennipman et al. (1990) is not natural. Thus, the generic classification of *Microsorium* cannot be studied in isolation but only by considering some closely related taxa, namely the similarly complex genus *Lepisorus* J.Sm. (Ching et al., 1983; Yu and Lin, 1997; Zhang et al., 2003; Zink, 1993) and some smaller, well-understood genera such as *Belvisia* Mirbel (Hovenkamp and Franken, 1993) and *Lecanopteris* Reinw. (Haufler et al., 2003). Two additional genera have to be considered because they represent the two sister lineages to all other microsoroids, the genera *Goniophlebium* C.Presl and *Thylacopteris* Kunze ex J.Sm. Both genera were revised by Rödl-Linder (1990, 1994) but the classification of the former genus is still controversial (Lu and Li, 2006).

This study aims to employ the strategy that was used successfully to address the relationships among the Neotropical segregates of *Polypodium*. Sequences of up to four regions of the plastid genome were obtained and analyzed using standard phylogenetic approaches such as maximum parsimony, maximum likelihood, and

Bayesian inference of phylogeny. The taxon-sampling was designed in consideration of the results of previous DNA-based studies (Haufler et al., 2003; Lu and Li, 2006; Schneider et al., 2004a,c, 2006a) and taxonomic morphology-based studies (Bosman, 1986, 1991; Ching, 1978a,b; Ching and Shing, 1983a,b; Ching and Wu, 1980; Ching et al., 1983; Hovenkamp, 1998; Hennipman et al., 1990; Hetterscheid and Hennipman, 1984; Hovenkamp and Franken, 1993; Lu, 1999; Nootboom, 1997, 1999; Rödl-Linder, 1990, 1994; Shi, 1999; Shi and Zhang, 1999a,b,c; Zhang et al., 2003; Zink, 1989, 1993). We sampled more than 80 spp. of microsoroid ferns, including at least one representative of all suggested taxonomic units and we were successful in isolating and sequencing DNA from specimens of the type species of most genera. By doing so, we created a taxonomically comprehensive sampling including more than a third of all currently accepted species. This dataset has allowed us to infer the phylogenetic relationships of the microsoroid ferns and suggest a putatively natural generic classification. In addition, the sampling can be used to explore biogeographic patterns and compare them to the results of studies on the drynarioid ferns (Janssen and Schneider, 2005; Janssen et al., 2007) and the genus *Platycerium* (Kreier and Schneider, 2006a). The genera *Christiopteris* Copel. (Hennipman and Hetterscheid, 1984) and *Dictymia* J.Sm. were excluded from this study because those genera are not closely related to the drynarioid ferns and loxogrammioid ferns, respectively, as demonstrated independently (Schneider et al., 2004c, 2008).

2. Materials and methods

Material for generating DNA sequence data was collected either from specimens cultivated in Botanical Gardens or from material obtained from field collection and stored in silica. A few sequences were obtained from herbarium specimens. We were able to obtain material for several newly described species of *Microsorium* (Boonkerd and Nootboom, 2001; Smith and Hoshizaki, 2000), but other newly described taxa were not accessible. We were unsuccessful in isolating DNA from the type species of the monotypic genus *Cao-bangia* (Smith and Zhang, 2002) that is likely closely related to *Lemmaphyllum*. We took particular care to sample the type species of each genus accepted in the recent past for groups included in the microsoroids as defined in this paper (Table 1). Extraction of genomic DNA, amplification and sequencing of four chloroplast genome regions (cpDNA) were conducted as described in previous studies (Janssen and Schneider, 2005; Kreier and Schneider, 2006a,b; Kreier et al., 2007). The inferred cpDNA regions include two coding regions (*rbcl*, *rps4*) and two non-coding regions (*rps4-trnS* IGS and *trnL-F* IGS). GenBank accession numbers and voucher information are given in Table 2. Sequence assembly and editing were performed mainly with TreV (Staden Package, <http://sourceforge.net/projects/staden>). The final alignment was adjusted visually using MacClade 4.0 (Maddison and Maddison, 2002). Ambiguously aligned regions were excluded from all analyses and gaps were handled as missing data. Simple indel scoring was explored but not used in subsequent analyses because the result provided limited information.

We created two datasets, one large dataset containing all 104 samples of which at least one of the four sequences was available, and a small dataset containing only those 84 samples, of which we had sequences of all four regions. The second dataset is more likely to recover robust phylogenetic relationships, whereas the first dataset with a substantial amount of incomplete data may be more powerful with respect to taxonomic relevance because it included critical taxa lacking in the smaller dataset. For several species included in the first dataset, we were unable to obtain sequences for all regions because we did not have access to specimens with adequately preserved DNA and thus we were able to obtain se-

Table 1

Type species of microsoroid genera (as defined herein)

Genus	Species	Fig. 4
<i>Anapausia</i> C.Presl	<i>Leptochilus decurrens</i> Blume	24
<i>Belvisia</i> Copel.	<i>Belvisia spicata</i> (L.f.) Copel.	20
<i>Colysis</i> C.Presl	<i>Leptochilus hemionitideus</i> (Wall. Ex C.Presl) Noot.	25
<i>Dendroconche</i> Copel.	<i>Microsorium linguiforme</i> (Mett.) Copel.	7
<i>Drymotaenium</i> Makino	<i>Drymotaenium miyoshianum</i> Makino	19
<i>Goniophlebium</i> C.Presl	<i>Goniophlebium subauriculatum</i> (Blume) C.Presl	3
<i>Lecanopteris</i> Reinw.	<i>Lecanopteris carnosa</i> (Reinw.) Blume	8
<i>Lemmaphyllum</i> C.Presl	<i>Lemmaphyllum carnosum</i> (Hook.) C.Presl	11
<i>Lepidogrammitis</i> Ching	<i>Lemmaphyllum drymoglossoides</i> (Baker) Ching	
<i>Lepidomicrosorium</i> Ching	<i>Neocheiropteris superficialis</i> (Bedd.) Bosman	13
<i>Lepisorus</i> (J.Sm.) Ching	<i>Lepisorus nudus</i> (Hook.) Ching	18
<i>Leptochilus</i> Kaulf.	<i>Leptochilus axillaris</i> Kaulf.	23
<i>Metapolypodium</i> Ching	<i>Goniophlebium manmeiense</i> (H.Christ) Rödl-Linder	6
<i>Microsorium</i> Link	<i>Microsorium punctatum</i> (L.) Copel.	21
<i>Myrmecophila</i> (H.Christ) Nakai	<i>Lecanoperis sinuosa</i> (Hook.) Blume	9
<i>Neocheiropteris</i> H.Christ	<i>Neocheiropteris palmatopedata</i> H.Christ	12
<i>Neolepisorus</i> Ching	<i>Neocheiropteris ensatus</i> (Thunb.) Ching	15
<i>Paragramma</i> T.Moore	<i>Lepisorus longifolius</i> (Blume) Holttum	16
<i>Paraleptochilus</i> Copel.	<i>Leptochilus decurrens</i> Blume	24
<i>Phymatosorus</i> Pichi Serm.	<i>Microsorium scolopendrium</i> (Burm.f.) Copel.	22
<i>Platygyria</i> Ching & S.K.Wu	<i>Lepisorus waltonii</i> (Ching) S.L.Yu	17
<i>Polypodiastrum</i> Ching	<i>Goniophlebium argutum</i> (Hook.) Ching	4
<i>Polypodioides</i> Ching	<i>Goniophlebium amoenum</i> (Mett.) Bedd.	5
<i>Schellolepis</i> J.Sm.	<i>Goniophlebium percussum</i> (Cav.) Pichi Serm.	2
<i>Thylacopteris</i> Kunze ex J.Sm.	<i>Thylacopteris papillosa</i> (Blume) J.Sm.[1
<i>Tricholepidium</i> Ching	<i>Neocheiropteris normalis</i> Tagawa	14
<i>Weatherbya</i> Copel.	<i>Lemmaphyllum accedens</i> (Blume) Donk	10

Columns correspond to genus name plus authority, species name plus authority used in this paper, and number indicating the species position in Fig. 4. Only the type species of *Lepidogrammitis* was not included in this study.

quences for only some but not all regions, or obtained the sequences from GenBank.

Phylogenetic reconstructions were pursued using various software programs such as PAUP* (Swofford, 2002) for maximum parsimony, Modeltest (Posada and Crandell, 1998) for model selection, GARLI (Zwickl, 2006) for maximum likelihood, and MrBayes (Huelsenbeck and Ronquist, 2001) for Bayesian inference of phylogeny. Analyses with PAUP were performed as heuristic searches with 100 random-addition-starting trees (RAS) and TBR branch swapping to completion. Non-parametric bootstrap analyses were performed with 1000 bootstrap replicates and heuristic searches with 10 RAS and TBR to completion. Strict consensus trees were calculated if more than one most parsimonious tree was found. Maximum likelihood analyses were performed with GARLI with the GTR model implemented and all parameters estimated. The estimated parameters were compared with the parameters selected in independent runs of Modeltest using the Akaike information criterion. This approach is used to detect putative model violations. Bayesian inference of phylogeny was performed using a single model for all regions and separate models for coding versus non-coding partitions. Congruence among the chloroplast markers was tested by pairwise visual comparisons of the bootstrap consensus trees of all four regions. The evolution of several morphological characters was inferred by plotting these characters onto the obtained phylogenetic hypotheses using maximum parsimony reconstructions with ACCTRAN and DELTRAN optimizations as implemented in MacClade 4.0. These morphological characters were selected because they were either used as diagnostic features in the past or discussed as potential apomorphies. The same approach was used to infer the biogeographic distribution. The data for morphological and biogeographical reconstructions were mainly obtained from the literature (e.g., Bosman, 1991; Hennipman et al., 1990; Nooteboom, 1997, 1999) but always adjusted by our own observations. Two authors, X.-C. Zhang and H. Schneider, studied many of these species in their natural habitats. Other species were studied in cultivation and all species were studied

using herbarium specimens deposited in Goettingen (GOET) and in the NHM (BM).

3. Results

Maximum parsimony and maximum likelihood analyses found the same general topology for both the large and the small dataset, although maximum likelihood analysis of the large dataset contained several polytomies that were resolved by maximum parsimony analysis of the same dataset (Fig. 1). The maximum parsimony analysis of the large/small dataset resulted in 60/2 most parsimonious trees with a length of 2723/2515 steps (consistency index [CI] = 0.3879/0.4007, homoplasy index [HI] = 0.6121/0.5993, retention index [RI] = 0.7097/0.7563, rescaled consistency index [RC] = 0.3491/0.3524—CI and HI calculated without constant characters). The maximum likelihood analysis of the small dataset (Fig. 2) found a single tree with $-\ln = 18128.811$ (ML values calculated using GARLI). In comparison, the inclusion of taxa with incomplete sequence information reduced the support values (BS-MP) for several branches but the topology was not altered for taxa included in both datasets. The Bayesian inference of phylogeny of the large dataset recovered the stable phase after about 900–1100 generations (depending on the implemented models) and all measured parameters were stable after 500,000 generations (Fig. 3). In comparison, either a single model or more complex models performed similarly, yielding the same topologies, but differing slightly in the recovered support.

All analyses recovered the same topology (as summarized in Fig. 4) with minor differences in the relationships among species within well-supported clades. *Thylacopteris papillosa* and the monophyletic goniophlebioid clade were found as forming a grade leading to the core microsoroids which in turn split into four well-supported lineages: lecanopteroid clade, lepisoroid clade, membranaceoid clade, and microsoroid s.s. clade. These four lineages were found to cluster in two sister-pairs, lecanopteroid plus membra-

Table 2
List of material used in this study given as taxon name, voucher information, origin, collector, collector number, herbarium to which the voucher was deposited—GenBank accession numbers in the order *rbcL*, *rps4* plus *rps4-trnS* IGS, and *trnL-F* IGS

Taxon	Voucher	<i>rbcL</i>	<i>rps4</i>	<i>trnL-F</i>
<i>Belvisia annamensis</i> (C. Chr.) S.H. Fu	East Kalimantan; Hovenkamp 05-277 (L)	EU482931*	EU482976*	EU483025*
<i>Belvisia mucronata</i> (Fée) Copel.	Cult. BGZ; Kreier s.n. (GOET)	AY362562	AY362629	DQ642232
<i>Belvisia platyrhynchos</i> (Kunze) Copel.	cult. BGZ; Kreier s.n. (GOET)	DQ642152	DQ642190	DQ642233
<i>Belvisia spicata</i> (L.) Mirb. ex Copel.	Cult. BGG; Schneider s.n. (GOET)	DQ642153	DQ642191	DQ642234
<i>Drymotaenium miyoshianum</i> (Makino) Makino	Taiwan; Cranfill TW087 (UC)	AY362563	AY362630	DQ179640
<i>Goniophlebium amoenum</i> (Mett.) Bedd. var. <i>amoenum</i>	Yunnan; SG Lu B7 (PYU)	DQ078627	–	–
<i>Goniophlebium amoenum</i> var. <i>chinense</i> Ching	Yunnan; SG Lu X14 (PYU)	DQ078630	DQ078630	–
<i>Goniophlebium argutum</i> (Wall. ex Hook.) J. Sm. ex Hook.	Taiwan; Cranfill TW075 (UC)	DQ164442	DQ164473	DQ164505
<i>Goniophlebium formosanum</i> (Baker) Rödl-Linder	Taiwan; Cranfill TW043 (UC)	AB043100	AY096224	DQ642235
<i>Goniophlebium manmeiense</i> (H. Christ) Rödl-Linder	Yunnan; SG Lu K4 (PYU)	DQ078628	DQ078631	–
<i>Goniophlebium mehibitense</i> (C. Chr.) Parris	East Kalimantan; Hovenkamp 05-278 (L)	EU482932*	EU482977*	EU483026*
<i>Goniophlebium mengtzeense</i> (H. Christ) Rödl-Linder	Yunnan; Barrington 2085a (VT)	AY362560	AY362560	–
<i>Goniophlebium mengtzeense</i> (H. Christ) Rödl-Linder	Yunnan; SG Lu K9 (PYU)	DQ078624	DQ078633	–
<i>Goniophlebium microrhizomum</i> (Clarke ex Baker) Clarke ex Bedd.	Yunnan; SG Lu K8 (PYU)	DQ078627	DQ078632	–
<i>Goniophlebium niponicum</i> (Mett.) Bedd.	Unknown; Hirohara et al. 2000	ABO43098	–	–
<i>Goniophlebium niponicum</i> (Mett.) Bedd.	Japan; Kato s.n. (TI)	ABO43098	AY362626	EU483027*
<i>Goniophlebium niponicum</i> var. <i>wattii</i> Bedd.	Yunnan; SG Lu (PYU)	DQ078625	DQ078634	–
<i>Goniophlebium percussum</i> (Cav.) Wagner & Grether	cult. ASG; Smith s.n. (UC)	AY362561	AY362628	–
<i>Goniophlebium persicifolium</i> (Desv.) Bedd.	Malay Peninsula; Jaman 5890 (UC)	–	AY096225	–
<i>Goniophlebium persicifolium</i> (Desv.) Bedd.	Cult. BGB; 239-12-90-33 (B)	EU482933*	–	EU483028*
<i>Goniophlebium pseudocommutatum</i> (Copel.) Copel.	Cult. BGB; 239-36-90-30 (B)	EU482934*	Eu482978*	EU483029*
<i>Goniophlebium subauriculatum</i> (Blume) C.Presl	Cult. BGO; Smith s.n. (UC)	AF470342	DQ168812	AY083645
<i>Lecanopteris balgoyii</i> Hennipman	Sulawesi; Hennipman s.n. (L)	AF470328	EU482980*	AY083631
<i>Lecanopteris carnososa</i> Blume	Cult. RBGK; Cranfill 153 (UC)	AF470322	AY096227	AY083625
<i>Lecanopteris celebica</i> Hennipman	Cult. BGG; Schneider s.n. (GOET)	AF470323	EU482981*	AY083626
<i>Lecanopteris crustacea</i> Copel.	Cult. CAG; A.R. Smith s.n. (UC)	AF470329	EU482982*	AY083632
<i>Lecanopteris deparioides</i> (Ces.) Baker	Cult. BGU; Hennipman 7865 (U)	AF470324	–	AY083627
<i>Lecanopteris lomarioides</i> (Kunze ex Mett.) Copel.	Cult. BGU; Hennipman s.n. (U)	AF470326	–	AY083629
<i>Lecanopteris luzonensis</i> Hennipman	cult. BGG; Schneider s.n. (GOET)	AF470325	EU482983*	AY083628
<i>Lecanopteris mirabilis</i> (C. Chr.) Copel.	Cult. BGU; Hennipman s.n. (U)	AF470330	EU482984*	AY083633
<i>Lecanopteris pumila</i> Blume	Cult. BGU; Hennipman s.n. (UC)	AF470331	–	AY083634
<i>Lecanopteris sarcopus</i> (Teijsm. & Binn.) Copel.	Cult. RBGE; Ridl 171 (E)	EU482935*	EU482985*	EU483030*
<i>Lecanopteris sinuosa</i> (Hook.) Copel.	Cult. BGU; Hennipman 7821 (L)	AF470321	AY362634	AY083624
<i>Lecanopteris spinosa</i> Jermy & Walker	Cult. BGU; Hennipman s.n. (U)	AF470327	–	AY083630
<i>Lemmaphyllum accedens</i> (Blume) Donk ex. Holttum	East Kalimantan; Hovenkamp 05-298 (L)	EU482936*	EU482986*	EU483031*
<i>Lemmaphyllum carnosum</i> (J. Sm. ex Hook.) C. Presl	Cult. BGUI; A.R. Smith s.n. (UC)	AF470332	AY362631	AY083635
<i>Lemmaphyllum diversum</i> (Rosenst.) Tagawa	Taiwan; Ranker 2079 (COLO)	EU482937*	EU482987*	EU483032*
<i>Lemmaphyllum microphyllum</i> C. Presl	Cult. BGZ; Schneieder s.n. (GOET)	EU482938*	EU482988*	EU483033*
<i>Lepidogrammitis diversa</i> (Rosenst.) Ching	China; Zhang 1854 (PE)	EU482939*	EU482989*	EU483034*
<i>Lepisorus clathratus</i> (C.B. Clarke) Ching	Tibet; Dickoré 12430 (GOET)	DQ642154	DQ642192	DQ642236
<i>Lepisorus excavatus</i> (Willd.) Ching	Tanzania; Herp 3561 (DSM)	DQ642155	DQ642193	DQ642237
<i>Lepisorus excavatus</i> (Willd.) Ching	Grande Comore; Rakotondrainibe 6785 (P)	DQ642156	DQ642194	DQ642238
<i>Lepisorus kawakamii</i> (Hayata) Tagawa	Taiwan; Ranker 2051 (COLO)	EU482940*	EU482990	EU483035*
<i>Lepisorus longifolius</i> (Bl.) Holtt.	Cult. BGM; Schneider s.n. (GOET)	DQ642157	DQ642195	DQ642239
<i>Lepisorus macrosphaerus</i> (Baker) Ching	Taiwan; Cranfill TW018 (UC)	EU482941*	EU482991*	EU483036*
<i>Lepisorus megasorus</i> (C. Chr.) Ching	Taiwan; Cranfill TW069 (UC)	DQ642158	DQ642196	DQ642240
<i>Lepisorus monilisorus</i> (Hayata) Tagawa	Taiwan; Cranfill TW012 (UC)	EU482942*	EU482992*	EU483037*
<i>Lepisorus nudus</i> (Hook.) Ching	Cult. UCGB; Smith s.n. (UC)	AY362564	–	–
<i>Lepisorus pseudo-ussuriensis</i> Tagawa	Taiwan; Cranfill TW093 (UC)	EU482943*	EU482993*	EU483038*
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Cult. BGZ; Kreier s.n. (GOET)	U05629	AY096226	DQ642241
<i>Lepisorus waltonii</i> (Ching) S.L. Yu	China; Cranfill 94-266-29 (UC)	EU482944*	EU482994*	EU483039*
<i>Leptochilus axillaris</i> (Cav.) Kaulf.	Java; Walker 11557 (BM)	–	–	EU483040*
<i>Leptochilus cantoniensis</i> (Baker) Ching	China; Dong 172 (PE)	EU482945*	EU482995*	EU483041*
<i>Leptochilus cantoniensis</i> (Baker) Ching	China; Dong 743 (PE)	EU482946*	EU482996*	EU483042*
<i>Leptochilus decurens</i> Blume	Cult. BGUI; Douglas 28 (UC)	AY096203	AY096228	DQ179640
<i>Leptochilus digitatus</i> (Baker) Noot.	China; Zhang 3509 (PE)	EU482947*	EU482997*	EU483043*
<i>Leptochilus digitatus</i> (Baker) Noot.	Vietnam; A.R. Smith 00-036 (UC)	EU482948*	EU482998*	EU483044*
<i>Leptochilus elliptica</i> (Thunb.) Ching	China; Zhang 1923 (PE)	EU482949*	EU482999*	EU483045*
<i>Leptochilus hemionitideus</i> (Wall. ex C. Presl) Noot.	Japan; Hasebe 26551 (TI)	U05612	–	–
<i>Leptochilus hemionitideus</i> (Wall. ex C. Presl) Noot.	Cult. NYBG; Moran s.n. (NY)	–	EU503044*	EU503045*
<i>Leptochilus hemitoma</i> (Hance) Ching	China; Zhang 3302 (PE)	EU482951*	EU483001*	EU483047*
<i>Leptochilus henryi</i> (Baker) Ching	China; Zhang 2541 (PE)	EU482952*	EU483002*	EU483048*
<i>Leptochilus simplifrons</i> (H. Christ) Tagawa	Cult. JNU; Zhang 3800 (PE)	EU482953*	EU483003*	EU483049*
<i>Leptochilus macrophyllum</i> (Blume) Noot. var. <i>wrightii</i> (Hook. & Baker) Noot.	Japan (Okinawa); Tsutsumi 1067 (CT)	EU482954*	EU483004*	EU483050*
<i>Microsorium commutatum</i> (Bl.) Copel.	Cult. Whitehead; A.R. Smith 2901 (UC)	AY362571	EU483005*	EU483051*
<i>Microsorium cuspidatum</i> (D. Don) Tagawa	Cult. NYBG; A.R. Smith 1738194 (UC)	AF470335	AY096230	AY983638
<i>Microsorium fortunei</i> (T.Moore) Ching	Taiwan; Ranker 2087 (COLO)	DQ642159	DQ642197	DQ642242
<i>Microsorium fortunei</i> (T.Moore) Ching	China; Zhang 3446 (PE)	EU482955*	EU483006*	EU483052*
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Hawaii; Lorence 9155 (DL)	EU482956*	EU483007*	EU483053*
<i>Microsorium grossum</i> (Langsd. & Fisch.) S.B. Andrews	Moorea; Ranker 1941 (COLO)	DQ179633	DQ179636	DQ179642
<i>Phymatosorus hainanensis</i> (Noot.) S.G.Lu	cult. SCIB; Wang 1348 (PE)	EU482960	EU483011*	EU483059*
<i>Microsorium insigne</i> (Blume) Copel.	China; Liu 204 (PE)	EU482957*	EU483008*	EU483054*
<i>Microsorium insigne</i> (Blume) Copel.	China; Liu 214 (PE)	EU482958*	EU483009*	EU483055*
<i>Microsorium insigne</i>	China; Zhang 3510 (PE)	EU482959*	EU483010*	EU483056*
<i>Microsorium lastii</i> (Baker) Tardieu	Perier 7937 (P)	EU482961*	EU483012*	EU483058*
<i>Microsorium linguiforme</i> (Mett.) Copel.	New Guinea; Ranker 1176 (UC)	AF470334	AY362635	AY083637

Table 2 (continued)

Taxon	Voucher	<i>rbcL</i>	<i>rps4</i>	<i>trnL-F</i>
<i>Microsorium membranaceum</i> (D.Don) Ching	Cult. Xishuanbanna; Li 95 (PE)	EU482962 [*]	EU483013 [*]	EU483059 [*]
<i>Microsorium membranaceum</i> (D.Don) Ching	Taiwan; Cranfill TW042 (UC)	EU482963 [*]	DQ642198	DQ642244
<i>Microsorium membranifolium</i> (R.Br.) Ching	Cult. BGG; Schneider s.n. (GOET)	DQ642161	DQ642200	DQ642245
<i>Microsorium membranifolium</i> (R.Br.) Ching	Hawaii; Dunn 458 (LOA)	EU482964 [*]	EU483014 [*]	EU483060 [*]
<i>Microsorium musifolium</i> (Blume) Copel.	Cult. BGUI; A.R. Smith s.n. (UC)	AF470335	AY362636	AY083636
<i>Microsorium novo-zealandiae</i> (Baker) Copel.	New Zealand; Perrie WELT P20873	DQ401116	DQ401126	DQ401121
<i>Microsorium pappei</i> (Mett. ex Kuhn) Tardieu	Cult. BGL; 901812 (L)	AF470336	–	AY083639
<i>Microsorium papuanum</i> (Baker) Parris	Cult. BGB; Schuettelpelz 603 (GOET)	DQ642162	EU483015 [*]	DQ642246
<i>Microsorium pteropus</i> (Blume) Copel.	Cult. BGG; Kreier s.n. (GOET)	EU482965 [*]	EU483016 [*]	EU483061 [*]
<i>Microsorium punctuatum</i> (L.) Copel.	Cult. BGH; Schneider s.n. (GOET)	DQ164444	DQ164475	DQ164508
<i>Microsorium punctuatum</i> (L.) Copel.	Taiwan; Ranker 2096 (COLO)	EU482966 [*]	EU483017 [*]	EU483063 [*]
<i>Microsorium pustulatum</i> (G. Forst.) Copel.	New Zealand; Perrie WELT P20874	DQ401117	DQ401122	EU483066 [*]
<i>Microsorium scandens</i> (G. Forst.) Tindale	New Zealand; Perrie WELT P20875	DQ401118	DQ401128	DQ401123
<i>Microsorium scandens</i> (G. Forst.) Tindale	Cult. BGG; Kreier s.n. (GOET)	DQ212057	DQ212058	DQ179641
<i>Microsorium scolopendrium</i> (Burm.f.) Copel.	Cult. BGG; Schneider s.n. (GOET)	DQ642163	DQ642201	DQ642247
<i>Microsorium scolopendrium</i> (Burm.f.) Copel.	Mayotte; Rakotondrainibe 6601 (P)	DQ642164	DQ642202	DQ642248
<i>Microsorium spectrum</i> (Kaulf.) Copel.	Hawai'i; Wood 10936 (LOA)	EU482967 [*]	EU483018 [*]	EU483064 [*]
<i>Microsorium spectrum</i> (Kaulf.) Copel.	Hawaii; Hoshizaki 1350 (UC)	EU482968 [*]	EU483019 [*]	EU483065 [*]
<i>Microsorium thailandicum</i> T. Booknerd & Noot.	Cult. BGG; Schwertfeger s.n. (GOET)	EU482969 [*]	EU483020 [*]	EU483066 [*]
<i>Microsorium varians</i> (Mett.) Henniipman & Hett.	Cult. BGG; Schneider s.n. (GOET)	AY362566	AY362638	DQ179643
<i>Microsorium viellardii</i> (Mett.) Copel.	Cult. BGD; Schneider s.n. (GOET)	DQ179635	DQ179638	DQ179645
<i>Microsorium whiteheadii</i> A.R. Sm. & Hoshiz.	Sumatra; Whitehead s.n. (UC)	EU482970 [*]	EU483021 [*]	EU483067 [*]
<i>Microsorium zippellii</i> (Blume) Ching	Indonesia; Tsutsumi IN112 (TI)	AB23241	DQ642203	DQ642249
<i>Microsorium superficiale</i> (Blume) Bosman	Taiwan; Cranfill 030 (UC)	EU482971 [*]	EU483022 [*]	EU483062 [*]
<i>Neocheiropteris palmatopedata</i> (Baker) H.Christ	Cult. BGZ; Schneider s.n. (GOET)	AY362567	AY362640	DQ212059
<i>Neocheiropteris superficiale</i> (Blume) Bosman	Taiwan; Cranfill TW073 (UC)	AY725055	AY725048	AY725049
<i>Neolepisorus phyllomanes</i> (H. Christ) Ching	Cult. RBGE; Nicholson s.n. (E)	EU482973 [*]	EU483024 [*]	EU483069 [*]
<i>Neolepisorus ovatus</i> (Wall. ex Bedd.) Ching	China; Zhang 728/1 (PE)	EU482972 [*]	EU483024 [*]	EU483068 [*]
<i>Thylacopteris papillosa</i> (Blume) Krause ex J.Sm.	Java; Gravendeel 559 (L)	AY459174	AY459188	AY459183
<i>Tricholepidium maculatum</i> (H.Christ) Ching	China; Zhang 3100 (PE)	EU482974 [*]	–	EU483070 [*]
<i>Tricholepidium normale</i> (D.Don) Ching	China; Shen S4-1 (PE)	EU482975 [*]	–	EU483071 [*]

Sequences marked with ^{*} were generated for this study. Voucher information given as: Locality or cultivated in the Botanical Garden of xxx; Collector collector number or garden collection number (herbarium); Abbreviations: ASG, Private Garden of Alan R. Smith (Berkeley); BGB, Botanical Garden Berlin-Dahlem; BGBO, Botanical Garden Bogor; BGG, Old Botanical Garden Göttingen; BGH, Botanical Garden Heidelberg; BGL, Botanical Garden Leiden; BGU, Botanical Garden Utrecht; BGUI, Botanical Garden University of California at Berkeley; BGZ, Botanical Garden Zurich; CAG, Garden of Charles Alford (Florida); NYBG, Botanical Garden New York; RBGE, Royal Botanic Garden Edinburgh; and RBGK, Royal Botanic Garden Kew.

naceoid clade and leporoid plus microsoid s.s. clade but these sister-pairs lacked robust bootstrap support (<75%).

The goniophleboid clade includes all species sampled that were recognized by previous authors as belonging to the genus *Goniophlebium* or its segregates such as *Metapolypodium*. Within this clade, we found five well-supported subclades that correspond to putative segregates, e.g. *Goniophlebium* s.s., *Metapolypodium*, *Polypodiastrium*, *Polypodioides*, and *Schellolepis*. The subclades *Goniophlebium* s.s. and *Schellolepis* formed an unsupported sister clade whereas the other three subclades formed together a clade without bootstrap support.

The membranaceoid clade consists of two species, the Asian *Microsorium membranaceum* and the Madagascan *Microsorium lastii*. This clade is the sister to the *Lecanopteris* clade but this branch is unsupported. The lecanopterid clade consists of three subclades as previously reported in Schneider et al. (2006a). The relationships among these three well-supported subclades are resolved but lack bootstrap support values. The *Microsorium linguiforme* and *Microsorium scandens* clade form a grade below the monophyletic ant-fern genus *Lecanopteris*.

The leporoid clade shows a division into two subclades but these two branches are unsupported. One subclade consists of the monophyletic genus *Lemmaphyllum* and species recognized by some authors (Henniipman et al., 1990) as belonging to *Neocheiropteris*. Two putative segregates of the latter genus, *Neolepisorus* and *Tricholepidium*, were recovered as strongly supported clades. The other branch of the leporoid clade consists of the monophyletic genus *Belvisia*, the monotypic genus *Drymotaenium*, and *Lepisorus*. *Lepisorus* appears to be paraphyletic. One of the two putative segregates of *Lepisorus*, the genus *Paragramma*, was found to be the putative sister clade of *Lepisorus* plus *Drymotaenium* and *Belvisia*, but this branch is poorly supported. The second included putative segregate, *Platygyria*, was found to be sister to *Lepisorus clathratus*.

Within the microsoid s.s. clade all deeper nodes are unsupported, whereas several higher nodes are strongly supported. Supported nodes are: *Microsorium cuspidatum* clade, *Microsorium insigne* clade, *Microsorium punctatum* clade, *M. scolopendrium* clade, *Leptochilus* plus *Microsorium pteropus*, and *Leptochilus*. The following sister-pairs are found in most reconstructions but lack support: *M. cuspidatum* clade plus *M. membranifolium* clade, *Microsorium commutatum* plus *Microsorium insigne* clade, and *Microsorium punctatum* plus *M. scolopendrium* clade. The well-supported *Leptochilus* clade is nested within a grade formed by species assigned to the paraphyletic genus *Microsorium*. However, the branches within the *Microsorium* grade are unsupported.

4. Discussion

4.1. Phylogenetic relationships

In general, our results agree with those published in previous phylogenetic studies, especially Schneider et al. (2004a,c, 2006a). However, the increased taxonomic sampling—doubling the number of sampled species—did significantly improve the precision of inferred clade relationships. In the following, we will focus on three key issues of these results: taxonomic implications, biogeographical aspects, and ecological disparity. Before discussing these three points, we want to stress the limitations of this study. Many species still need to be included in phylogenetic studies. An increase of taxonomic coverage appears particularly important for delineating the two putatively unnatural genera *Lepisorus* and *Microsorium*. Some progress will also depend on production of additional DNA sequence markers that are more informative for some branches, such as the leporoid clade. Careful study of the morphology of these clades is also required to gain additional evi-

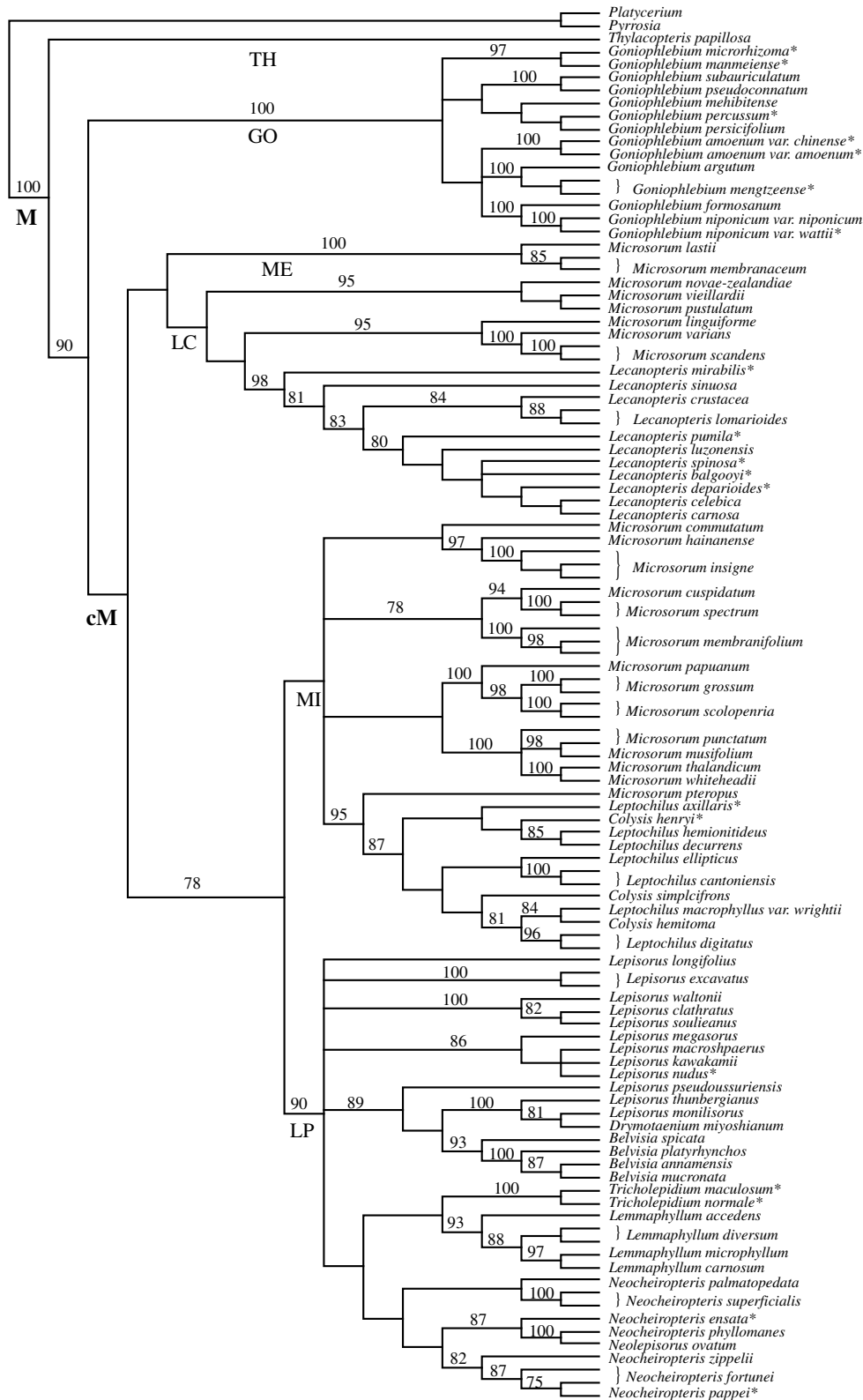


Fig. 1. Strict consensus tree based on 60 maximum parsimonious trees obtained by a maximum parsimony analysis of the large dataset (including taxa with incomplete sequence data indicated with *). Numbers above branches correspond to maximum parsimony bootstrap values. Abbreviations: M, microsoroids; cM, core microsoroids; GO, goniophlebioid clade; LC, lecanopteroid clade; LP, leporoid clade; ME, membranaceoid clade; MI, microsoroid s.s. clade; TH, thylacopteroid clade.

dence. The presented results are certainly not sufficient to discuss the status of some species that are nested within species complexes such as the *Microsorium punctatum* complex, *Microsorium scolopendrium* complex, and the *Neocheiropteris superficiale* com-

plex. These lineages require focused studies to delineate species boundaries. The need for more exhaustive studies is also recommended with respect to two other discussed topics. The biogeographical analysis was designed to illuminate the larger scale

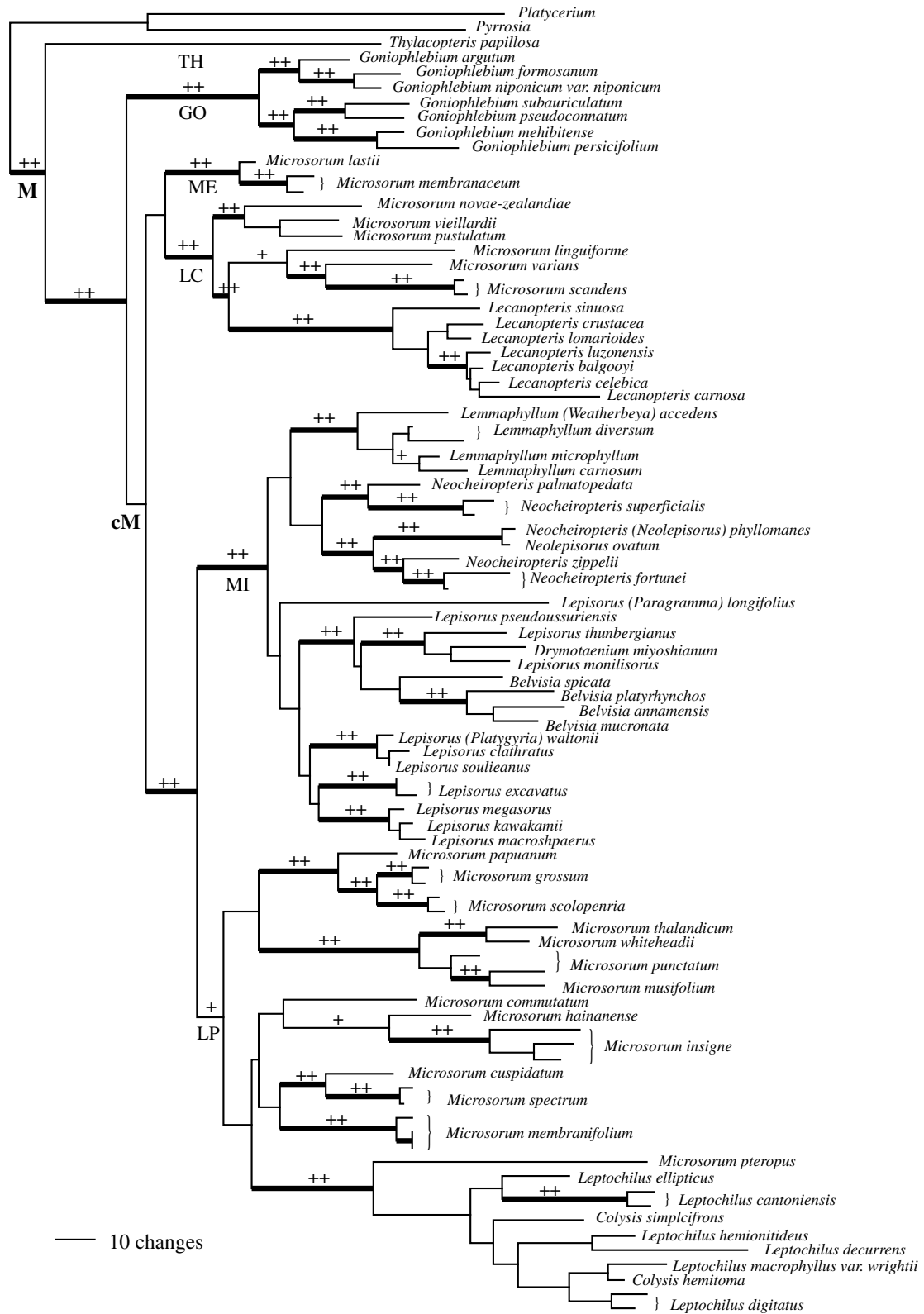


Fig. 2. Phylogram generated in a maximum likelihood analysis of the small dataset (including only taxa with complete sequence data). Thickened branches indicate bootstrap support values of 100%. ++ = ML-BS of 100%, + = ML-BS \geq 95%.

patterns, without considering approaches that reconstruct ancestral node distribution with models that include processes of biogeographic evolution such as dispersal. The selection of large areas of putative endemism reduces the ambiguity introduced

by widespread species but hampers the integration of process-based analyses. Future studies may focus on this issue. Similarly, the discussion on ecological strategies was designed in order to illuminate large-scale patterns.

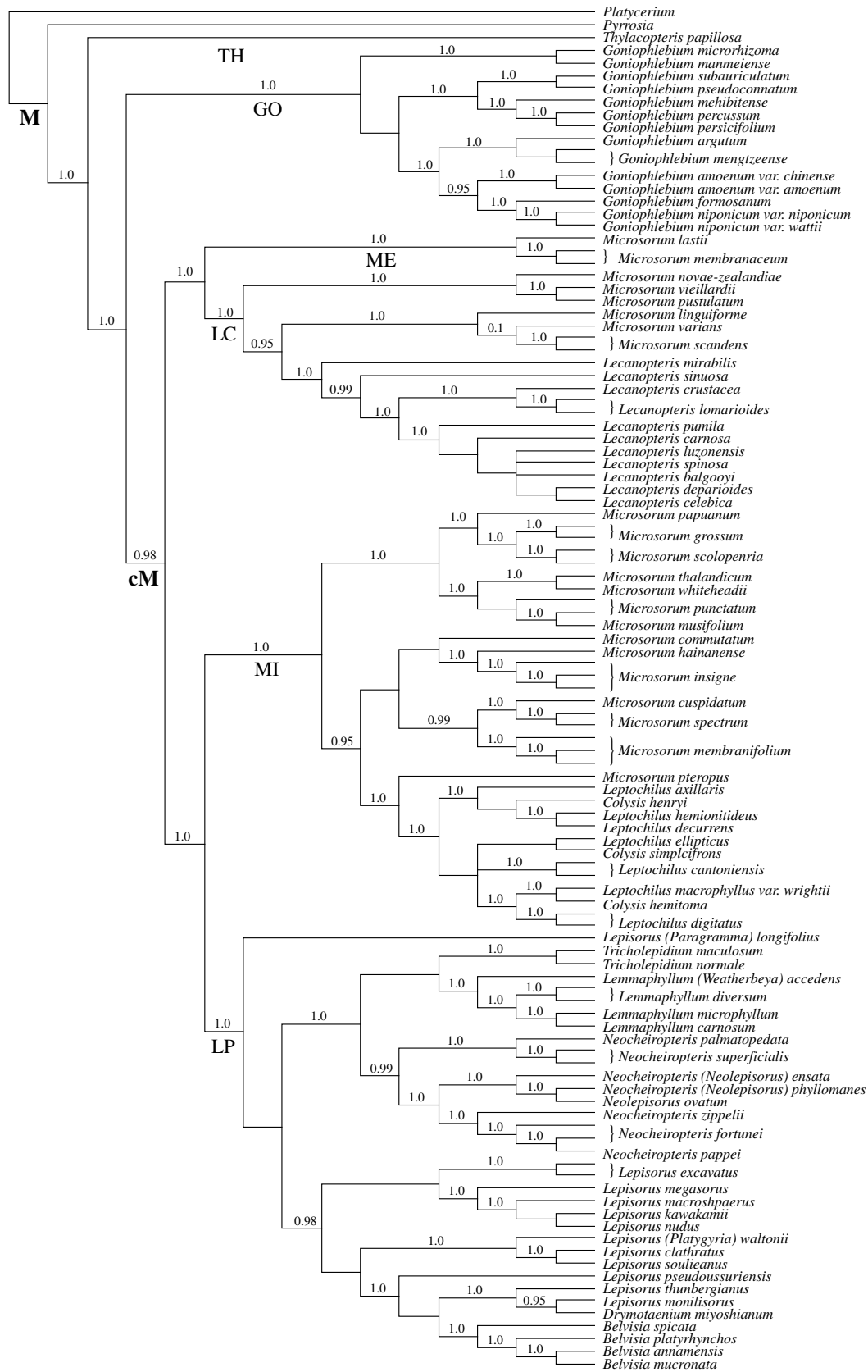


Fig. 3. Majority Consensus tree based on 1,000,000 generations (without the burn-in phase of about 1000 generations) obtained using MrBayes. Posterior support values are given above branches if $p \geq 0.95$.

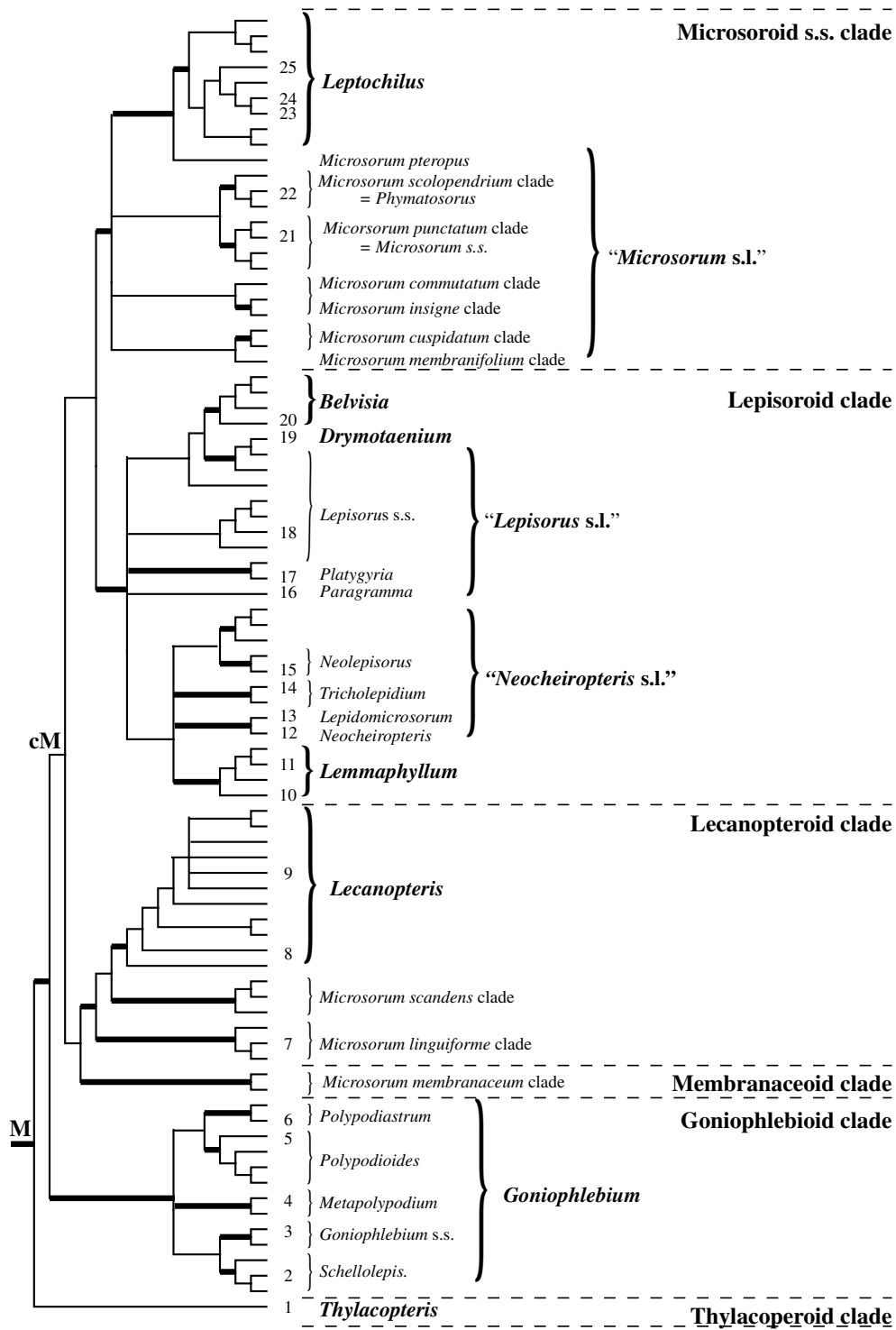


Fig. 4. Taxonomic summary trees based on the results shown in Figs. 1–3. Abbreviations at internal branches correspond to microsoroids (M) and core microsoroids (cM). Thickened branches indicate bootstrap support values of $\geq 90\%$. Dotted lines frame major clades recognized and named on the left side of the figure. Currently widely recognized genera are printed in bold. Paraphyletic taxa are indicated using hyphens. The genus *Microsorium* is shown excluding species belonging to the lecanopteroid clade, lepisoroid clade, or membranaceoid clade. Segregates of larger genera are indicated using accepted generic names. Informal names are given to clades mentioned in the text without existing genus names. Only two exceptions are made to reduce confusion and both the informal and existing genus name are given. This information is presented in a hierarchical fashion if possible from right to the left. Numbers attached to terminal clades correspond to type species of genera (see Table 1).

4.2. Taxonomic evaluation

Although we discuss taxonomic implications, we do not see the present taxonomic sampling as sufficient to propose a new classi-

fication. Instead, we want to identify congruence and incongruence of the phylogenetic hypothesis with existing classification schemes. We hope that these arguments will trigger the studies necessary to illuminate the natural relationships of these ferns.

To simplify the discussion, we have summarized the results in Fig. 4.

Taxa belonging to the microsorioids were treated by Hennipman et al. (1990) as members of three different tribes: Lepisoreae, Microsoreae, and Polypodieae. All three are unnatural taxonomic units as already discussed previously (Schneider et al., 2004c). Genera that were placed in the Lepisoreae and Microsoreae are all nested within the core microsorioids, whereas the members of the basal microsorioid grade, *Goniophlebium* and *Thylacopteris*, were treated as members of the otherwise neotropical and temperate Polypodieae. Taxa placed into the Microsoreae are found in all four lineages within the core microsorioids while genera treated as Lepisoreae are exclusively nested within the leporoid lineage. This lineage includes genera previously assigned to Lepisoreae such as *Belvisia*, *Drymotaenium*, *Lemmaphyllum*, and *Lepisorus* in addition to the *Neocheiropteris* assemblage that was classified as belonging to the Microsoreae by Hennipman et al. (1990). With *Lemmaphyllum* sister to the *Neocheiropteris* clade, the Lepisoreae according to Hennipman et al. (1990) are paraphyletic. Close relationships between *Lepisorus* and *Neocheiropteris* have been suspected before (Ching, 1933). Based on the results, we propose a classification with six monophyletic lineages: *Thylacopteris* lineage, *Goniophlebium* lineage, *Membranaceum* lineage, *Lecanopteris* lineage, *Lepisorus* lineage, and *Microsorium* lineage.

Similar to the higher-level classification, our results shed new light on the generic classification of these taxa. As an example, Nooteboom's concept of *Microsorium* is polyphyletic and needs to be replaced, whereas his concept of *Leptochilus* describes a monophyletic unit (Nooteboom, 1997). The latter includes species treated by other authors under various generic names such as *Colysis* and *Paraleptochilus*. The type species of all these genera, including the type of *Leptochilus*, are nested within a well-supported clade. In contrast, the genus *Microsorium* has to be redefined with various segregates. One of the well-supported segregates corresponds to *Neocheiropteris* s.l. as suggested by Bosman (1991). Alternatively, members of the *Neocheiropteris* clade may be treated as several smaller genera that were all found to be monophyletic such as *Neolepisorus* and *Tricholepidium*. *Tricholepidium* was often found to be sister to *Lemmaphyllum*, and thus this species complex should be treated as an independent genus.

The isolated membranaceoid clade has never been recognized as a distinct taxon and thus no generic name exists for it. Two other segregates were already discussed in a study focusing on *Microsorium* in New Zealand (Schneider et al., 2006a). One of these two clades includes *M. linguiforme*, the type of *Dendroconche*, but this species is morphologically very distinct from the remaining members of this clade. The option to include all species of the *Lecanopteris* clade into the ant-fern genus *Lecanopteris* does not appear desirable for practical reasons. The genus *Lecanopteris* is well defined through apomorphic character states whereas the apomorphic morphological characters have still to be identified for the lecanopteroid clade. The relationships between the two putative sister clades of *Lecanopteris* are poorly resolved (see also Schneider et al., 2006a) and we are therefore hesitant to decide if one or two new genera should be recognized.

The membranaceoid clade is likely sister to the lecanopteroid clade but it is sufficiently different in its plastid genome as well as in biogeography, and morphology to be recognized as a separate lineage. A new genus needs to be established for this clearly separate group. Currently, we are aware of two members of this new genus, the Asian *M. membranaceum* and the Madagascan *M. lastii*. Morphological similarities suggest *M. leandrianum* from Madagascar as an additional member (Bosman, 1991). Bosman (1991) suggested close relationships between these three species but did not argue for their segregation as a new genus.

The polyphyly of *Microsorium* could be resolved by excluding all species belonging either to the lecanopteroid clade, or the leporoid clade, or the membranaceoid clade, but the recognition of *Leptochilus* would still make the reduced *Microsorium* paraphyletic. The current phylogeny is consistent with two alternative taxonomic solutions: either to include all species of the *Microsorium* clade in a single genus, or to recognize at least three genera besides *Leptochilus*. In the latter scenario, *M. pteropus* needs to be transferred to *Leptochilus* or to be established as a monotypic new genus. *Microsorium* itself may be defined as including the *M. punctatum* group and the *M. scolopendrium* group. Alternatively, these two lineages may be treated as segregate genera. The genus name *Microsorium* would apply to the *M. punctatum* clade whereas the *M. scolopendrium* clade includes *M. scolopendrium* and type of *Phymatosorus*. The other two to four lineages did not include any species that are the type of any already described genus. Currently, the branching within the *Microsorium* clade is poorly supported and many candidate species need to be sampled. Thus, additional evidence may allow us to resolve these questions. Any taxonomy of this group must address the issue of there being no obvious morphological differences allowing the unambiguous definition/identification of these genera (Copeland, 1947).

A similar problem was discovered for the definition of the genus *Lepisorus* because the recognition of *Drymotaenium* and *Belvisia* render this genus paraphyletic. Some authors had already suspected that *Belvisia* and *Drymotaenium* may be offshoots from *Lepisorus* (e.g., Zink, 1989, 1993). The current evidence adds the genus *Platygyria* as a further component to the *Lepisorus* complex (Schneider et al., 2004c). Interestingly, *L. longifolia*, the type of the genus *Paragramma*, is at least in some phylogenetic analyses found as sister to the remaining leporoid clade. The poor support for most branches and the limited taxon-sampling suggest the need of an exhaustive study of this group.

Our results provide support for many previously recognized groups despite the conflicts that were discussed previously (see above). The genera *Belvisia*, *Goniophlebium* (as defined by Rödl-Linder, 1990), *Lecanopteris*, and *Lemmaphyllum* (including *Weatherbya*), all were found to be monophyletic. *Neocheiropteris* as defined by Hennipman et al. (1990) is likely monophyletic after the exclusion of *Tricholepidium*. Two of these putative natural genera, *Goniophlebium* and *Neocheiropteris*, are replaced by some authors with a set of smaller genera such as *Polypodides* and *Polypodiastrum* for *Goniophlebium* and *Neolepisorus* for *Neocheiropteris*, respectively. These smaller genera were also found to be monophyletic and thus the phylogeny did not provide strong evidence for more inclusive or more restricted definitions of these two genera. However, studies focused on these groups, similar to the study of Lu and Li (2006), are needed to reveal further details. The broad definition of *Neocheiropteris* given in Fig. 3 is very much in accordance with the concept employed by Bosman (1991); Hennipman et al. (1990).

The dataset was not designed to infer issues concerning the definition of species, but one interesting case may be mentioned here. According to the plastid sequence data, the Afromadagascan *Neocheiropteris pappei* is nested within the Asiatic *N. fortunei*. Morphological similarities support a close relationship between these taxa and more research is required to determine the status of *N. pappei*. The data used here may be misleading based on sampling bias or problems inherited by low variation of plastid DNA such as incomplete coalescence.

4.3. Biogeographic history of microsorioids

Reconstructions of ancestral node distributions indicate an origin of microsorioids in the Asiatic tropics with putative deep splits separating predominantly Malesian clades from predominantly

continental Asiatic clades (Fig. 5). This is particularly visible in the goniophlebioid clade (*Goniophlebium* in Fig. 5). Thus, microsoroid ferns are clearly distinguished from other paleotropical clades of Polypodiaceae such as drynarioids, loxogramroids, and platyceroids, which show deep separations between Afromadagascan and Asian/Australasian clades (Janssen and Schneider, 2005; Janssen et al., 2007; Kreier and Schneider, 2006a,b). Afromadagascan species appear instead to be nested within the tip groups as sister clades to continental Asiatic species (*M. lastii*/*M. membranaceum*; *Membranaceum* in Fig. 5), as sister clades nested within continental Asiatic species (*N. pappei*/*N. fortunei*; *Neolepisorus* in Fig. 5, see also Figs. 1–3), or as widespread species complexes occurring in more than one area of putative endemism (*Belvisia spicata*, *M. punctatum*, *M. scolopendrium*, see for their relationships Figs. 1–3). Only one (*L. excavatus*) out of nine African species (according to Zink, 1993) was included, rendering the interpretation of the African species of *Lepisorus* impossible (see Figs. 1–3; dark green line within *Lepisorus* in Fig. 5). This part of the phylogenetic hypothesis is also weakly supported. In general, the results suggest repeated colonization of Afromadagascar by microsoroid ferns via continental Asia but long distance dispersals from Malesian islands to Madagascar are plausible for some widespread species such as *M. punctatum* and *M. scolopendrium*.

The lecanopterid clade (*Lecanopteris* + *M. scandens* clade + *M. linguiforme* clade in Fig. 5) has a distribution nearly completely restricted to Malesia and the Austral regions, extending to New Zealand in the south. Only two widespread species (*L. sinuosa* and *M. linguiforme*) are also found in Indochina and India, respectively. The putative sister clade to the lecanopterid clade is distributed from Madagascar to continental Asia with the distribution range of *M. membranaceum* (*Membranaceum* in Fig. 5) extending to the northern parts of the Malesian region.

A similar separation into Malesian and continental Asian clades is also found in *Goniophlebium* (*Goniophlebium* plus *Schellolepis* in Malesia and *Metapolypodium* plus *Polypodiastrum*, plus *Polypodioides* in continental Asia; see Figs. 4 and 5). The putative frequent switch between a more Malesian (i.e., tropical) and a continental Asian (increasingly subtropical to temperate) range is further indicated by the exclusively Malesian distribution of the *Thylacopteris* clade (Fig. 5), the predominantly continental Asian distribution of the lepisoroid clade, and the more mixed patterns recovered in the microsoroid s.s. clade. Focusing on particular clades, this pattern of frequent exchanges between these areas despite clear preferences among the lineages has found further support. The majority of species within the lepisoroid clade shows a continental Asian distribution with the putative offshoot *Belvisia* (Fig. 5) as the only sublineage that includes several species occurring exclusively in Malesia (Hovenkamp, 1998; Hovenkamp and Franken, 1993). The most basal segregate of the *Belvisia* clade, *B. spicata*, has the largest distribution of this genus—ranging from Tropical Africa throughout Malesia to China and Taiwan in the north and to Moorea in the south. Only a few species of the other genera within the lepisoroid clade are found in Malesia. Most of these are restricted to northern parts of the archipelago such as Luzon, Malay Peninsula, and Sumatra (Hovenkamp, 1998). In addition, these species, such as *L. longifolius*, have extensive distributions covering both Malesia and the southern parts of continental Asia. A comparable but more complex pattern is found in the microsoroid s.s. clade. Similar to the lepisoroid clade, *Leptochilus* appear as a mainly continental Asian diversification, whereas two other recovered clades may be mainly the results of diversification in the tropics, e.g. *M. punctatum* and *M. scolopendrium* clade. However, sampling of this group may be insufficient as support for this hypothesis because several species of this lineage occur as widespread in both regions. The observed pattern may be, therefore, an artifact created by a denser coverage of Malesian taxa.

Core microsoroids successfully colonized the Pacific islands such as Hawai'i several times independently, but only one of these colonization events resulted in an unambiguous speciation event. The Hawaiian endemic *M. spectrum* is sister to *M. lucidum*, a species with a widespread occurrence on Pacific islands. A second putative speciation event requires further study. The current data suggest a separation between *M. grossum* and *M. scolopendrium* but it is not clear if this separation reflects a speciation event or intraspecific phylogeographic variation in a single species, *M. scolopendrium*.

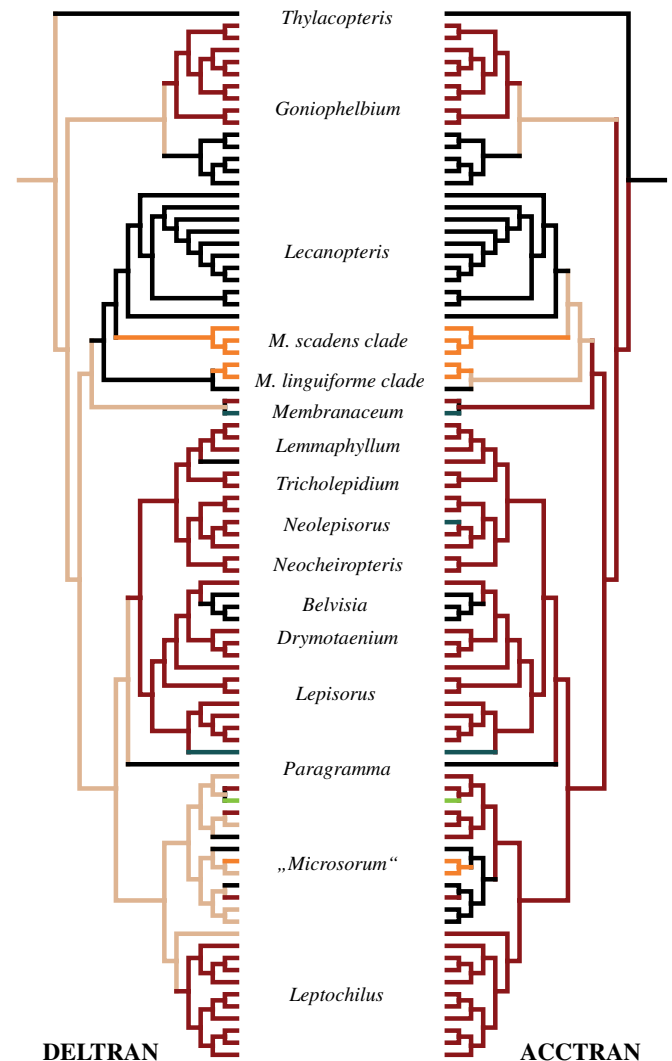


Fig. 5. Inference of biogeographic patterns by plotting the distribution of extant taxa onto a single tree obtained in the Bayesian inference of phylogeny using a maximum parsimony approach. The left tree corresponds to DELTRAN character state optimization, whereas the right tree shows ACCTRAN optimization. This approach does not assume any specific processes of biogeographical evolution. We recognized the following areas of putative endemism: (a) Afromadagascar (dark green), (b) Continental Asia including Japan, Sri Lanka, and Taiwan but excluding southern Indochina (red), (c) Malesia plus southern Indochina (black), (d) Austral region including Australia, New Zealand, New Caledonia, and New Guinea (orange), and (e) Pacific islands that are not part of the Austral region such as Hawai'i (bright green). Unresolved nodes are given in brown. In some cases, the regions overlap to some extent (e.g. Malesia and Austral region in New Guinea). Taxa occurring in these overlapping areas were initially treated as polymorphic but considered as belonging to one of the alternative regions if an unambiguous reconstruction of the related nodes were obtained. Widespread taxa occurring in more than one of these regions were treated as polymorphic in all analyses. To reduce ambiguity, we simplified the distribution of taxa that occur nearly exclusively in one region but have small range extensions in another region by ignoring these extensions.

The status of these two species is disputed. For example, Nootboom (1997) accepted a single species.

In conclusion, extensive studies of the biogeographic history of these ferns are needed to determine the area of origin and migration routes for the microsoroid ferns. The current data are compatible with previous ideas about an origin in southern China (Ching, 1978a) although this study in addition to other studies on Polypodiaceae (Janssen and Schneider, 2005; Kreier and Schneider, 2006a) have provided increasing evidence for a major role of the northern parts of Malesia and Indochina in the history of these ferns.

4.4. Evolution of ecological strategies in microsoroid ferns

The majority of species belonging to the microsoroid ferns grow either as epiphytes or mainly on rocks. The rock habit is especially common in the lepisoroid clade and the genus *Leptochilus* but also in other members of the microsoroid s.s. clade. The habit of growing on rocks is less common in the non-core microsoroids and thus the ancestral ecological specificity is likely an epiphytic habit. This scenario would indicate a tendency towards saxicolous growth in the evolution of these ferns. However, the inference is ambiguous because some species grow successfully as epiphytes or saxicolous ferns.

The lepisoroid clade is also characterized by putative adaptations to xeric conditions experienced by epiphytes growing in rather open conditions such as those on the trunks of isolated standing trees and on rock surfaces. The majority of species of this clade show entire leaves with often rather thick leathery laminae such as those found in species *Lepisorus longifolius* and *L. megasorus*. Other species such as *Belvisia spicata* also show thick waxy surfaces although other species of the same clade lack these features. For example, *Neocheiropteris superficialis* grows successfully in shady forests where it forms clonal undergrowth patches that climb up the lower parts of trees. Not all epiphytes show obvious adaptations to xeric conditions with the exception of leaf articulation, which is in turn a character present in most Polypodiaceae. Epiphytes with limited adaptation to drought stress are especially found in the genus *Goniophlebium*.

The hemiepiphytic and/or climbing habit evolved independently several times in the microsoroids. Well-documented examples are *Leptochilus axillaries*, *Microsorium pustulatum*, *M. scandens*, *Tricholepidium normale* and relatives, and some of the forms of *Neocheiropteris superficialis*. However, the separation of climbing, hemiepiphytism, and epiphytism is not always easily defined for ferns with a long creeping rhizome (Dubuisson et al., 2003). In contrast, adaptation to rheophytic habitats (as defined by van Steenis, 1981) is mainly restricted to the *Leptochilus/Microsorium pteropus* clades. These clades include two species growing frequently as rheophytes, *L. macrophyllus* sensu Nootboom and *M. pteropus*.

Finally, some microsoroid ferns show apparent adaptation to nutrient deficiency in epiphytic habitats. The ant-fern *Lecanopteris* evolved domatia, which are colonized by ants and provide additional nitrate and phosphate resources (Gay, 1993). A different strategy appears to be present in *M. linguiforme* and *M. musifolium*. Both species possess sessile to subsessile leaves with expanded bases of the lamina forming pockets for litter collection. This is similar to, but less elaborate than, the litter collectors found in drynarioids (Janssen and Schneider, 2005) and *Platyterium* (Kreier and Schneider, 2006a).

Besides morphological characters, other apparently adaptive features may be harder to document. Recent reports recovered evidence for the occurrence of physiological adaptations to water stress such as the crassulacean acid metabolism (CAM) in *Microsorium punctatum* (Holttum and Winter, 1999; Martin et al., 2005).

Other physiological adaptations may involve substrate specificity in some saxicolous species. This is expected for taxa occurring on limestone, e.g., *M. whiteheadii*, because the majority of microsoroids are found on acidic substrates.

4.5. Evolution of spore wall characters in these ferns

Differences in the exine (=exospore) and perine (=perispore) ultrastructure were described and subsequently have been employed to classify certain microsoroids. Hennipmaqn (1990) distinguished four types of exine and two types of perine of which all four exine and both perine types were found in the microsoroid lineage (Hennipman and Roos, 1983; Hennipmaqn, 1990; Van Uffelen, 1993, 1997). The *M. membranaceum* exine is currently only known from *M. membranaceum* (Van Uffelen, 1993, 1997). The *Belvisia*-type exine is known only from species belonging to the core microsoroids. It is found in all species belonging to Hennipman's Lepisoreae, e.g., *Belvisia*, *Drymotaenium*, *Lemmaphyllum*, and *Lepisorus*, but it is also found in some species of Hennipman's Microsoreae. This indicates a tendency toward modification of the spore wall during the evolution of these ferns. The taxonomic significance, however, needs to be confirmed with additional studies, addressing issues such as whether the *M. membranaceum*-type exine is apomorphic in the membranaceoid clade. The results concerning the relationships among genera of the lepisoroid clade suggest the need for further studies on spores of taxa nested within the *Neocheiropteris* clade. Van Uffelen (1993) reported a *Blechnum spicant* exine type for *N. ensata*, *N. normalis*, and *N. palmatopedata*, whereas she reported a *Belvisia* exine type for *N. ovatus* and *N. pappi*. The conflicting evidence is obvious in particular if the close relationships of *N. ensata* and *N. ovatus* are taken into account. Furthermore, the *Belvisia* type is not restricted to the lepisoroid clade but was also reported for members of the microsoroid s.s. clade, e.g., *M. papuana* and *M. scolopendria* (Hennipmaqn, 1990; Van Uffelen, 1993). The putative sister lineage to the *M. scolopendria* complex is the *M. punctatum* complex which also has spores with a *Blechnum spicant* exine type. In conclusion, the spore wall characters appear to be highly homoplastic and will require an extensive re-investigation within a robust phylogenetic framework. Van Uffelen (1993, 1997) pointed out issues concerning the interpretation of spore types, which may be resolved by comparing spores of sister taxa. The Polypodiaceae provide a unique opportunity to study the evolution of spore walls because spore walls tend to be highly conserved within most extant fern lineages (Tryon and Lugardon, 1991).

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