



# A molecular phylogeny and a revised classification of tribe Lepisoreae (Polypodiaceae) based on an analysis of four plastid DNA regions

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Phylogenetic relationships within the palaeotropical tribe Lepisoroideae (Polypodiaceae) were investigated by studying sequence variation of four plastid DNA regions: *rbcL*, *rps4* plus *rps4-trnS* IGS, *trnL* intron plus *trnL-F* IGS, *rbcL-atpB* IGS plus part of *atpB*. In total, over 4000 nucleotides were sequenced for 39 species. Seven well-supported clades were found in the analyses of the combined data set. We provide a new classification of Lepisoroideae by integrating phylogenetic results and known variation of morphological characters. The two small genera *Neocheiropteris* and *Tricholepidium* are supported as monophyletic, the genus *Paragramma* is resurrected and the genera *Lepisorus*, *Neolepisorus*, *Lemmaphyllum* and *Lepidomicrosorium* are re-circumscribed. We proposed 14 new combinations, among which *Caobangia* is treated as a synonym of *Lemmaphyllum*. A key for identifying the recognized genera is presented. © 2010 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2010, **162**, 28–38.

**ADDITIONAL KEYWORDS:** *Caobangia* – *Lemmaphyllum* – *Lepidomicrosorium* – *Lepisorus* – *Neolepisorus* – *Paragramma* – south-east Asia – taxonomic treatment.

## INTRODUCTION

The application of DNA sequence data to the analysis of phylogenetic relationships has led to major improvements in our understanding of intrafamilial relationships of the most species-rich fern family, Polypodiaceae. Schneider *et al.* (2004) resolved the broad relationships within the family by reporting evidence for four main lineages. Successive studies focused on the relationships within selected lineages of Polypodiaceae, for example, drynarioids (Janssen & Schneider, 2005), grammitids (Ranker *et al.*, 2004),

loxogrammioids (Kreier & Schneider, 2006b), microsoroids (Schneider *et al.*, 2006a; Kreier *et al.*, 2008b), platycerioids (Kreier & Schneider, 2006a) and various neotropical genera (Smith *et al.*, 2006a; Schneider *et al.*, 2006b; Kreier *et al.*, 2007, 2008a; Salino *et al.*, 2008; Otto *et al.*, 2009). Less attention has been paid to poorly understood, mainly south-east Asian lineages such as selliguioids and lepisorioids. To date, lepisorioids have been studied only in the context of deeper phylogenetic relationships such as the family Polypodiaceae (Schneider *et al.*, 2004) and the microsoroid clade (Kreier *et al.*, 2008b). In both studies, the lepisorioids were found to be monophyletic and nested within the paraphyletic microsoroids. This clade appeared to be nearly identical in its taxonomic

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breadth to tribe Lepisoreae as defined by Hennipman, Veldhoen & Kramer (1990), but with the inclusion of several species treated by Nootboom (1997, 1998) as part of the microsoroid genus *Microsorium* Link (Kreier *et al.*, 2008b).

The lepisoroid ferns are distributed throughout continental Asia, Australasia and Afromadagascar and constitute one of the most abundant and species-rich fern lineages in south-east Asia. The circumscription and classification of genera within this lineage are still poorly understood. Each author studying this group has suggested a different number of genera, although these various circumscriptions were based on the same morphological evidence (Ching, 1978a, b; Hennipman *et al.*, 1990; Shi, 1999; Shi and Zhang, 1999; Smith *et al.*, 2006b). Hennipman *et al.* (1990) accepted only four genera (*Lepisorus* (J.Sm.) Ching, *Belvisia* Mirb., *Drymotaenium* Makino, and *Lemmaphyllum* C.Presl), whereas Ching and his students (Ching, 1978c; Ching & Wu, 1980; Ching & Shing, 1983a, b) accepted several small genera, including *Lepidogrammitis* Ching, *Neolepisorus* Ching, *Tricholepidium* Ching, *Lepidomicrosorium* Ching & K.H.Shing, and *Platygyria* Ching & S.K.Wu. Ching treated *Neocheiropteris* Christ as belonging to the lepisoroids, whereas Nootboom (1997, 1998) reduced the genus to a synonym of the microsoroid genus *Microsorium*.

Recent phylogenetic studies (Schneider *et al.*, 2004, Kreier *et al.*, 2008b), however, rejected Nootboom's concept of *Microsorium* and found several species of *Microsorium*, for example, *Microsorium fortunei* (T.Moore) Ching, *M. zippelii* (Blume) Ching, *M. pappei* (Mett ex Kuhn) Tardieu and *M. superficiale* (Blume) Ching, to have close relationships with *Neolepisorus* or *Neocheiropteris*. These findings echoed Bosman's interpretation of the relationships (1991) but rejected Nootboom's treatment (1997). At the same time, these findings emphasized the need to redefine lepisoroid genera.

The taxonomic ambiguity also extends to the genus *Lemmaphyllum* and its putative segregates. Hennipman *et al.* (1990) treated the monotypic genus *Weatherbya* Copel. as a synonym of *Lemmaphyllum*. *Weatherbya accedens* (Blume) Copel. (= *Lemmaphyllum accedens* (Blume) Donk) is distinguished from other species of *Lemmaphyllum* by the distinctive shape of the fertile leaves (Copeland, 1947; Rahaman & Sen, 2000). Most recently, Smith & Zhang (2002) described the monotypic genus *Caobangia* A.R.Sm. & X.C.Zhang, which is undoubtedly closely related to species belonging to *Lemmaphyllum*, as sharing many morphological similarities, although differing in its distinctive dense indumentum on the leaves. The status of Ching's genus *Lepidogrammitis* (Ching, 1940) is another problematic issue. The segregation of *Lemmaphyllum* and other entities belonging to the

*Lemmaphyllum* lineage are based on the occurrence of coenosori and leaf dimorphisms. However, these characters are prone to convergent evolution in Polypodiaceae (Hovenkamp & Franken, 1993; Janssen & Schneider, 2005). Considering conflicting interpretations of generic limits, the application of DNA sequences in a phylogenetic context was needed to elucidate a more natural classification of this lineage.

## MATERIAL AND METHODS

### TAXONOMIC SAMPLING

A total of 34 described species, representing all currently recognized genera of lepisoroids, was included in this study (Ching, 1978a, b; Ching & Wu, 1980; Ching & Shing, 1983a, b; Hennipman *et al.*, 1990; Smith & Zhang, 2002). Five representatives belonging to the genera *Microsorium*, *Leptochilus* C.Presl and *Lecanopteris* Reinw. were included as outgroups; these were selected on the basis of previous phylogenetic studies (Kreier *et al.*, 2008b; Schneider *et al.*, 2004). Voucher information for all included samples is given in the Supporting Information (Appendix).

### DNA ISOLATION, AMPLIFICATION, AND SEQUENCING

Total genomic DNA was extracted from silica-gel-dried leaves using the modified cetyl trimethyl ammonium bromide (CTAB) procedure of Doyle & Doyle (1987). For each taxon, four plastid genome regions (*rbcL*, *rbcL-atpB*, *rps4+rps4-trnS*, *trnL-trnF*) were amplified separately with standard polymerase chain reaction (PCR) by using published primer sets: *rbcL-atpB* intergenic spacer (IGS) plus part of the *atpB* coding region (<http://www.pryerlab.net/>), the *rbcL* gene (Olmstead *et al.*, 1992; Gastony & Rollo, 1995), *rps4+rps4-trnS* IGS (Nadot *et al.*, 1995; Smith & Cranfill, 2002) and the *trnL-trnF* region including the *trnL* intron and the *trnL-trnF* IGS (Taberlet *et al.*, 1991; Treweek *et al.*, 2002). To simplify discussion, the following terms will be used: *trnL-F* for the *trnL-trnF* region, *rbcL-atpB* IGS for *rbcL-atpB* IGS + parts of *atpB*, and *rps4-trnS* for *rps4+rps4-trnS*.

GFX™ PCR DNA and the Gel Band Purification Kit (Amersham Pharmacia Biotech, Piscataway, NJ, USA) were used to prepare the PCR products for direct sequencing using the DYEnamic™ ETDye Terminator Cycle Sequencing Kit (Amersham Pharmacia Biotech) and the MegaBACE™1000 DNA Analysis Systems, following the manufacturer's protocols. Sequence data were edited and assembled in ContigExpress program from the Vector NTI Suite 6.0 (Informax Inc., North Bethesda, MD, USA). The resulting sequences were aligned using CLUSTAL X with default settings (Thompson *et al.*, 1997) and further adjusted manually in MacClade 4.0 (Maddi-

son & Maddison, 2002). Ambiguous positions were identified visually and excluded from all phylogenetic analyses. All sequences have been deposited in GenBank (see Table 1 for accession numbers).

#### PHYLOGENETIC ANALYSES

Maximum parsimony (MP) analyses of the four plastid DNA regions were conducted separately with the same settings as for the combined data matrix

**Table 1.** Information regarding taxon names, collecting localities, collector, voucher deposition and GenBank accession numbers for sequences included in the phylogenetic analyses

| Taxon   | Voucher   | <i>rbcL</i> | <i>rbcL-atpB</i> | <i>rps4-trnS</i> | <i>trnL-F</i> |
|---|---|-------------|------------------|------------------|---------------|
| <i>Leptochilus henryi</i> (Baker) Ching   | China, Sichuan; Zhang 2541 (PE)                   | EU482952    | GU126709         | EU483002         | GU126732      |
| <i>Lemmaphyllum accedens</i> (Blume) Donk ex Holttum  | Indonesia; Hovenkamp 05-298 (L)                   | EU482936    |                  | EU482986         | EU483031      |
| <i>Lemmaphyllum adnascens</i> Ching   | China, Sichuan; Zhang 4237 (PE)                   | GU126694    | GU126702         | GU126713         | GU126724      |
| = <i>Lepidogrammitis adnascens</i> (Ching) Ching  |   |             |                  |                  |               |
| <i>Lemmaphyllum carnosum</i> (Hook.) C.Presl  | Japan; Zhang 4364 (PE)                            | GU126698    | GU126706         | GU126717         | GU126728      |
| <i>Lemmaphyllum microphyllum</i> C.Presl  | China, Guangxi; X.C. Deng 31753 (PE)              | GQ256314    | GQ256154         | GQ256390         | EU483033      |
| <i>Lemmaphyllum diversum</i> (Rosenst.) Tagawa  | Taiwan; Ranker 2079 (COLO)                        | EU482937    | GU126707         | EU482987         | GU126729      |
| = <i>Lepidogrammitis diversum</i> (Rosenst.) Ching  |   |             |                  |                  |               |
| <i>Lemmaphyllum drymoglossoides</i> (Baker) Ching   | China, Guizhou; Zhang <i>s.n.</i> (PE)            |             | GQ256155         | GQ256391         | GQ256241      |
| = <i>Lepidogrammitis drymoglossoides</i> (Baker) Ching  |   |             |                  |                  |               |
| <i>Lemmaphyllum intermedium</i> (Ching) Li Wang   | China, Sichuan; Zhang 5162 (PE)                   | GU126696    | GU126704         | GU126715         | GU126726      |
| = <i>Lepidogrammitis intermedia</i> Ching   |   |             |                  |                  |               |
| <i>Lemmaphyllum pyriforme</i> Ching   | Cult. TBG; Zhang 4363 (PE)                        | GU126695    | GU126703         | GU126714         | GU126725      |
| = <i>Lepidogrammitis pyriformis</i> (Ching) Ching   |   |             |                  |                  |               |
| <i>Lemmaphyllum rostratum</i> (Bedd.) Tagawa  | China, Yunnan; Shui 80676 (PE)                    | GU126697    | GU126705         | GU126716         | GU126727      |
| = <i>Lepidogrammitis rostrata</i> (Bedd.) Ching   |   |             |                  |                  |               |
| <i>Lepidomicrosorium buergerianum</i> (Miq.) Ching & K.H.Shing ex S.X.Xu                                    | China, Yunnan; Shui 80894 (PE)                    | GQ256315    | GQ256156         | GQ256392         | GQ256242      |
| <i>Lemmaphyllum squamatum</i> (A.R.Sm. & X.C.Zhang) Li Wang = <i>Caobangia squamata</i> A.R.Sm. & X.C.Zhang | China, Guangxi; W.B. Xu 07087 (PE)                | GU126692    | GU126699         | GU126710         | GU126721      |
| <i>Lepidomicrosorium subhemionitideum</i> (H.Christ) P.S.Wang   | China, Yunnan; D.Li 80 (PE)                       |             | GU126700         | GU126711         | GU126722      |
| <i>Lepidomicrosorium subhemionitideum</i> (H.Christ) P.S.Wang   | China, Guangxi; Zhang 4111 (PE)                   | GU126693    | GU126701         | GU126712         | GU126723      |
| <i>Lepidomicrosorium superficiale</i> (Blume) Li Wang = <i>Microsorium superficiale</i> (Blume) Ching       | Taiwan; Cranfill TW030 (UC)                       | EU482971    | GU126708         | EU483022         | GU126730      |
| <i>Lepisorus clathratus</i> (C.B.Clarke) Ching  | China, Yunnan; Zhang 4533 (PE)                    | GQ256263    | GQ256094         | GQ256336         | GQ256181      |
| <i>Lepisorus contortus</i> (H.Christ) Ching   | China, Chongqing; Zhang 5204 (PE)                 | GQ256265    | GQ256096         | GQ256338         | GQ256183      |
| <i>Lepisorus excavatus</i> (Bory ex Willd.) Ching   | Tanzania; Hemp 3561 (DSM)                         | DQ642155    | GQ256101         | DQ642193         | GQ256188      |
| <i>Lepisorus kawakamii</i> (Hayata) Tagawa  | Taiwan; Ranker 2051 (COLO)                        | EU482940    | GQ256106         | DQ482990         | GQ256193      |
| <i>Lepisorus likiangensis</i> Ching et S.K.Wu   | China, Yunnan; Zhang 4488 (PE)                    | GQ256274    | GQ256109         | GQ256348         | GQ256196      |
| <i>Paragramma longifolia</i> (Blume) T.Moore = <i>Lepisorus longifolius</i> (Blume) Holttum                 | Malaysia; Jaman RJ5838 (UC)                       | DQ642157    | GQ256113         | DQ642195         | GQ256200      |
| <i>Lepisorus loriformis</i> (Wall. ex Mett) Ching   | China, Yunnan; Zhang 4440 (PE)                    | GQ256278    | GQ256114         | GQ256352         | GQ256201      |
| <i>Lepisorus macrosphaerus</i> (Baker) Ching  | China, Tibet; Zhang 4794 (PE)                     | GQ256280    | GQ256116         | GQ256354         | GQ256203      |
| <i>Lepisorus monilisorus</i> (Hayata) Tagawa  | Taiwan; H.M. Zhang 20050117 (PE)                  | GQ256283    | GQ256120         | GQ256357         | GQ256207      |
| <i>Lepisorus spicatus</i> (L.f.) Li Wang  | Tahiti; Ranker 1915 (COLO)                        | EF463244    | GQ256083         | DQ642191         | GQ256170      |
| = <i>Belvisia spicata</i> (L.f.) Mirb. ex Copel.  |   |             |                  |                  |               |
| <i>Lepisorus thunbergianus</i> (Kaulf.) Ching   | Japan; Koichi Ohora 2005042404 (TI)               | GQ256305    | GQ256145         | GQ256381         | GQ256232      |
| <i>Lepisorus miyoshianus</i> (Makino) Fraser-Jenk. & Subh.Chandra = <i>Drymoglossum miyoshianum</i> Makino  | China, Sichuan; C.C. Liu DB06104 (PE)             | GQ256255    | GQ256085         | GQ256327         | GQ256172      |
| <i>Lepisorus uchiyamae</i> (Makino) H.Ito   | Japan; Fujimoto 2005042902 (TI)                   | GQ256310    | GQ256150         | GQ256386         | GQ256237      |
| <i>Lepisorus ussuriensis</i> (Regel et Maack) Ching   | China, Heilongjiang; B.D.Liu <i>s.n.</i> (PE)     | GQ256311    | GQ256151         | GQ256387         | GQ256238      |
| <i>Microsorium punctatum</i> (L.) Copel.  | China, Hainan; Zhang 4194 (PE)                    | GQ256316    | GQ256158         | GQ256394         | GQ256244      |
| <i>Microsorium scolopendrium</i> (Burm.f.) Copel.   | Mayotte; Rakotondrainibe <i>et al.</i> , 6601 (P) | DQ642164    | GQ256159         | DQ642202         | GQ256245      |
| <i>Neochirolepis palmatopedata</i> (Baker) H.Christ   | China, Yunnan; Zhang 4482 (PE)                    | GQ256318    | GQ256160         | GQ256396         | GQ256246      |
| <i>Neolepisorus ensatus</i> (Thunb.) Ching  | Korea; Zhang 3611 (PE)                            | GQ256319    | GQ256161         | GQ256397         | GQ256247      |
| <i>Neolepisorus fortunei</i> (T.Moore) Li Wang  | China, Yunnan; Shui 80768 (PE)                    | EU482955    | GQ256157         | GQ256393         | GQ256243      |
| = <i>Microsorium fortunei</i> (T.Moore) Ching   |   |             |                  |                  |               |
| <i>Neolepisorus zippelii</i> (Blume) Li Wang  | Indonesia; Tsutsumi <i>et al.</i> , IN112 (TI)    | AB232411    |                  | AB232439         | GU126731      |
| = <i>Microsorium zippelii</i> (Blume) Ching   |   |             |                  |                  |               |
| <i>Tricholepidium maculosum</i> (H.Christ) Ching  | China, Yunnan; Shui 80596 (PE)                    | GQ256323    | GQ256165         | GQ256401         | GQ256251      |

TBG, Tuebingen Botanic Garden.

Herbaria abbreviation follows Index Herbariorum (<http://sciweb.nybg.org/science2/IndexHerbariorum.asp>).

analysis (see below). The four majority-rule consensus topologies were inspected for topological conflicts using a threshold of 90% bootstrap value or higher values (Johnson & Soltis, 1998). We observed no topological conflict among data sets and hence all four regions were combined into a single data set.

MP analyses of the combined data set were run using PAUP 4.0b10 (Swofford, 2002). All characters were weighted equally and gaps were treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1000 replicates with random sequence addition, tree bisection–reconnection (TBR) branch swapping and saving 10 trees from each random sequence addition. Bootstrap support (BS) values were calculated with 1000 simple addition sequence replicates with TBR branch swapping and 10 trees saved per replicate.

MrMTgui (<http://genedrift.org/mtgui.php>) was used to determine the best-fitting DNA substitution model using the Akaike Information Criterion (AIC). Maximum likelihood (ML) trees were generated using the program GARLI (Zwickl, 2006) with the GTR model plus GAMMA and Invariant site variable implemented. All parameters were estimated simultaneously for the tree search. GARLI analyses were performed with the default settings and repeated several times. The default setting of this software was also employed to calculate bootstrap values for ML analyses based on 100 bootstrap replicates. Bayesian inference of phylogeny (BI) was performed using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck, 2003) using a single model for all regions and separate models for coding vs. non-coding partitions. Four chains were run, each for 2 000 000 generations and were sampled every 1000 generations, starting with a random tree. The convergence of runs and estimation of burn-in were checked using Tracer ver. 1.4 (Rambaut & Drummond, 2007). Bayesian posterior probabilities (PP) were calculated as the majority consensus of all sampled trees after discarding the trees sampled within the burn-in phase. Two sets of posterior probabilities are reported. The first set is based on analyses of a data set partitioned into non-coding vs. coding regions (PP-PA), whereas the second set is based on analyses of the unpartitioned data set (PP-NP).

## RESULTS

The combined four-region data matrix consists of 4508 nucleotides, of which 501 (11.1%) are variable and parsimonious uninformative and 568 (12.6%) are variable and potentially parsimony informative. Parsimony analysis results in 36 most parsimonious trees with a tree length of 1785 steps. Consistency and retention indices (CI = 0.67, RI = 0.75) are rela-

tively high. The best model selected by MrMTgui based on AIC criterion for the combined data set is TVM+I+G. The ML tree ( $-\ln L = 1.6665.e^{-4}$ ) has a nearly identical topology with the MP tree and differs only in the bootstrap support value of some clades. The burn-in phase is determined to comprise 200 000 generations and the mean likelihood is determined as  $-\ln L = 1.718 e^{-4}$ .

All lepisoroid ferns included in the analysis form a well-supported clade with PP-PA = 1.00; PP-NP = 1.00; MP-BS = 96; ML-BS = 100 (Fig. 1). Clade I, consisting of *Paragramma* (*Lepisorus*) *longifolia* T.Moore alone, is sister to all other lepisoroid ferns, with strong support values: PP-PA = 1.00; PP-NP = 1.00; MP-BS = 93; ML-BS = 98 (Fig. 1). The remaining ingroup taxa are divided into two major sister lineages. The first main branch, clade II, comprises the genera *Lepisorus*, *Belvisia* and *Drymotaenium*. The latter two genera are found to nest within *Lepisorus*. The second main branch (A) consists of clades III–VII. The relationships among these clades are poorly resolved or at least poorly supported in each of the four analyses carried out, but each clade consistently has strong support in all phylogenetic analyses performed (Fig. 1). Clade III consists of *Neolepisorus* and two species often included in *Microsorium*; clades IV and V correspond to traditionally recognized genera *Tricholepidium* and *Neocheiropteris*; clade VI includes the contentious genus *Lepidomicrosorium* and *Microsorium superficiale*; clade VII includes four recognized genera: *Lemmaphyllum*, *Lepidogrammitis*, *Caobangia* and *Weatherbya*. *Lemmaphyllum* (*Weatherbya*) *accedens* is sister to the other species belonging to this clade. The next clade separates *Caobangia squamata* A.R.Sm. & X.C.Zhang [= *Lemmaphyllum squamatum* (A.R.Sm. & X.C.Zhang) Wang Li; see below] from the remaining species. These relationships are strongly supported in the results of Bayesian inference of phylogeny but not in MB-BS and ML-BS.

Clades III–VII form three well-supported clades using Bayesian inference of phylogeny with independent models for two partitions (coding vs. non-coding regions). Clade III is sister to a clade that includes clade VII as sister to the clade comprising clades IV–VI in the sequence IV–V–VI (Fig. 1). Alternative relationships are found in the three other analyses performed for this data set.

## DISCUSSION

### PHYLOGENY AND GENERIC DELIMITATIONS

As in most current studies, we used DNA sequence variation to reconstruct the relationships of the lepisoroid ferns. We also took morphological evidence





**Figure 1.** Results of Bayesian inference of phylogeny: majority consensus tree based on 1 000 000 generations (excluding the burn-in phase of 200 000 generations) generated using MrBayes with the data set of four plastid genome regions partitioned into coding vs. non-coding regions. The newly proposed classification for Lepisoroideae, to generic level, is shown. Generic names in parentheses are previously accepted names. The main clades discussed in the text are identified using a number from I to VII. Support values are given as posterior values (++) corresponds to  $P = 1.0$ ; + corresponds to  $P \geq 0.95$ ) above branches and bootstrap percentages (++) corresponds to 100%; + corresponds to  $\geq 95$ ) below branches. The first posterior values (above branches) were obtained with a data set partitioned into coding vs. non-coding regions, whereas the second posterior values correspond to the result of a Bayesian inference of phylogeny with a single model applied to the whole data set. The first bootstrap values (below branches) correspond to the result of the maximum parsimony bootstrap analysis (MP-BS), whereas the second bootstrap values correspond to the result of the maximum likelihood bootstrap analysis (ML-BS). ‘-’ indicates branches are not present in the given phylogenetic analyses.

into consideration. Conflicting generic delimitations are mostly not the result of conflicts between genotype and phenotype but rather the result of ambiguity concerning the information provided by the morphological variation. DNA sequence variation, i.e. genotype, is here used to segregate putative apomorphic characters from homoplastic characters. The latter have often misled systematists in their attempts to ascertain the natural classification of these ferns.

The small genus *Paragramma* is found to be sister to all other lepisoroid ferns, with strong support: MP-BS = 93, ML-BS = 98, PP<sup>1</sup> = 1.00, PP<sup>2</sup> = 1.00; this result was weakly supported by Kreier *et al.* (2008b). Our molecular phylogenetic results support the acceptance of *Paragramma* as an independent genus. This small genus was often treated as part of *Lepisorus* (Hennipman *et al.*, 1990; Hovenkamp, 1998). The separation of *Paragramma* from other lepisoroid ferns is consistent with the occurrence of several ancestral phenotypic character states, such as the basic chromosome number of  $n = 36$  (Manton, 1954) and the strongly clathrate rhizome scales. Further studies are needed to assess the relationships of the other putative member of *Paragramma*, the New Guinea endemic *P. balteiformis* (Brause) Copel. Unfortunately, we were unable to obtain material suitable for DNA sequencing of this species.

The main branch A includes several clades comprising species that were treated either as small genera, for example, *Lepidomicrosorium*, *Neocheiropteris*, *Neolepisorus* and *Tricholepidium*, or as members of the unnatural genus *Microsorium* (Hennipman *et al.*, 1990; Bosman, 1991; Nootboom, 1997, 1998). Nootboom's concept of *Microsorium* was shown to be polyphyletic in Kreier *et al.* (2008b) and our study provides further evidence for this conclusion. Our increased taxonomic coverage enables us to address the question about the segregation of the four mentioned genera. A further component of branch A is the genus *Lemmaphyllum* and its relatives. Conflicting opinions have existed concerning the generic delimitations in this group (Ching, 1978a, b; Hennipman

*et al.*, 1990; Saiki, 1984; Rahaman & Sen, 1999). Only some authors have recognized *Lemmaphyllum accedens* as the monotypic genus *Weatherbya* (Saiki, 1984; Rahaman & Sen, 2000). Similarly, the separation of *Lepidogrammitis* and *Lemmaphyllum* has not been widely accepted. Our study is the first to include the monotypic genus *Caobangia*, only recently described (Smith & Zhang, 2002).

*Neolepisorus ensatus* (Thunb.) Ching (clade III in Fig. 1), the type of *Neolepisorus*, and *Neocheiropteris palmatopedata* (Baker) Christ (clade V in Fig. 1), the type of *Neocheiropteris*, were embedded in different clades. Our analysis does not provide support for the treatment of *Neolepisorus* as a synonym of *Neocheiropteris* (Hennipman *et al.*, 1990; Bosman, 1991) and supports the acceptance of *Neolepisorus* as an independent genus (Ching & Shing, 1983a; Lin, 2000). *Microsorium fortunei* and *M. zippelii* were found to be included in clade III, corresponding to the genus *Neolepisorus*. These relationships were already suspected by Bosman (1991), who treated the two species as belonging to *Neocheiropteris s.l.* If one accepts monophyly, the transfer of these two species to *Neolepisorus* is desirable. The African species, *M. pappei*, has been suggested to be conspecific with *M. fortunei* (Kreier *et al.*, 2008b), but it is tentatively accepted here as an independent species, pending further investigation.

*Tricholepidium* was found to be distinct from *Lemmaphyllum* and *Neocheiropteris* and thus we treat this species complex as a separate genus. This genus is recognized by the hair-bearing rhizome scales (Ching, 1978c), but this character occurs also in some species of *Lepisorus* and *Neocheiropteris* among lepisoroid ferns and has evolved several times within Polypodiaceae. *Tricholepidium* shares some characteristics with *Microsorium*, such as more than one row of sori (sometimes one irregular row), and some with *Lepisorus*, such as peltate paraphyses. Nootboom (1997, 1998) treated this genus as a single species, *Microsorium normale* Ching, with marked variability. Further studies are needed to confirm the species number of *Tricholepidium*.

Clades V and VI form well-supported sister groups. The distinction of the lamina morphology, entire vs. palmate, and the different habit, climbing vs. creeping, support recognition of two independent genera, *Lepidomicrosorium* and *Neocheiropteris*, although the phylogenetic relationships would allow the treatment of both clades as a single genus *Neocheiropteris* with *Lepidomicrosorium* reduced to a synonym. Nootboom (1997, 1998) treated species belonging to Ching's genus *Lepidomicrosorium* as synonyms of *Microsorium superficiale*. Our results suggest a close relationship among species of *Lepidomicrosorium* and *Microsorium superficiale*. Our present sampling is insufficient to resolve questions concerning the number of species belonging to *Lepidomicrosorium*. Nootboom (1997, 1998) recognized a single species, *Microsorium superficiale*, whereas Chinese pteridologists recognize up to 18 species (Lin, 2000).

Clade VII comprises four previously recognized genera: *Lemmaphyllum*, *Lepidogrammitis*, *Weatherbya* and *Caobangia*. The latter two monotypic genera form the first two segregated taxa within this clade, whereas *Lepidogrammitis* and *Lemmaphyllum* are intercalated, forming a poorly supported clade (MP-BS = 54) that collapses in ML analysis as a result of a zero-length branch. Our new data provide strong support for synonymizing *Lepidogrammitis* under *Lemmaphyllum*, a view held by Hennipman *et al.* (1990). *Lepidogrammitis* was a genus based on having separate sori, contrasting with the coenosori in species of *Lemmaphyllum* (Pichi Sermolli, 1977; Rahaman & Sen, 1999; Lin, 2000), but this character is a poor indication of relationships in Polypodiaceae (Hovenkamp & Franken, 1993). For the two monotypic genera, *Weatherbya* and *Caobangia*, there are two alternative taxonomic solutions: either to treat these two genera as synonyms of *Lemmaphyllum*, or to recognize them as two independent genera. *Weatherbya*, distributed in Malaysia to Polynesia, was merged with *Lemmaphyllum* by some authors (Holttum, 1954; Hennipman *et al.*, 1990), but others (Rahaman & Sen, 2000) argued that it should be maintained as a genus, distinct from *Lemmaphyllum* by the evident midvein on the adaxial surface and fertile leaves that are abruptly constricted towards the distal end. The monotypic genus *Caobangia* (Smith & Zhang, 2002), the phylogenetic position of which is resolved for the first time in our study, is restricted to limestone ridges in northern Vietnam and southern China (Xu *et al.*, 2008). The genus shows some different characters from *Lemmaphyllum*: persistent scales on both surfaces of the lamina and lack of paraphyses. However, considering the high support values of clade VII and the low support values for its subclades, we are inclined to accept the four traditionally defined genera as a single genus, *Lemmaphyllum*.

The phylogenetics of *Lepisorus*–*Belvisia*–*Drymotaenium* clade was addressed in an independent study comprising a much denser taxonomic sampling of the most species-rich lineage of leporoids (Wang *et al.*, 2009). The present analysis focuses on the phylogenetic relationships of the other clades of leporoid ferns.

## CHECKLIST

1. *Paragramma* T.Moore, Index Filic. xxxii. 1857. – TYPE: *P. longifolius* (Blume) T.Moore [= *Lepisorus longifolius* (Blume) Holttum = *Grammitis longifolius* Blume] *Species number*: 2, but relationships of *P. balteiformis* need confirmation. Its inclusion in *Paragramma* is based on arguments by Copeland (1947). *Distribution*: Tropical Asia, throughout Malesia, north to southern Thailand.  
*Paragramma balteiformis* (Brause) Copel.  
*Paragramma longifolia* (Blume) T.Moore
2. *Neocheiropteris* Christ, Bull. Soc. Bot. France 62: Mem. 1: 21. 1905. – TYPE: *N. palmatopedata* (Baker) Christ  
[= *Polypodium palmatopedatum* Baker] *Species number*: 2.  
*Distribution*: Southern China: Yunnan, Guizhou and Sichuan Provinces.  
*Neocheiropteris palmatopedata* (Baker) Christ  
*Neocheiropteris triglossa* (Baker) Ching
3. *Tricholepidium* Ching, Acta Phytotax. Geobot. 28: 41. 1978 – TYPE: *T. normale* (D.Don) Ching  
[= *Polypodium normale* D.Don] *Species number*: Taxonomy unclear, seven names are listed here provisionally.  
*Distribution*: China (Xizang, Yunnan and Guangxi), Nepal, Northern India, Sikkim, Bhutan and Northern Vietnam.  
*Tricholepidium angustifolium* Ching  
*Tricholepidium chapaense* (C.Chr. & Tardieu) Ching  
*Tricholepidium maculosum* (Christ) Ching  
*Tricholepidium normale* (D.Don) Ching  
*Tricholepidium pteropodium* Ching  
*Tricholepidium tibeticum* Ching & S.K.Wu  
*Tricholepidium venosum* Ching
4. *Lepisorus* (J.Sm.) Ching, Bull. Fan Mem. Institute. Biol. 4: 47. 1933. – TYPE: *L. nudus* (Hook.) Ching  
[= *Pleopeltis nuda* Hook.] *Species number*: c. 60–70. Species to be addressed in an independent study (Wang *et al.*, 2009).

## KEY TO THE GENERA OF TRIBE LEPISOREAE

The characters of the tribe as defined by Hennipman *et al.* (1990) include a usually entire lamina, clathrate stem scales and spores with a *Belvisia*-type exospore and thin perispore. However, the ultrastructure of the spores was studied only for species belonging to *Lepisorus* (van Uffelen, 1997).

- 1a. Rhizomes short-creeping, leaves approximate; lamina strap-shaped, 75–150 cm long; sori oblong or linear-oblong, deeply immersed; paraphyses ranging from simple hairs to dark, circular and peltate, or irregularly shaped, mostly basifixed scales.....*Paragramma*
- 1b. Rhizomes long- or short-creeping, leaves distant or approximate; lamina various in shape, rarely up to 70 cm long; sori discrete, round, oblong or confluent into coenosori; with uniform paraphyses peltate, circular or irregularly shaped, rarely without peltate paraphyses.....2
- 2a. Blades pedatifid or trifid.....*Neochheiropteris*
- 2b. Blades simple, sometimes irregularly and pinnatifidly lobed.....3
- 3a. Plants climbing; rhizome scales bearing a tuft of long, stiff, needle-like, reddish brown, hairs near the centre of a scale.....*Tricholepidium*
- 3b. Plants epiphytic, terrestrial or climbing; rhizome scales glabrous, occasionally bearing a tuft of short, soft, brown hairs at point of attachment.....4
- 4a. Sori arranged into two straight lines, each on one side of midrib, discrete or coenosoral.....5
- 4b. Sori scattered or arranged into more or less straight lines, never merging into coenosori.....6
- 5a. Plants epiphytic or terrestrial; rhizomes short- to long-creeping; sori discrete, sometimes coenosoral; always with paraphyses, these clathrate, peltate, of thin to thick texture and entire to irregular margin.....*Lepisorus*
- 5b. Plants climbing; rhizomes long and slender; sori discrete or coenosoral, with or rarely without paraphyses, these clathrate, peltate, of thick texture and irregular margin.....*Lemmaphyllum*
- 6a. Plants terrestrial; sori arranged into (1–)2–4 lines on each side of midrib.....*Neolepisorus*
- 6b. Plants climbing; sori scattered over laminae.....*Lepidomicrosorium*

*Distribution:* Tropical Africa and Asia, but most diversified in subtropical Asia, one species extending to Hawaii.

*Note:* Our results confirm previous reports (Kreier *et al.*, 2008b; Wang *et al.*, 2009) that *Belvisia* and *Drymotaenium* are nested within *Lepisorus*. These species are now treated as belonging to *Lepisorus*. *Drymotaenium miyoshianum* Makino has already been transferred to *Lepisorus*, but new combinations are proposed here for species previously treated as *Belvisia* (Hovenkamp & Franken, 1993). Given the principle of priority, the genus name *Belvisia* should be used with two synonyms *Lepisorus* and *Drymotaenium*, but considering the evidently large size of *Lepisorus* and the conservation of stability of nomenclature, it is better to keep the genus name *Lepisorus* with *Belvisia* and *Drymotaenium* merged into it.

***Lepisorus abbreviatus*** (Fée) Li Wang, **comb. nov.**  
 = *Belvisia abbreviata* (Fée) Hovenkamp & Franken, Blumea 37: 519. 1993.

= *Drymoglossum abbreviatum* Fée, Mem. Foug. 5: 26. 1852.

***Lepisorus annamensis*** (C.Ch.) Li Wang, **comb. nov.**

= *Belvisia annamensis* (C.Ch.) S.H.Fu, Gen. Pterid. China: 159. 1954

= *Hymenolepis annamensis* C.Ch., Dansk. Botanisk Arkiv 6: 68. 1929.

***Lepisorus henryi*** (Hieron. ex C.Ch.) Li Wang, **comb. nov.**

= *Belvisia henryi* (Hieron. ex C.Ch.) S.H.Fu, Gen. Pterid. China: 159. 1954.

= *Hymenolepis henryi* Hieron. ex C.Ch., Dansk Bot. Ark. 6: 67/ 1929.

*Lepisorus miyoshianus* (Makino) Fraser-Jenk. & Subh.Chandra

***Lepisorus mucronatus*** (Fée) Li Wang, **comb. nov.**

= *Belvisia mucronata* (Fée) Copel., Gen. Fil. 192. 1947.

= *Hymenolepis mucronata* Fée, Mem. Fam. Foug. 5: 82. 1852.

***Lepisorus novoguineensis*** (Rosenst.) Li Wang, **comb. nov.**

= *Belvisia novoguineensis* (Rosenst.) Copel., Gen. Fil. 192. 1947.

= *Paltonium novoguineense* Rosenst., Nova Guinea 8: 729. 1912.

***Lepisorus platyrhynchos*** (Kunze) Li Wang, **comb. nov.**

= *Belvisia platyrhynchos* (Kunze) Copel., Gen. Fil. 192. 1947.

= *Hymenolepis platyrhynchos* Kunze, Farnkr. 1: 111. 1842.

***Lepisorus spicatus*** (L.f.) Li Wang, **comb. nov.**

= *Belvisia spicata* (L.f.) Mirbel ex Copel., Gen. Fil. 192. 1947.

= *Acrostichum spicatum* L.f., Suppl. Plant. 444. 1781.



***Lepisorus validinervis* (Kunze) Li Wang, comb. nov.**

≡ *Belvisia validinervis* (Kunze) Copel., Gen. Fil. 192. 1947.

≡ *Hymenolepis validinervis* Kunze, Bot. Zeit. (Berlin) 6: 122. 1848.

**5. *Lemmaphyllum* C.Presl., Epim. Bot. 157.**

1849. – TYPE: *L. spathulatum* C.Presl

*Species number*: c. 8–10.

*Distribution*: Diversity centre in southern China, with a few species also occurring in Korea, Japan, Thailand, Myanmar, India and Malesia.

*Lemmaphyllum accedens* (Blume) Donk

*Lemmaphyllum adnascens* Ching

*Lemmaphyllum carnosum* (Wall. ex Hook.) C.Presl

*Lemmaphyllum diversum* (Rosenst.) Tagawa

*Lemmaphyllum drymoglossoides* (Baker) Ching

***Lemmaphyllum intermedium* (Ching) Li Wang, comb. nov.**

≡ *Lepidogrammitis intermedia* Ching, Fl. Tsinling 2: 231. 1974.

*Lemmaphyllum microphyllum* C.Presl

*Lemmaphyllum pyriforme* (Ching) Ching

*Lemmaphyllum rostratum* (Bedd.) Tagawa

***Lemmaphyllum squamatum* (A.R.Sm. & X.C.Zhang) Li Wang, comb. nov.**

≡ *Caobangia squamata* A.R.Sm. & X.C.Zhang, Novon 12: 549. 2002.

**6. *Neolepisorus* Ching, Bull. Fan Mem. Institute. Biol. Bot.**

10: 11. 1940. – TYPE: *N. ensatus* (Thunb.) Ching

[≡ *Polypodium ensatum* Thunb.]

*Species number*: 4–14, taxonomy unclear.

*Distribution*: Subtropical East Asia plus one species in Afromadagascar.

*Neolepisorus dengii* Ching & P.S.Wang

*Neolepisorus emeiensis* Ching & K.H.Shing

*Neolepisorus ensatus* (Thunb.) Ching

***Neolepisorus fortunei* (T.Moore) Li Wang, comb. nov.**

≡ *Microsorium fortunei* (T.Moore) Ching, Bull. Fan Mem. Institute. Biol. Bot. 4: 304–304. 1933.

≡ *Drynaria fortunei* T.Moore, Gard. Chron. 1855: 708–709, f. s.n. 1855.

*Neolepisorus lancifolius* Ching & K.H.Shing

*Neolepisorus minor* W.M.Zhu

*Neolepisorus ovatus* (C.Presl) Ching

***Neolepisorus pappei* (Mett. ex Kuhn) Li Wang, comb. nov.**

≡ *Polypodium pappei* Mett. ex Kuhn, Filic. Afr. 150. 1868.

*Neolepisorus sinensis* Ching

*Neolepisorus tenuipes* Ching & K.H.Shing

*Neolepisorus truncatus* Ching & P.S.Wang

*Neolepisorus tsaii* Ching & K.H.Shing

***Neolepisorus zippelii* (Blume) Li Wang, comb. nov.**

≡ *Microsorium zippelii* (Blume) Ching, Bull. Fan. Mem. Institute. Biol. 308. 1933.

≡ *Polypodium zippelii* Blume, Fl. Javae 2: 172. 1847.

**7. *Lepidomicrosorium* Ching & K.H.Shing, Bot. Res.**

1: 1–14. pl. 1–5. 1983. – TYPE: *L. buergerianum*

(Miq.) Ching & K.H.Shing

[≡ *Polypodium buergerianum* Miq.]

*Species number*: 2–5, taxonomy unclear.

*Distribution*: The constituent species are mainly distributed in China, with some species ranging to Japan and tropical Asia.

*Lepidomicrosorium buergerianum* (Miq.) Ching & K.H.Shing

*Lepidomicrosorium hymenodes* (Kunze) L.Shi & X.C.Zhang

*Lepidomicrosorium subhemionitideum* (Christ) P.S.Wang

***Lepidomicrosorium superficiale* (Blume) Li Wang, comb. nov.**

≡ *Microsorium superficiale* (Blume) Ching, Bull. Fan Mem. Institute. Biol. 4: 299. 1933.

≡ *Polypodium superficiale* Blume Fl. Javae 136, 1828 [1830].

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