

# Origin and diversification of African ferns with special emphasis on Polypodiaceae

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**Abstract.** Although Africa harbors low species diversity compared to the neotropics or South East Asia, the African fern flora is of interest because of its specific composition and geographic location between the neotropics and Asia. We address the question of how the evolution of the African fern flora may have been enriched by repeated input from the neotropics and Asia. For the purpose of this paper we consider three major biogeographic regions: the neotropics, Africa and Madagascar, and Asia including Malesia and Australasia. We interpret distribution data for six clades of Polypodiaceae in a molecular phylogenetic framework. We conclude that African fern taxa shared with or closely related to ones in the neotropics or Asia have been brought about by ancient and recent dispersal events with or without subsequent speciation. The African fern flora is interpreted as being composed of endemic, neotropical, and Asian elements and as being situated in a zone of overlap of typical neotropical and Asian fern floras.

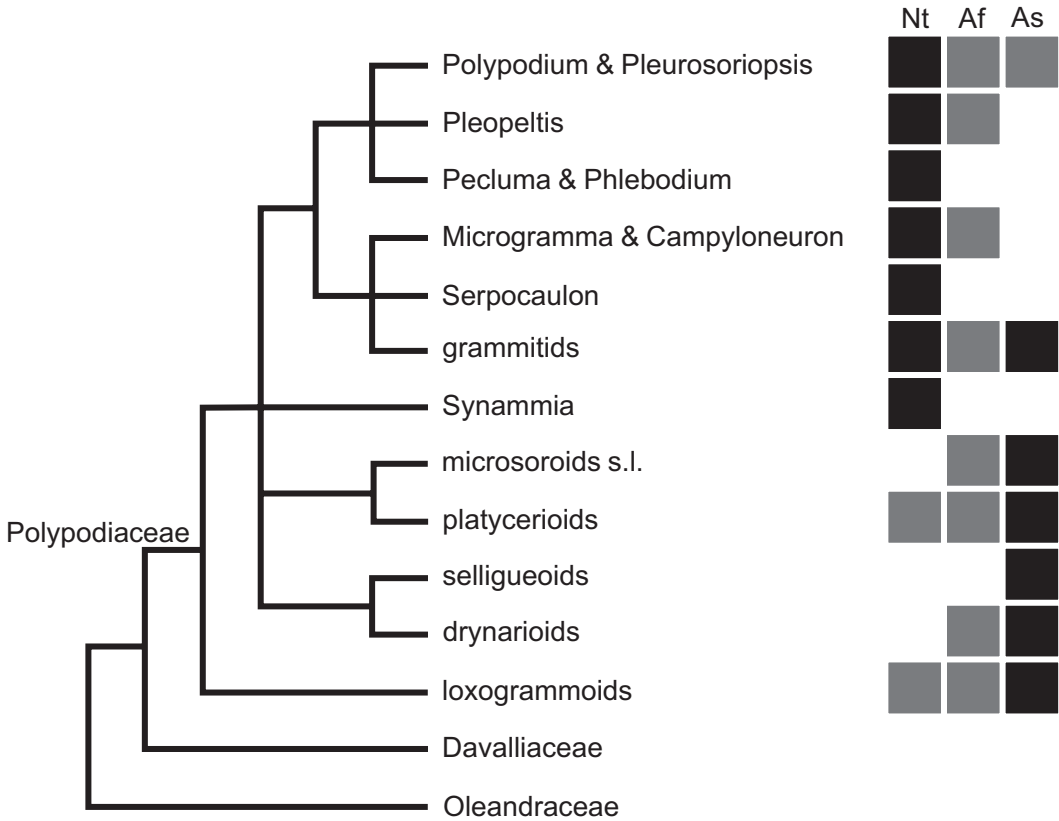
**Key Words:** Africa, dispersal, ferns, historical biogeography, polygrammoids, vicariance.

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Compared to South America or South East Asia, the fern flora of continental Africa is considerably less species rich, whereas Madagascar and the islands of the Indian Ocean represent hotspots of fern diversity (e.g., Christensen, 1912; Tardieu-Blot, 1964a, 1964b; Badré & Cadet, 1978; Lorence, 1978; Kubitzki, 1990; Johns, 1991; Roux, 2001; Rakotondrainibe, 2003). Understanding historical biogeographical dynamics at a global scale is a prerequisite to the comprehension of the evolution of regional diversity. Several studies have dealt with intercontinental floristic and faunistic relationships in a phylogenetic context (e.g., Renner et al., 2001; Davis et al., 2002, 2004; Zhang & Renner, 2003; Plana et al., 2004; Renner, 2004; Sanmartín & Ronquist, 2004; Sparks, 2004; Sparks &

Smith, 2004; Sytsma et al., 2004; Yuan et al., 2005). Although valuable accounts on the relationships of African ferns exist (Smith, 1972; Moran & Smith, 2001; Parris, 2001), these accounts did not use a molecular phylogenetic framework and were, except Parris (2001), focused on neotropical affinities, not Asian ones.

Polypodiaceae sensu Smith et al. (2006) are a monophyletic lineage of leptosporangiate ferns comprising the Grammitidaceae and Polypodiaceae sensu Kubitzki (1990), for which the temporary name “polygrammoid ferns” was employed until recently (Fig. 1; Schneider et al., 2004c). The paleotropical davallioid ferns include only few representatives in Africa and are sister to the Polypodiaceae, suggesting a possible origin



**FIG. 1.** Overview of Polypodiaceae (polygrammoid ferns). Phylogenetic tree modified from Schneider et al. (2006b, 2004c). Diversity centers are indicated by black squares, whereas secondary distributions (i.e., of a minority of clade members) are indicated by grey squares. Clades shown are either composed of representatives that are mainly or exclusively neotropical or paleotropical in distribution. There are no predominantly African clades on the phylogenetic level illustrated in this figure. **Nt** neotropics; **Af** Africa, Madagascar and adjacent islands; **As** Asia, SE Asia and Australia.

of that lineage in the Asian region. All clades of the Polypodiaceae are predominantly to exclusively neotropical or paleotropical except for the grammitid clade, which has a more or less even pantropical distribution (Fig. 1). It is noteworthy that although many clades of Polypodiaceae comprise African members, there are no predominantly African clades among major lineages. A large derived clade including grammitids and diverse polypodioid subclades is almost entirely neotropical in composition, but also contains the northern temperate species of *Polypodium*, paleotropical grammitids, and some African taxa.

Polypodiaceae are a pantropical fern fam-

ily, adapted to diverse ecological conditions (dry or wet, epiphytic or terrestrial habitats), and show a diverse range of global distribution patterns. This, together with a high sampling density, makes the family particularly suited to study the biogeographical relationships of the African fern flora in a phylogenetic framework. In Africa, Madagascar, and nearby oceanic islands, Polypodiaceae are represented by approximately 77 species (Christensen, 1912; Tardieu-Blot, 1964a, 1964b; Lorence, 1978; Kubitzki, 1990; Johns, 1991; Roux, 2001; Rakotonrainibe, 2003). The most species-rich lineages of Polypodiaceae are the taxonomically difficult microsorioid and gram-

mitid clades (Schneider & al., 2004c). Ranker et al. (2004) recovered neotropical grammitid taxa in a basal position within the grammitid clade and found evidence for several dispersal events to the paleotropics. They also showed that palaeotropical grammitids formed a derived subclade. Grammitids, however, are currently taxonomically and phylogenetically insufficiently understood to hypothesize about the historical biogeography of the clade. The grammitid lineage, although a major component of Polypodiaceae, is consequently not analyzed in the present paper. It includes about 35 African species, the majority of which show affinities to the derived Old World clade (Ranker et al., 2004), whereas some are related to neotropical taxa. Microsoroid ferns, with approximately 15 species, are the second most species rich representatives of the polygrammoid clade in the African region. It is important to point out, that all genera of Polypodiaceae present in Africa comprise taxa with close relationships to either the neotropics or tropical Asia, except for a taxonomically doubtful disjunct South African occurrence of the northern temperate *Polypodium* cf. *vulgare* L.

By its geographic position, the African – Madagascan region is likely to be situated in a contact zone between the neotropics and the Asian – Australian region. Accordingly, apart from endemics, its fern flora is characterized by the presence of Old and New World species that are either shared with or have close relatives in the neotropics or Asia. For the present paper, we will limit discussion of distribution data to three biogeographical mega-regions: (1) the neotropics, (2) Africa and Madagascar including adjacent islands (herein referred to as Africa), and (3) Asia, Malesia, and Australia (herein referred to as Asia).

It has been argued that fern spores disperse over long distances shaping distribution patterns and triggering fern speciation (Smith, 1972; Tryon, 1986; Brownsey, 2001). However, vicariance occurs in ferns and must be regarded as an *a priori* equally likely process (Barrington, 1993; Kato, 1993; Wolf et al., 2001). Extinction as a result of aridification during the later Cenozoic has considerably influenced the observed species composition in

Africa (Aldasoro et al., 2004) but the poor fossil record of epiphytic ferns in Africa and elsewhere prevents a sufficient study of patterns of extinction in Polypodiaceae. We herein discuss the phylogenetic and biogeographical affinities of the African representatives in selected predominantly neotropical or predominantly Asian lineages of Polypodiaceae and interpret the underlying processes with respect to space and time. We do not present dated analyses, but base our inferences of biogeographical processes on well supported results of previous studies indicating an age of Polypodiaceae of about 40 Ma (Schneider et al., 2004b). Divergence time estimates presented by Schneider et al. (2004b) are congruent with the fossil record of Polypodiaceae with the oldest fossils dating back to the Eocene (van Uffelen, 1991; Collinson, 2001). These age estimates do not support hypotheses that explain the current distribution patterns as a result of the Gondwana breakup, which began in the mid Jurassic (~ 167 Ma).

## Materials and Methods

### DATA SETS

Data sets were compiled for the drynarioid, loxogrammoid, *Microgramma*, microsoroid, platycerioid, and *Pleopeltis* lineages of Polypodiaceae. The matrices included four chloroplast markers: *rbcL* and *rps4* (two coding genes) as well as *rps4-trnS* IGS and *trnL-trnF* IGS (two non-coding regions). Sequences were obtained from GenBank or generated for this study (Appendix). The data sets are in large part based on recently published studies (Schneider et al., 2004a, 2006a, 2006b; Janssen & Schneider, 2005; Kreier & Schneider, 2006a, 2006b). Taxon sampling density (Table I) covers at least 50 % of the known species in these lineages, except for the species-rich microsoroid and the poorly collected loxogrammoid lineages. Distribution data for all taxa have been gathered from various floristic treatments (Hennipman & Roos, 1982; Roos, 1985; Hovenkamp 1986; Zink, 1993; Nooteboom, 1997; Roux, 2001; Moran & Smith, 2001; Rakotonrainibe, 2003) and from the Missouri Botanical Garden's Tropicos database (<http://mobot.mobot.org/W3T/Search/vast.html>).

TABLE I  
OVERVIEW OF THE DATASETS EMPLOYED IN THIS STUDY

Lineage	Outgroup <sup>a</sup>	# taxa (estimated) <sup>b</sup>	# taxa in ingroup <sup>c</sup>
drynarioids	<i>Arthromeris</i> , <i>Selliguea</i>	~32	23 (24)
loxogrammoids	<i>Dictymia</i>	~36	6 (7)
<i>Microgramma</i>	<i>Niphidium</i>	~20	9 (12)
microsoroids s.l.	<i>Thylacopteris</i>	~150	34 (36)
platycerioids	<i>Thylacopteris</i>	~66	37 (37)
<i>Pleopeltis</i>	<i>Phlebodium</i>	~60	18 (21)

<sup>a</sup> Outgroup assignment is based on current understanding of the phylogenetic relationships of Polypodiaceae (Schneider et al., 2004a, 2004c).

<sup>b</sup> Taxon numbers have been estimated based on Mickel and Smith (2004), Kubitzki (1990), and Roos (1985). *Pleopeltis* as recognized here corresponds to the *Pleopeltis* clade sensu Schneider et al. (2004c).

<sup>c</sup> Taxon numbers for the ingroup of each data set are given excluding and (in parentheses) including multiple accessions for a single species.

## DNA SEQUENCING

DNA was extracted from silica-dried leaf material or herbarium specimens using the Invisorb<sup>®</sup> Plant Spin Mini Kit (Invitex). PCR reactions were carried out according to standard protocols using the same primers for the *rps4* + *rps4-trnS*, *rbcL*, and *trnL-trnF* regions as in Janssen and Schneider (2005) and Kreier and Schneider (2006a). Purified PCR products were sequenced and analyzed on an ABI capillary sequencer 3100 (Applied Biosystems) according to established protocols.

## DATA ANALYSIS

Alignments were produced manually in MacClade (Maddison & Maddison, 2000). Ambiguously aligned regions were excluded from all analyses. Phylogenetic analyses were performed with PAUP\* 4.0b10 (Swofford, 2000). Maximum parsimony analyses were carried out as heuristic searches with 1000 random additions and TBR branch swapping. Results were summarized as strict consensus trees if more than one tree was found. Branch support was estimated by nonparametric bootstrap (Felsenstein, 1985) calculated for 10,000 replicates, each performed as a heuristic search with 10 random additions and TBR branch swapping. Maximum likelihood (ML) analyses were conducted for each dataset applying settings corresponding to models suggested by the hierarchical likelihood ratio test (hLRT) cri-

terion implemented in Modeltest 3.7 (Posada & Crandall, 1998). The Akaike information criterion (AIC) favored the same models in most cases. Deviating models were closely related and their implementation in PAUP\* yielded identical topologies. Naming of models used in the results section is based on Posada and Crandall (1998) and the documentation to Modeltest 3.7. Searches were carried out in the heuristic mode, obtaining starting trees by neighbor joining and performing TBR branch swapping. Search parameters are given in the results section for each data set. Nonparametric bootstrap trees were calculated for 1000 or 500 replicates according to dataset size and performed as heuristic searches obtaining starting trees by neighbor joining and performing TBR branch swapping. Rearrangements were limited to 100 per replicate in ML bootstrap analyses of the larger datasets (>20 taxa).

Biogeographical patterns in the drynarioid, loxogrammoid, and platycerioid lineages have been analyzed using DIVA 1.2 (Ronquist, 1997) reducing distribution data to the three mega-regions the present paper focuses on.

## Results

### DRYNARIOID LINEAGE

Based on the hierarchical likelihood ratio test (hLRT) criterion as implemented in Modeltest 3.7 we determined as the best fit model for the drynarioid data set the

K81uf+I+ $\Gamma$  model with the following parameter values: A-C=G-T=1.0000, A-G=C-T=3.8279, A-T=C-G=0.5304, I=0.4709,  $\Gamma$ =1.0220. After maximum likelihood (ML) analysis, we obtained a tree with a log likelihood (ln L)=-6717.82 (Fig. 2).

Maximum parsimony (MP) analysis yielded 72 most parsimonious trees, 504 steps long, with the following tree statistics: CI=0.8234, HI=0.1766, RI=0.8708, RC=0.7171. The strict consensus tree is topologically identical to the ML-tree, with the exception that the branch subtending the basal node of the (*Drynaria descensa* - *D. volkensii*) clade in the ML-tree is collapsed creating a polytomy in the MP-consensus.

The drynarioid lineage has its diversity center in tropical SE-Asia and Malesia. Two taxa are endemic to the African continent and one (*D. willdenowii*) to Madagascar. The African-Madagascan taxa form a monophyletic group separated from the other clade members by a deep split. Biogeographic analysis with DIVA 1.2 (Ronquist, 1997) was unable to unambiguously assign ancestral distributions to the root node of the lineage. The group originated either in Africa or Asia, but the sister clade of drynarioids is restricted to Asia.

#### LOXOGRAMMOID LINEAGE

The hLRT criterion as implemented in Modeltest 3.7 indicated the TIM+ $\Gamma$  model as the best fit for the loxogrammoid data set with the following parameter values: A-C=G-T=1.0000, A-G=3.1365, A-T=C-G=0.2187, C-T=4.4151,  $\Gamma$ =0.3197. One tree with a log likelihood (ln L)=-5683.78 was recovered by ML analysis (Fig. 3).

Phylogenetic analysis under the MP criterion yielded a single tree, 451 steps long (CI=0.8869, HI=0.1131, RI=0.8381, RC=0.7433), topologically identical to the ML-tree.

Most loxogrammoid ferns are endemic to Asia. The African representatives included in this study together with the only neotropical species (*Loxogramme mexicana*) form a sister clade to the Asian loxogrammoids. Reconstruction of an ancestral distribution for the root node of the lineage with DIVA 1.2 (Ronquist, 1997) was unable to distinguish between an origin in Africa or Asia.

#### MICROGRAMMA LINEAGE

The K81uf+ $\Gamma$  model was estimated using the hLRT criterion as implemented in Modeltest 3.7 as a best fit for the *Microgramma* data set with the following parameter values: A-C=G-T=1.0000, A-G=C-T=3.3363, A-T=G-C=0.4607,  $\Gamma$ =0.2191. ML analysis recovered a tree with a log likelihood (ln L)=-5544.81 (Fig. 4).

MP analysis yielded a single tree, 377 steps long (CI=0.8568, HI=0.1432, RI=0.7000, RC=0.5997), topologically deviating from the ML-tree in several instances: *M. megalophylla* is sister to both accessions of *M. mauritiana* (51% bootstrap support) and both accessions of *M. vacciniifolia* are sister to the clade thus formed (58% bootstrap support). *Microgramma percussa* is sister to all other taxa with 65% bootstrap support in the MP-tree.

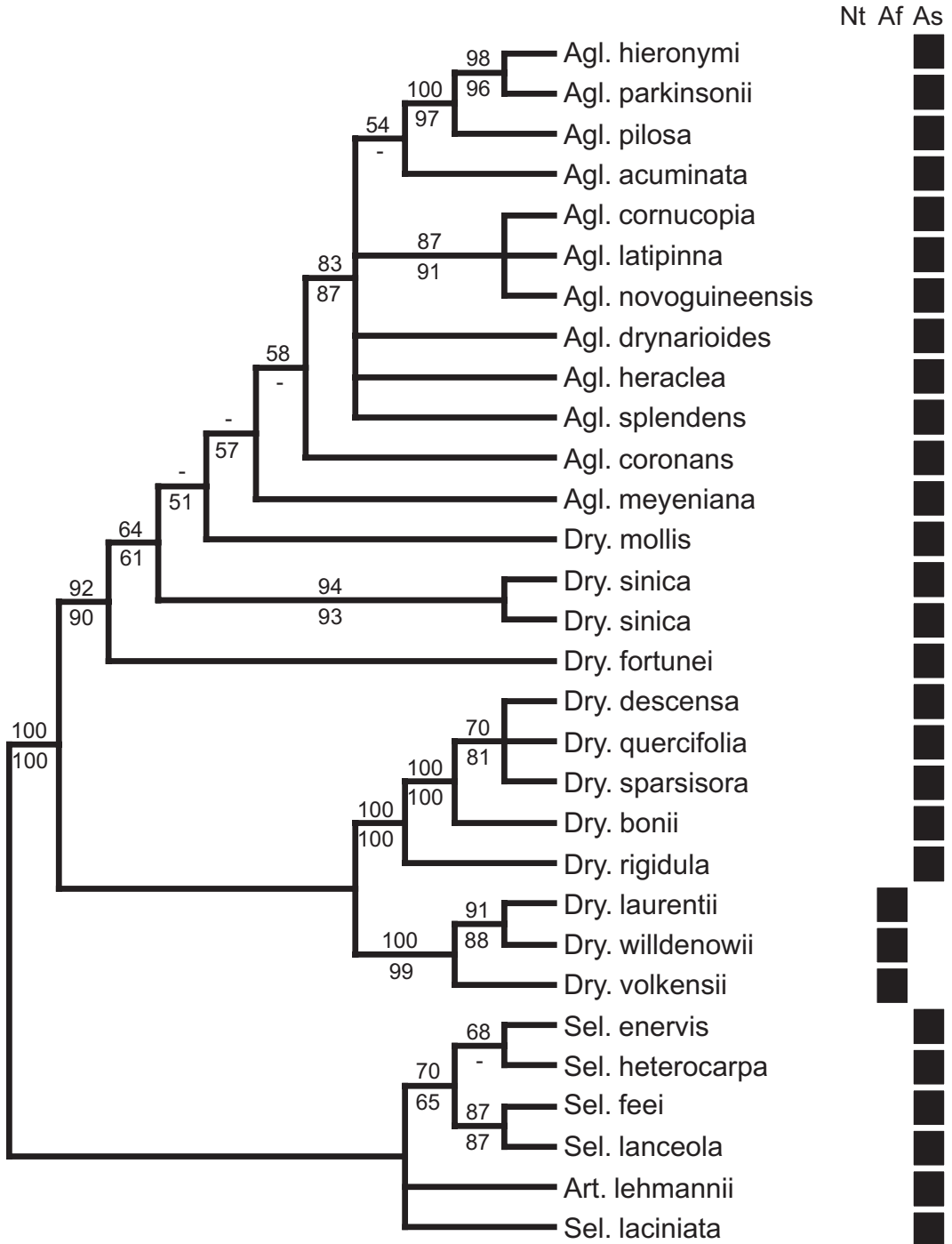
*Microgramma* is an essentially neotropical lineage with one or two African species nested among the neotropical taxa. The African accessions were not sister to the neotropical *M. lycopodioides*. Analysis of distribution data with DIVA 1.2 suggest a neotropical origin of this lineage.

#### MICROSOROID LINEAGE

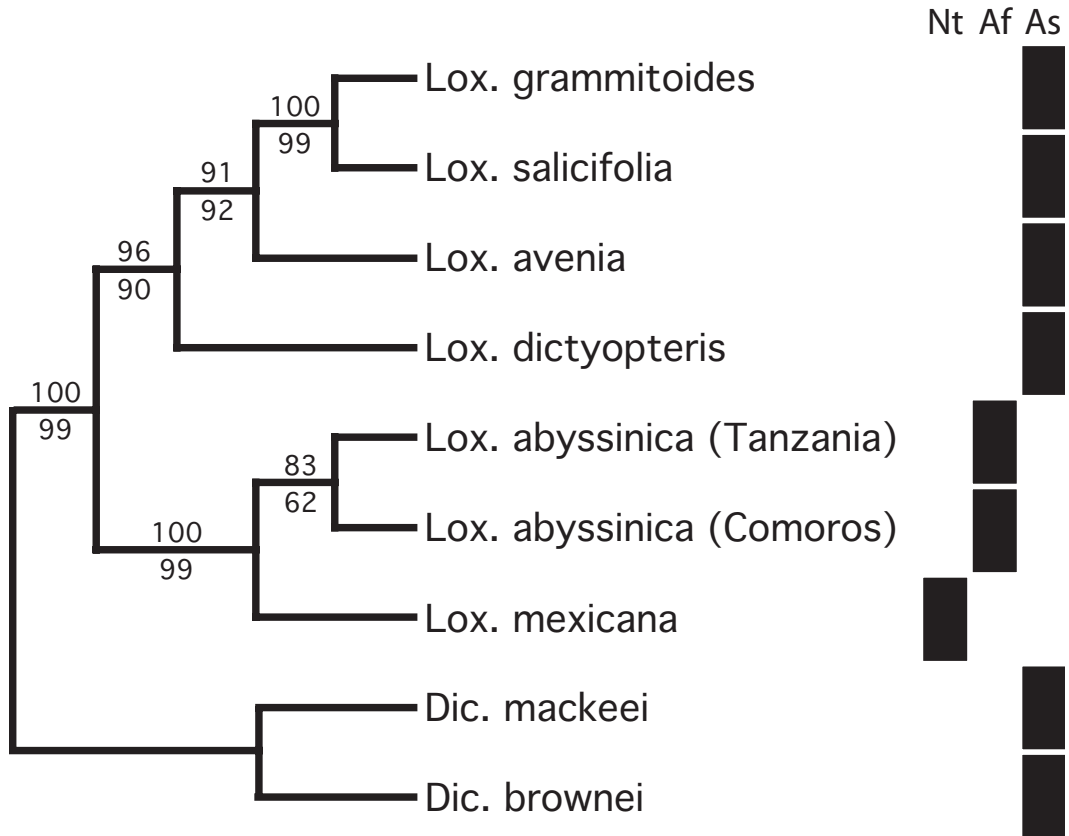
The GTR+I+ $\Gamma$  model was recovered under the hLRT criterion as implemented in Modeltest 3.7 as a best fit for the microsoroid data set with the following parameter values: A-C=1.0501, A-G=4.7058, A-T=0.3689, C-G=0.8070, C-T=6.6995, G-T=1.0000, I=0.3642,  $\Gamma$ =0.7645. The tree obtained after ML analysis had a log likelihood (ln L)=-11453.30 (Fig. 5).

Analysis of the data set under the MP criterion produced ten most parsimonious trees, 1443 steps long (CI=0.6043, HI=0.3957, RI=0.6283, RC=0.3797). The strict consensus tree shows (*Microsorium fortunei* - *Neocheiropteris ensata*) united in a polytomy and the branch subtending the basal node of the (*Belvisia mucronata* - *Lepisorus clathratus*) clade collapsed creating another polytomy. Otherwise it is topologically identical to the ML-tree.

The microsoroid lineage has its diversity center in SE Asia and is absent from the



**FIG. 2.** Phylogenetic hypothesis and distribution data for the dryarioid lineage. The tree was obtained under maximum likelihood (ML). Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (500 replicates) below branches. Agl *Aglamorpha*, Art *Arthromeris*, Dry *Drynaria*, Sel *Selliguea*. Nt neotropics; Af Africa, Madagascar and adjacent islands; As Asia, SE Asia and Australia



**FIG. 3.** Phylogenetic hypothesis and distribution data for the loxogrammoid lineage. The tree was obtained under maximum likelihood (ML). Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (1000 replicates) below branches. Dic *Dictymia*, Lox *Loxogramme*. **Nt** neotropics; **Af** Africa, Madagascar and adjacent islands; **As** Asia, SE Asia and Australia.

neotropics (except for *M. scolopendrium* (Burm. f.) Copel., which is introduced). Several species also occur in or are endemic to the African region. These do not form a monophyletic group, but are nested among the other taxa. Analysis of distribution data with DIVA 1.2 indicated this lineage to be of Asian origin.

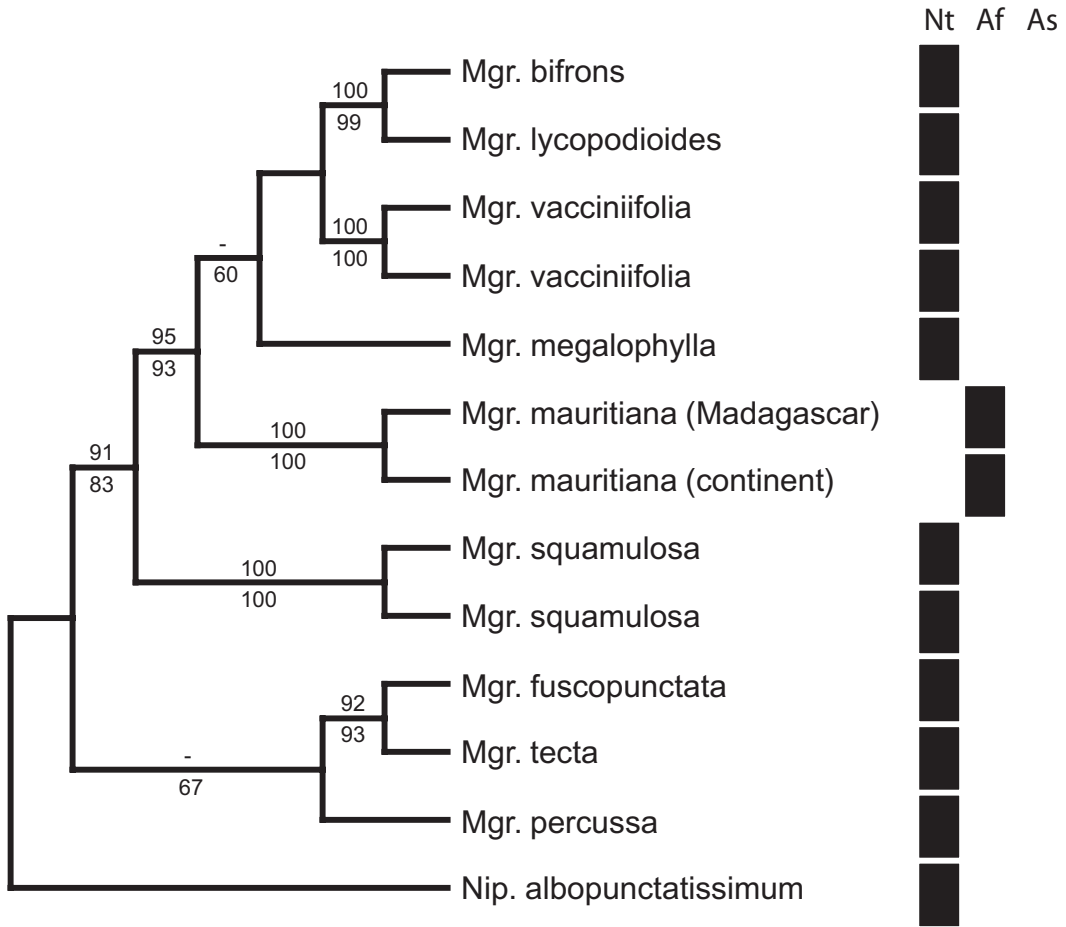
#### PLATYCERIOID LINEAGE

The TIM+I+ $\Gamma$  model was determined by the hLRT criterion as implemented in Modeltest 3.7 as best fit model for the platyceroid dataset with the following parameter values: A-C=G-T=1.0000, A-G=3.2370, A-T=C-G=0.3862, C-T=4.2861, I=0.4222,  $\Gamma$ =0.7861. The tree obtained by ML analysis had a log likelihood (ln L)=-10209.62.

Twelve most parsimonious trees, 1189 steps

long, were obtained by MP analysis (CI=0.6417, HI=0.3583, RI=0.8426, RC=0.5407). The strict consensus tree (Fig. 6) is topologically identical to the ML-tree except for the position of the African species of *Pyrrosia*. In the MP-tree *Pyrrosia niphoboloides* is placed in a subbasal position in the *Pyrrosia* clade, whereas in the ML-tree it is sister to *Platycerium*. *Pyrrosia liebuschii* is located at the base of the *Pyrrosia* clade in the MP-tree, but sister to all other platyceroids in the ML-tree. Neither of the positions in the ML-tree received ML-bootstrap support, whereas a putative basal position of both taxa in the *Pyrrosia*-clade receives more than 80% bootstrap support under maximum parsimony.

The platyceroid lineage is most diverse in southeastern Asia and Malesia. *Platycerium* and *Pyrrosia* are monophyletic. African rep-



**FIG. 4.** Phylogenetic hypothesis and distribution data for *Microgramma*. The tree was obtained under maximum likelihood (ML). Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (1000 replicates) below branches. *Mgr* *Microgramma*, *Nip* *Niphidium*. **Nt** neotropics; **Af** Africa, Madagascar and adjacent islands; **As** Asia, SE Asia and Australia.

representatives of *Pyrrosia* are most likely in a basal position, i.e., they form a paraphyletic grade at the base of the *Pyrrosia*-clade. The African representatives of *Platyserium* are monophyletic and sister to the Asian species. One neotropical species of *Platyserium* (*P. andinum*) is nested within that clade. Biogeography of the *Platyserium* clade has been explored by Kreier and Schneider (2006a).

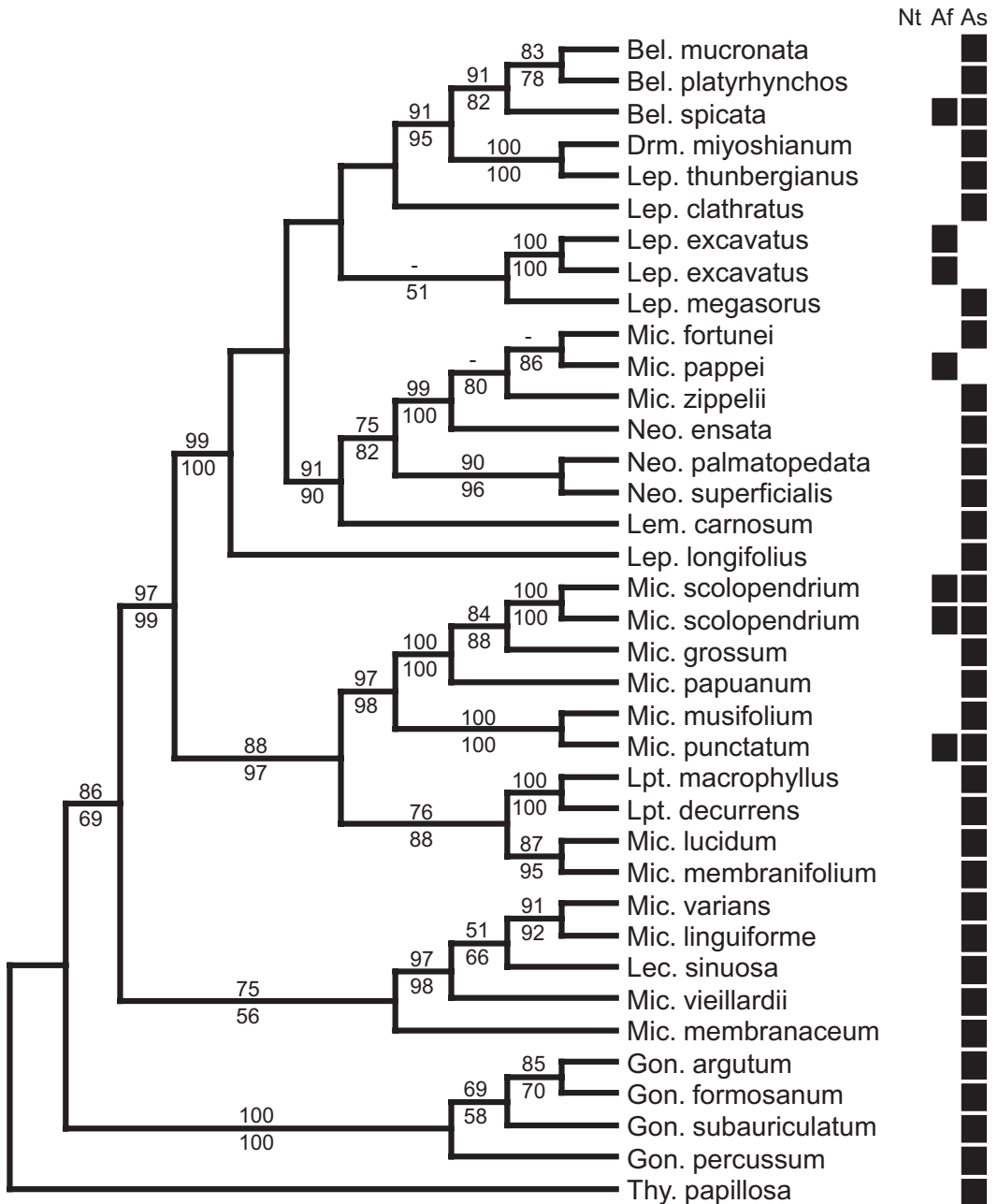
#### PLEOPELTIS LINEAGE

The hLRT as implemented in Modeltest 3.7 suggested the K81uf+ $\Gamma$  model as best fit model for the *Pleopeltis* data set with the fol-

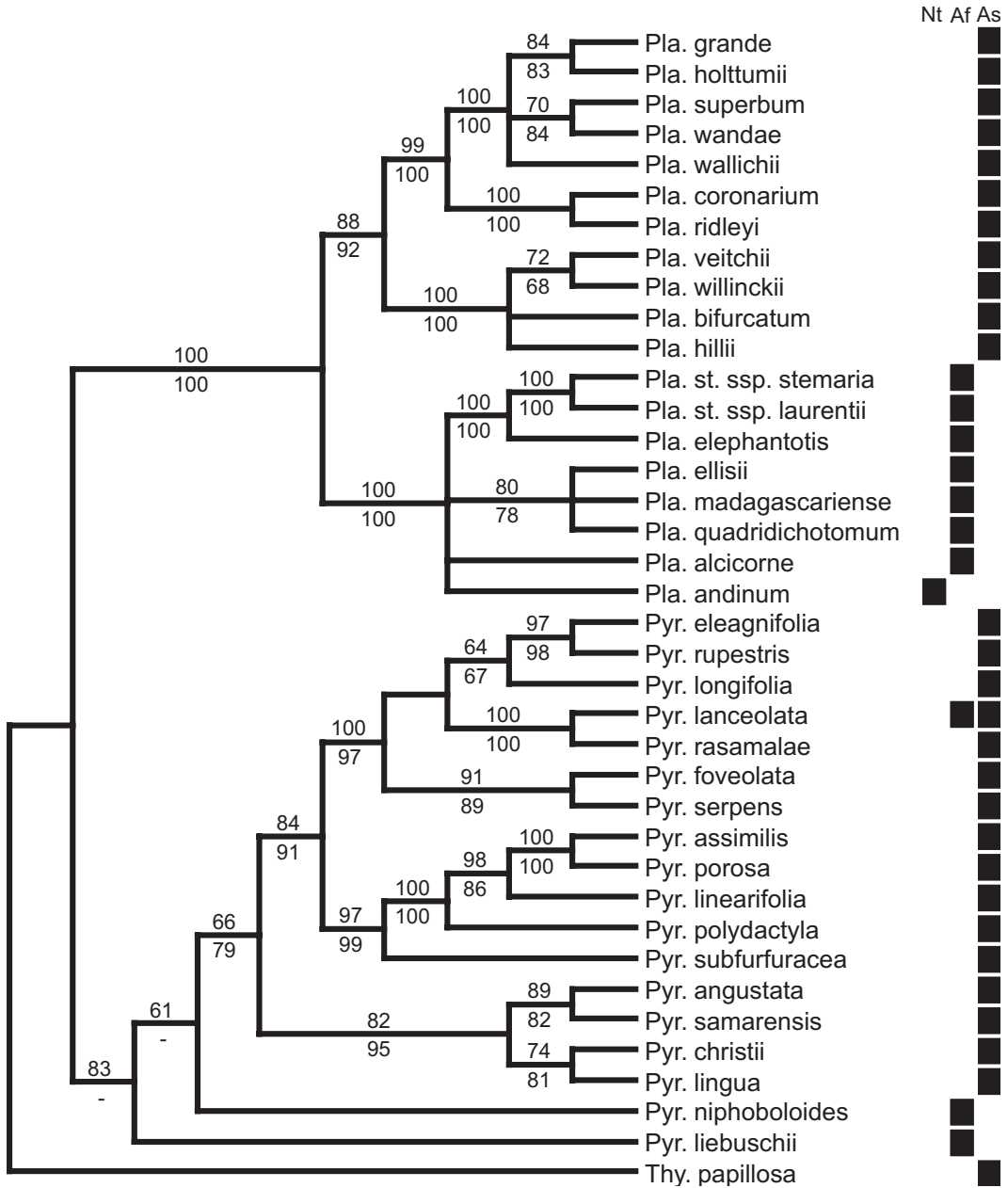
lowing parameter values: A-C=G-T=1.0000, A-G=C-T=3.2992, A-T=C-G=0.4614,  $\Gamma$ =0.0910. ML analysis found two trees with a log likelihood (ln L)=-5756.16 (Fig. 7). Topological differences between both trees concern relationships among the four accessions of *P. macrocarpa* and are presumably artifacts owed to extremely low sequence divergence among all four accessions for the markers used.

MP analysis produced 45 trees, 394 steps long (CI=0.8350, HI=0.1650, RI=0.7994, RC=0.6675), with the strict consensus topologically identical to the ML-tree, except for the position of *P. bombycinum* (Maxon) A.R.





**FIG. 5.** Phylogenetic hypothesis and distribution data for the microsoroid lineage. The tree was obtained under maximum likelihood (ML). Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (500 replicates) below branches. Bel *Belvisia*, Drm *Drymotaenium*, Gon *Goniophlebium*, Lec *Lecanopteris*, Lem *Lemmaphyllum*, Lep *Lepisorus*, Lpt *Leptochilus*, Mic *Microsorium*, Neo *Neochiropteris*, Thy *Thylacopteris*. Nt neotropics; Af Africa, Madagascar and adjacent islands; As Asia, SE Asia and Australia.



**FIG. 6.** Phylogenetic hypothesis and distribution data for the platyceroid lineage. Strict consensus of 12 most parsimonious trees. Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (500 replicates) below branches. *Pla* *Platycerium*, *Pyr* *Pyrrosia*, *Thy* *Thylacopteris*. **Nt** neotropics; **Af** Africa, Madagascar and adjacent islands; **As** Asia, SE Asia and Australia.

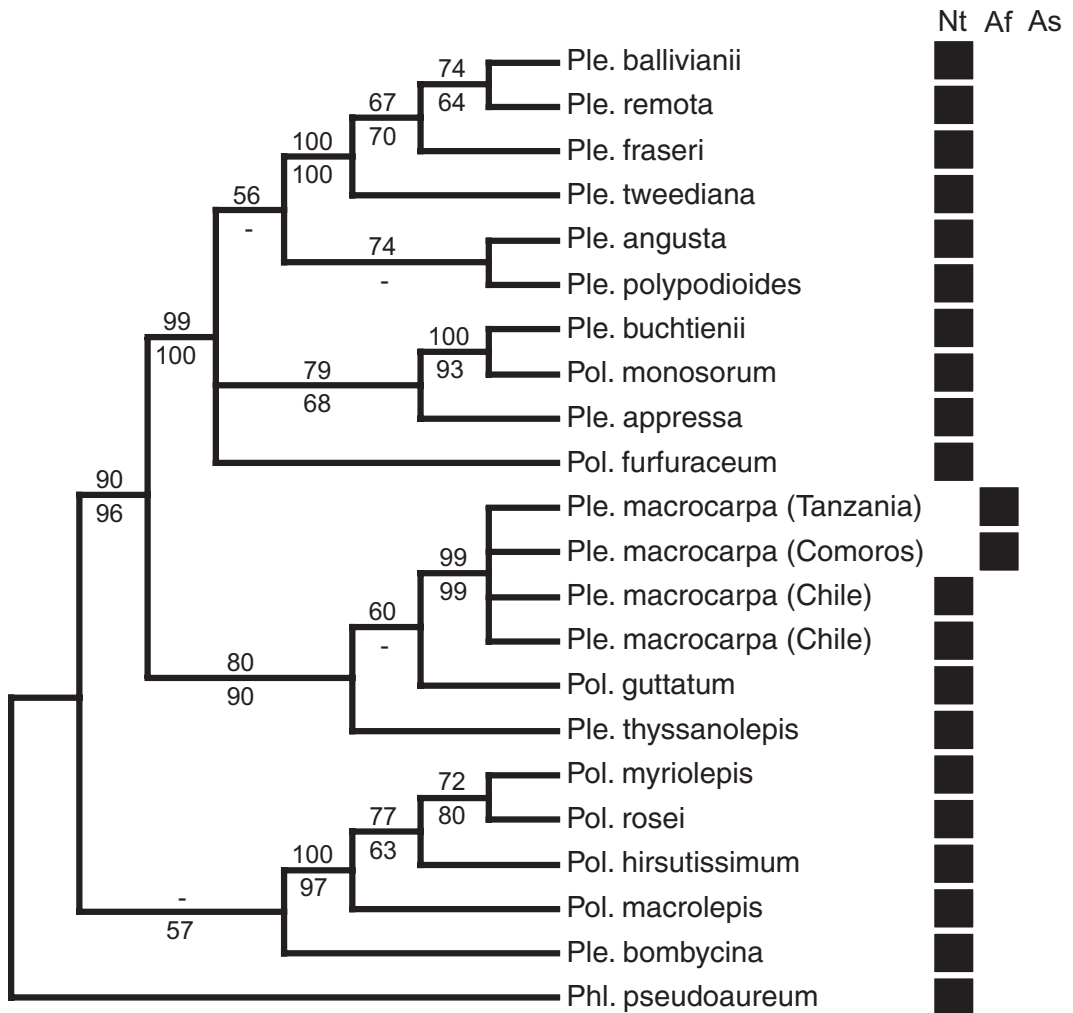


FIG. 7. Phylogenetic hypothesis and distribution data for *Pleopeltis*. Strict consensus of two trees obtained under maximum likelihood (ML). Maximum parsimony bootstrap support values (10,000 replicates) are shown above, and ML bootstrap support values (500 replicates) below branches. Phl *Phlebodium*, Ple *Pleopeltis*, Pol *Polypodium*. Nt neotropics; Af Africa, Madagascar and adjacent islands; As Asia, SE Asia and Australia.

Sm., the branch subtending the (*Polypodium myriolepis* – *Pleopeltis bombycina*) clade being collapsed creating a polytomy.

The *Pleopeltis* clade as circumscribed in Schneider et al. (2004c) is in need of taxonomic study. Its species are almost exclusively neotropical, with *Pleopeltis macrocarpa* representing the only African taxon (out of three) included in the current data set. Analysis of simplified distribution data with DIVA 1.2 confirmed the neotropics as most likely ancestral distribution at the root node.

## Discussion

### AFRICA – ASIA RELATIONSHIPS

**Drynarioid lineage.** The drynarioid lineage contains an entirely African clade of *Drynaria* splitting off near the base. Biogeographic analysis yielded ambiguous reconstructions for the root node of this lineage; thus it cannot be hypothesized whether drynarioids are originally an Asian or African lineage. The latter seems less probable if the

distribution of sister groups in Polypodiaceae is taken into account.

**Loxogrammoid lineage.** We use the name *Loxogramme abyssinica* (Baker) M.G. Price for continental African and Comoran accessions. For a discussion on the distinction of *L. abyssinica* and *L. lanceolata* (Sw.) C. Presl, see Verdcourt (2001). The loxogrammoids represent, especially in Asia, a taxonomically poorly understood and undercollected group. Therefore the phylogeny presented here covers only part of its actual diversity. Taking into account distribution data for the majority of loxogrammoid ferns and their sister lineages, it is probable that the loxogrammoid lineage is of Asian origin, even though with the current taxon sampling we cannot put forward a sound hypothesis concerning a possible African or Asian origin of the lineage.

**Platynerioid lineage.** This lineage comprises two monophyletic genera: *Platynerium* and *Pyrrosia*. The pattern observed in the lineages discussed above occurs doubly in platynerioids (i.e., both lineages exhibit a deep split in African and Asian species). The single neotropical species of *Platynerium*, *P. andinum* Baker, is nested within the African subclade and thus very likely gained its current distribution range by a dispersal event from Africa. The alternative scenario of a dispersal from Asia via the neotropics to Africa has not found support in exhaustive analyses of the phylogeny of *Platynerium* (Kreier and Schneider, 2006a, and references given therein) and is also unlikely considering the distribution of the sister clade *Pyrrosia* and the physical map of Earth in the mid Cenozoic. As in the previous cases, it cannot be decided whether *Platynerium* is an originally African or Asian lineage (Kreier & Schneider, 2006a). The current sampling includes only two African species of *Pyrrosia* forming a grade at the base of the *Pyrrosia* clade (Fig. 6). Hovenkamp (1986) postulated a phylogenetically basal position for the African representatives of *Pyrrosia*. This hypothesis is here confirmed for *P. liebuschii* (Hieron.) Schelpe. Hence, an African origin of the genus *Pyrrosia*, if not of the entire platynerioid lineage, seems probable. A larger sampling of African species is desirable to corroborate this finding.

**Microsoroid lineage.** This taxonomically poorly understood group is represented in the present phylogeny with only about 20% of its actual diversity. Five species native to Africa (two of which are endemic to the region) have been included in the data set. The African microsoroid species are scattered over different subclades of the phylogenetic tree and attach to peripheral nodes. The lineage being chiefly Asian in distribution and taking into account distribution data of sister lineages, it is most likely of Asian origin. The pattern of African taxa in the tree indicates at least five independent and comparatively recent dispersal events from Asia to Africa. Lacking data on the ages of individual lineages of microsoroids, it is uncertain whether all colonization events took place at different times or whether they partly coincided. In only two out of the five instances illustrated here, colonization of the African region was likely followed by speciation, although the alternative of extinction subsequent to dispersal in the region of origin cannot be excluded.

**Outside Polypodiaceae.** Affinities of the African fern flora to the Asian region are evidenced not only by lineages of Polypodiaceae, but also by other groups: *Arthropteris* (Tectariaceae) with four or five species in the African and eight to ten species in the Asian region, *Coniogramme* (Pteridaceae) with one or two (*C. africana*, *C. madagascariensis*) species in the African region and about 30 in Asia, *Monogramma* (Pteridaceae) with one (*M. graminea*) African and about six Asian species, and *Onychium* (Pteridaceae) with one (*O. divaricatum*) African and about eight Asian species to name but a few examples (see also Parris, 2001). The genus *Todea* (Osmundaceae) is distributed in South Africa, Australia, New Zealand, and New Guinea—a classical Gondwana pattern.

#### AFRICA – NEOTROPICS RELATIONSHIPS

**Microgramma.** Although African species of *Microgramma* (i.e., those on the continent, Madagascar and Indian Ocean islands) are regarded as conspecific with the neotropical *M. lycopodioides* (L.) Copel. by some authors (e.g., Burrows, 1990; Verdcourt, 2001), the African plants are morphologically (Moran &

Smith, 2001) and phylogenetically (Fig. 4) distinct. Note that *M. mauritiana* (Willd.) Tardieu is not sister to the neotropical *M. lycopodioides* as postulated on the basis of morphology by Moran and Smith (2001). These authors also thought that the neotropical *M. nitida* appeared to be closely related to *M. mauritiana* — a relationship that remains to be tested. We include *M. owariensis* (Desv.) Alston (type from Nigeria) in *M. mauritiana* (type from Mauritius) because there is no evidence that specimens from Africa are distinguishable from those of the Indian Ocean. *Microgramma mauritiana* is nested within the *Microgramma* clade in a comparatively peripheral position (Fig. 4), indicating a relatively recent dispersal to Africa out of this originally neotropical lineage. Because *M. mauritiana* is absent from the neotropics, colonization was likely followed by speciation in the African region.

***Pleopeltis*.** We adopt the largely neotropical genus *Pleopeltis* in its most recent definition (Schneider et al., 2004c) including *Polypodium* species with scaly leaf blades. *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf. occurs in the neotropics and the African region. Although collected over the entire range of the species, all four accessions hardly show any sequence divergence for the markers analyzed (data not shown). This might be due to genetic conservation for ecophysiological reasons, but together with the absence of a deep split among the African representatives and the remainder of *Pleopeltis* in the tree (Fig. 7), this rather seems to indicate at least one recent dispersal event from the neotropics to Africa. The pattern observed is similar to that in the *Microgramma* clade, but speciation did not occur subsequent to colonization in *P. macrocarpa*, which may be owed to recency of dispersal or meeting environmental conditions in the newly gained area similar to those of the region of origin. The relationships of the other African representatives in the *Pleopeltis* clade, *Polypodium ensiforme* Thunb., and *Polypodium ecklonii* Kunze (also treated as a subspecies of *P. polypodioides*) remain to be tested.

**Outside Polypodiaceae.** Moran and Smith (2001) pointed out relationships of the African fern flora to the neotropics by listing

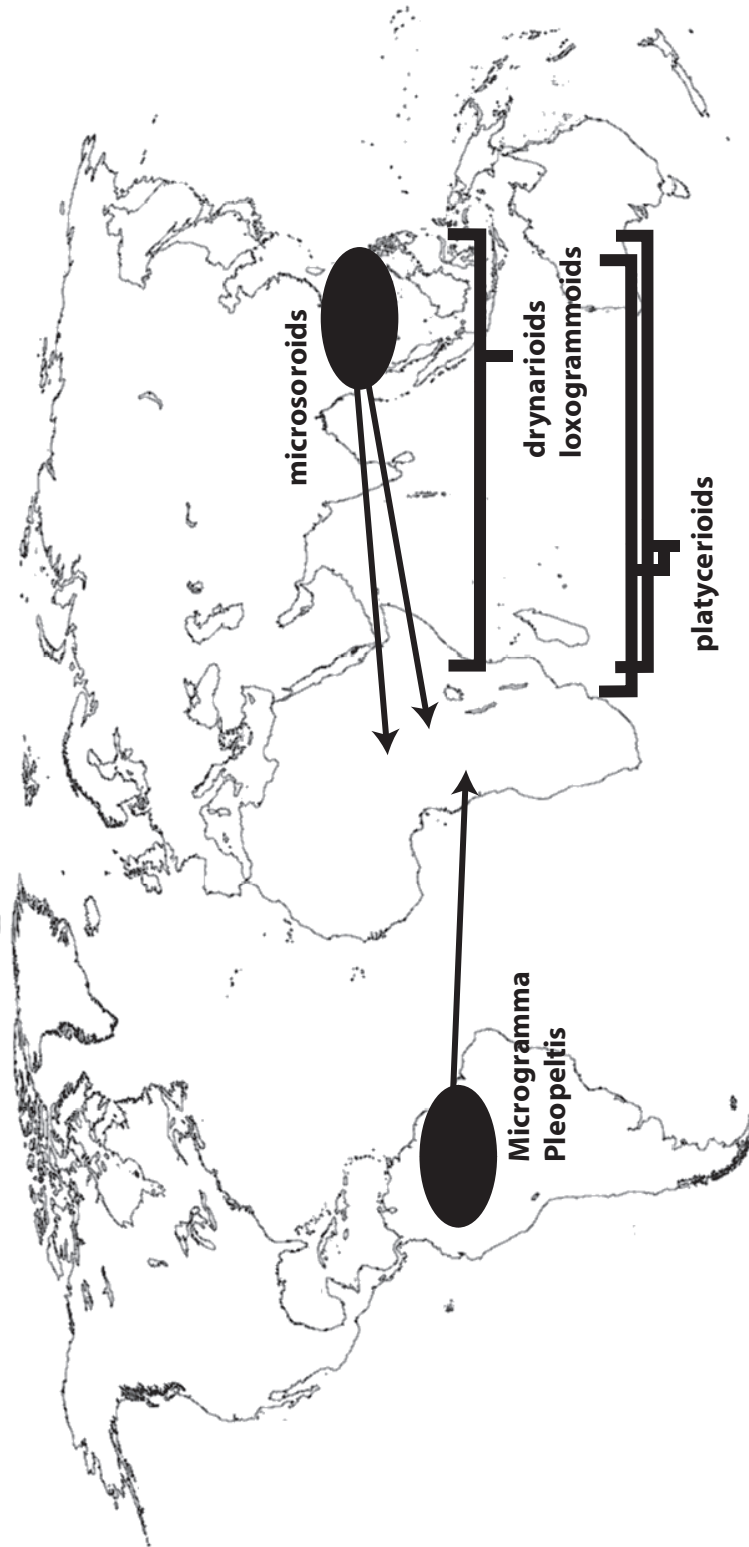
numerous shared or closely related fern taxa (see also Parris, 2001). Except for examples from Aspleniaceae, Elaphoglossaceae, Hymenophyllaceae and many others, the authors also discuss neotropical – African relationships evidenced by the grammitid lineage of Polypodiaceae that are not treated here for reasons detailed in the introduction: e.g. *Grammitis* subgen. *Grammitis*, *Lellingeria myosuroides* agg., *Melpomene flabelliformis*, *Terpsichore cultrata* - *T. elastica*. The scaly tree ferns (Cyatheaceae) represent a pantropical fern lineage with few species in Africa compared to its diversity centers in South America and Malesia. Morphologically, the African representatives are, at least in part, most likely related to neotropical species (Holtum, 1981; Conant, 1983).

#### INTERPRETATION OF OBSERVED PATTERNS IN POLYPODIACEAE

Our examination of selected lineages of Polypodiaceae has shown that African representatives exhibit close affinities to either neotropical (*Microgramma*, *Pleopeltis*) or Asian taxa (drynarioids, loxogrammoids, microsorioids, platycerioids). This leads us to the question of how such distribution patterns may have been created by biogeographical processes (Fig. 8).

Present distribution of biota may be seen as a result of three main biogeographic processes: dispersal, extinction, and vicariance. According to the age of the lineages in question and hence the prevailing past geographic and climatic conditions, contribution of any of the three aforementioned processes is likely to be unequal (Donoghue & Moore, 2003).

The African region was part of Gondwana, which started to break up during the Early Cretaceous (McLoughlin, 2001; Wells, 2003). By the end of the Cretaceous (65.5 Ma), Africa was separated from South America by a wide expanse of ocean. India was beginning to separate from Madagascar but may have been in close contact with Africa during its northward journey (Weijermars, 1989; Ridder-Numan, 1996). At the beginning of the Eocene (55.8 Ma), the developing floras of the neotropics, Africa and Asia are geographically isolated.



**Fig. 8.** Overview of the observed biogeographic patterns. The *Microgramma* and *Pleopeltis* clades are mainly neotropical with a few species in the African region, each of which presumably represents an independent dispersal event. The diversity center of the microsoroid lineage is in southeastern Asia, from which the African region was colonized several times. The loxogrammoid, drynarioid, and platyceroid lineages all include African clades sister to Asian ones. The deep splits in the phylogeny are indicated by brackets. The bracket is double for the platyceroid lineage, which shows parallel patterns in *Platyserium* and *Pyrrisia*. For this lineage, the “root” of the bracket is inserted near the African region because the current phylogeny makes an African origin of the lineage probable. No hypothesis, however, is implied by positioning on the north-south axis.

Well after a diversification burst of extant leptosporangiate fern lineages during the Late Cretaceous, Polypodiaceae most likely started to diversify during the Eocene, more precisely since about 40 Ma ago (Schneider et al., 2004b). This is consistent with the absence of fossils unequivocally assignable to Polypodiaceae before the Late Eocene (van Uffelen, 1991; Collinson, 2001). Therefore, it is probable that Polypodiaceae originated and diversified after the isolation of the neotropical, African, and Asian biogeographic regions. Although the presence of African clades splitting off at deep nodes in the drynarioid, loxogrammoid and platycerioid lineages suggests vicariance, the likely age of the Polypodiaceae argues otherwise; namely, that the observed patterns have been shaped by relatively old long distance dispersal events. The “vicariance-like” pattern observed in these three lineages illustrates the importance of incorporating temporal information in biogeographic analysis (Donoghue & Moore, 2003).

The three biogeographic regions discussed here remained, at least intermittently, connected at high latitudes by a climate that permitted the migration of tropical taxa through the Oligocene and Miocene (Wolfe, 1975; Collinson, 2001; Sanmartín et al., 2001; Tiffney & Manchester, 2001; Willis & McElwain, 2002; Davis et al., 2004). Consistent with this, the oldest known polypodiaceous fossil, *Protodrynaria*, has been described from the Moscow region and dates back to the Eocene – Oligocene boundary (Vikulin & Bobrov, 1987). This fossil was discussed as being related to the drynarioid or selliguioid ferns (van Uffelen, 1991). Boreotropic migration represents a plausible alternative for the explanation of presumably old, deep splits as observed in the drynarioid, loxogrammoid, and platycerioid lineages, but not for presumably recent and recurrent colonization events as evidenced by *Microgramma*, *Pleopeltis*, and especially the microsorioids.

Liverwort spores survive dispersal at high altitudes (van Zanten & Gradstein, 1988). If this holds true for fern spores and taking into account that wind has been shown to be a powerful dispersal vehicle in the southern hemisphere (Muñoz et al., 2004), relationships of African Polypodiaceae may indeed

result from long distance dispersal events at different geological times and at different points in the evolution of each lineage examined here. This is consistent with the arguments of Sanmartín and Ronquist (2004), who considered plant distribution patterns to be generally better explained as a result of dispersals, whereas animal distribution patterns may fit more often with a vicariance scenario. Whether and to which extent speciation occurs subsequent to colonization largely depends on the breeding system (Soltis & Soltis, 1990) and properties of the gametophyte (Dassler & Farrar, 2001) of the fern species in question. Additionally, speciation is more likely to occur with an increasing time of isolation (cf. platyceroids vs. *Pleopeltis*).

### Conclusion

The Polypodiaceae of the neotropics and Asia overlap in the African region; that is, the African polypodiaceous flora includes many lineages exhibiting close affinities to either the neotropics or Asia. The Polypodiaceae are too young for a vicariance interpretation to explain these affinities. Single or multiple long distance dispersal events at different times in the evolution of the lineages examined are most likely. Except for platyceroids, it is unlikely that the examined lineages of Polypodiaceae originated in Africa. Instead, at least a part of the diversity in African Polypodiaceae is derived from the neotropics or from Asia. Further examination of fern lineages outside Polypodiaceae in a phylogenetic framework is needed before a generalization of our findings for the entire African fern flora can be attempted.

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### Literature Cited

- Aldasoro, J. J., F. Cabezas & C. Aedo.** 2004. Diversity and distribution of ferns in sub-Saharan Africa, Madagascar and some islands of the South Atlantic. *Journal of Biogeography* 31: 1579–1604.
- Badré, F. & T. Cadet.** 1978. The pteridophytes of Réunion Island. *Fern Gazette* 11: 349–365.
- Barrington, D. S.** 1993. Ecological and historical factors in fern biogeography. *Journal of Biogeography* 20: 275–280.
- Brownsey, P. J.** 2001. New Zealand's pteridophyte flora - plants of ancient lineage but recent arrival? *Brittonia* 53: 284–303.
- Burrows, J. E.** 1990. *Southern African Ferns and Fern Allies*. Frandsen Publishers, Sandton.
- Christensen, C.** 1912. On the ferns of the Seychelles and the Aldabra group. *Transactions of the Linnean Society of London. Ser. 2, Botany*. 7: 409–425.
- Conant, D. S.** 1983. A revision of the genus *Alsophila* (Cyatheaceae) in the Americas. *Journal of the Arnold Arboretum* 64: 333–382.
- Collinson, M. E.** 2001. Cainozoic ferns and their distribution. *Brittonia* 53: 173–235.
- Dassler, C. L. & D. R. Farrar.** 2001. Significance of gametophyte form in long-distance colonization by tropical, epiphytic ferns. *Brittonia* 53: 352–369.
- Davis, C. C., C. D. Bell, P. W. Fritsch & S. Mathews.** 2002. Phylogeny of *Acridocarpus-Brachylophon* (Malpighiaceae): implications for tertiary tropical floras and afroasian biogeography. *Evolution* 56: 2395–2405.
- , P. W. Fritsch, C. D. Bell & S. Mathews. 2004. High-latitude Tertiary migrations of an exclusively tropical clade: evidence from Malpighiaceae. *International Journal of Plant Sciences* 165: S107–S121.
- Donoghue, M. J. & B. R. Moore.** 2003. Toward an integrative historical biogeography. *Integrative and Comparative Biology* 43: 261–270.
- Felsenstein, J.** 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Hennipman, E. & M. C. Roos.** 1982. A monograph of the fern genus *Platyserium* (Polypodiaceae). *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen. Afdeling Natuurkunde, Sectie 2*. 80: 1–126.
- Holtum, R. E.** 1981. The tree ferns of Africa. *Kew Bulletin* 36: 463–482.
- Hovenkamp, P.** 1986. A monograph of the fern genus *Pyrrosia*, Polypodiaceae. *Leiden Botanical Series* 9: 1–280.
- Janssen, T. & H. Schneider.** 2005. Exploring the evolution of humus collecting leaves in drynarioid ferns (Polypodiaceae, Polypodiidae) based on phylogenetic evidence. *Plant Systematics and Evolution* 252: 175–197.
- Johns, R. J.** 1991. Pteridophytes of tropical East Africa - a preliminary checklist of the species. *Royal Botanical Gardens, Kew*.
- Kato, M.** 1993. Biogeography of ferns - dispersal and vicariance. *Journal of Biogeography* 20: 265–274.
- Kreier, H.-P. & H. Schneider.** 2006a. Phylogeny and biogeography of the staghorn fern genus *Platyserium* (Polypodiaceae, Polypodiidae). *American Journal of Botany* 93: 217–225.
- & ———. 2006b. Reinstatement of *Loxogramme dictyopteris*, based on phylogenetic evidence, for the New Zealand endemic fern *Anarthropteris lanceolata* (Polypodiaceae, Polypodiidae). *Australian Systematic Botany* 19: 309–314.
- Kubitzki, K., editor.** 1990. The families and genera of vascular plants. Vol. I: Pteridophytes and Gymnosperms. K.U. Kramer & P. S. Green (vol. eds.). Springer-Verlag, Berlin.
- Lorence, D. H.** 1978. The pteridophytes of Mauritius (Indian Ocean): ecology and distribution. *Botanical Journal of the Linnean Society* 76: 207–247.
- Maddison, D. R. & W. P. Maddison.** 2000. *MacClade 4.05: Analysis of phylogeny and character evolution*. Sinauer Associates, Sunderland, Massachusetts.
- McLoughlin, S.** 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* 49: 271–300.
- Moran, R. C. & A. R. Smith.** 2001. Phytogeographic relationships between neotropical and African-Madagascan pteridophytes. *Brittonia* 53: 304–351.
- Muñoz, J., Á. M. Felcimo, F. Cabezas, A. R. Burgaz & I. Martínez.** 2004. Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science* 304: 1144–1147.
- Nooteboom, H. P.** 1997. The microsored ferns (Polypodiaceae). *Blumea* 42: 261–395.
- Parris, B. S.** 2001. Circum-Antarctic continental distribution patterns in pteridophyte species. *Brittonia* 53: 270–283.
- Plana, V., A. Gascoigne, L. L. Forrest, D. Harris & R. T. Pennington.** 2004. Pleistocene and pre-pleistocene *Begonia* speciation in Africa. *Molecular Phylogenetics and Evolution* 31: 449–461.
- Posada, D. & K. A. Crandall.** 1998. MODELTEST: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Rakotondrainibe, F.** 2003. Checklist of the pteridophytes of Madagascar. Pp. 295–313. *In*: S. M. Goodman & J. P. Benstead (eds.), *Natural history of Madagascar*. The University of Chicago Press, Chicago.
- Ranker, T. A., A. R. Smith, B. S. Parris, J. M. O. Geiger, C. H. Haufler, S. C. K. Straub & H. Schneider.** 2004. Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy. *Taxon* 53: 415–428.
- Renner, S. S.** 2004. Multiple Miocene Melastomataceae dispersal between Madagascar, Africa and India. *Philosophical Transactions of the Royal Society of*



- London, Series B - Biological Sciences 359: 1485–1494.
- , **G. Causing & K. Meyer**. 2001. Historical biogeography of Melastomataceae: The roles of tertiary migration and long-distance dispersal. *American Journal of Botany* 88: 1290–1300.
- Ridder-Numan, J. W. A.** 1996. The historical biogeography of the Southeast Asian genus *Spatholobus* (Leguminosae, Papilionoideae) and its allies. *Blumea Supplement* 10: 1–144.
- Ronquist, F.** 1997. Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology* 46: 195–203.
- Roos, M. C.** 1985. Phylogenetic systematics of the Drynarioideae (Polypodiaceae). *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen. Afdeling Natuurkunde, Sectie 2*. 85: 1–317.
- Roux, J. P.** 2001. *Conspectus of Southern African pteridophyta*. SABONET, Pretoria.
- Sanmartín, I., H. Enghoff & F. Ronquist**. 2001. Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society* 73: 345–390.
- Sanmartín, I. & F. Ronquist**. 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53: 216–243.
- Schneider, H., T. Janssen, P. Hovenkamp, A. R. Smith, R. B. Cranfill, C. H. Hauffer & T. A. Ranker**. 2004a. Phylogenetic relationships of the enigmatic Malesian fern *Thylacopteris* (Polypodiaceae, Polypodiidae). *International Journal of Plant Sciences* 165: 1077–1087.
- , **E. Schuettelpelz, K. M. Pryer, R. B. Cranfill, S. Magallon & R. Lupia**. 2004b. Ferns diversified in the shadow of angiosperms. *Nature* 428: 553–557.
- , **A. R. Smith, R. B. Cranfill, T. J. Hildebrand, C. H. Hauffer & T. A. Ranker**. 2004c. Unraveling the phylogeny of polygrammoid ferns (Polypodiaceae & Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molecular Phylogenetics and Evolution* 31: 1041–1063.
- , **H.-P. Kreier, L. R. Perrie & P. J. Brownsey**. 2006a. The relationships of *Microsorium* (Polypodiaceae) species occurring in New Zealand. *New Zealand Journal of Botany* 44: 121–127.
- , ———, **R. Wilson & A. R. Smith**. 2006b. The *Synammia* enigma: evidence for a temperate lineage of polgrammoid ferns (Polypodiaceae, Polypodiidae) in Southern South Africa. *Systematic Botany* 31: 31–41.
- Smith, A. R.** 1972. Comparison of fern and flowering plant distributions with some evolutionary interpretations for ferns. *Biotropica* 4: 4–9.
- , **K. M. Pryer, E. Schuettelpelz, P. Korall, H. Schneider & P. G. Wolf**. 2006. A classification for extant ferns. *Taxon* 55: 705–731.
- Soltis, P. S. & D. E. Soltis**. 1990. Evolution of inbreeding and outcrossing in ferns and fern-allies. *Plant Species Biology* 5: 1–11.
- Sparks, J. S.** 2004. Molecular phylogeny and biogeography of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Chichlidae). *Molecular Phylogenetics and Evolution* 30: 599–614.
- & **W. L. Smith**. 2004. Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Melanotaeniidae): Gondwanan vicariance and evolution in freshwater. *Molecular Phylogenetics and Evolution* 33: 719–734.
- Swofford, D. L.** 2000. PAUP\*: phylogenetic analyses using parsimony (\* and other methods), version 4b10. Sinauer Associates, Sunderland, Massachusetts.
- Sytsma, K. J., A. Litt, M. L. Zjhra, J. C. Pires, M. Nepokroeff, E. Conti, J. Walker & P. G. Wilson**. 2004. Clades, clocks, and continents: historical and biogeographical analysis of Myrtaceae, Vochysiaceae, and relatives in the southern hemisphere. *International Journal of Plant Sciences* 165: S85–S105.
- Tardieu-Blot, M.-L.** 1964a. Ptéridophytes. *In: A. Aubréville (ed.) Flore du Cameroun*. Muséum national d'Histoire naturelle, Paris.
- Tardieu-Blot, M.-L.** 1964b. Ptéridophytes. *In: A. Aubréville (ed.) Flore du Gabon*. Muséum national d'Histoire naturelle, Paris.
- Tiffney, B. H. & S. R. Manchester**. 2001. The use of geological and paleontological evidence in evaluating plant phylogeographic hypotheses in the northern hemisphere Tertiary. *International Journal of Plant Sciences* 162: S3–S17.
- Tryon, R. M.** 1986. The biogeography of species with special reference to ferns. *Botanical Review* 52: 117–155.
- van Uffelen, G. A.** 1991. Fossil Polypodiaceae and their spores. *Blumea* 36: 253–272.
- van Zanten, B. O. & S. R. Gradstein**. 1988. Experimental dispersal geography of neotropical liverworts. *Beiheft zur Nova Hedwigia* 90: 41–94.
- Verdcourt, B.** 2001. Polypodiaceae. *In: H. J. Beentje (ed.), Flora of Tropical East Africa*. Balkema, Rotterdam.
- Vikulin, S. V. & A. E. Bobrov**. 1987. A new fossil genus *Protodrynaria* (Polypodiaceae) from the paleogene flora of Tim (the south of the middle Russian upland). [in Russian]. *Botanicheskii Zhurnal* 72: 95–98.
- Wells, N. A.** 2003. Some hypotheses on the Mesozoic and Cenozoic palaeoenvironmental history of Madagascar. Pp. 16–34. *In: S. M. Goodman and J. P. Benstead (eds.), Natural history of Madagascar*. The University of Chicago Press, Chicago.
- Weijermars, R.** 1989. Global tectonics since the breakup of Pangea 180 million years ago: Evolution maps and lithospheric budget. *Earth-Science Reviews* 26: 113–162.
- Willis, K. J. & J. C. McElwain**. 2002. *The evolution of plants*. Oxford University Press, Oxford.
- Wolf, P. G., H. Schneider & T. A. Ranker**. 2001. Geographic distributions of homosporous ferns: does dispersal obscure evidence of vicariance? *Journal of Biogeography* 28: 263–270.
- Wolfe, J. A.** 1975. Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanical Garden* 62: 264–279.
- Yuan, Y.-M., S. Wohlhauser, M. Möller, J. Klackenberg, M. W. Callmänder & P. Küpfer**. 2005. Phy-

- logeny and biogeography of *Exacum* (Gentianaceae): a disjunctive distribution in the Indian Ocean Basin resulted from long distance dispersal and extensive radiation. *Systematic Biology* 54: 21–34.
- Zhang, L.-B. & S. S. Renner.** 2003. The deepest splits in Chloranthaceae as resolved by chloroplast sequences. *International Journal of Plant Sciences* 164: S383–S392.
- Zink, M. J.** 1993. Systematics of the fern genus *Lepisorus* (J.Smith) Ching (Polypodiaceae-Lepisoreae). Inaugural-Dissertation, Universität Zürich. ADAG Administration und Druck AG, Zürich.

APPENDIX  
 GENBANK ACCESSION NUMBERS AND VOUCHER INFORMATION FOR THE DATA SETS EMPLOYED IN THIS STUDY. ACCESSION NUMBERS OF SEQUENCES PRODUCED FOR THIS STUDY ARE IN BOLD FACE. ALL OTHER SEQUENCES HAVE BEEN PUBLISHED IN RECENT WORKS ON POLYPODIACEAE (KREIER & SCHNEIDER, 2006A, 2006B; JANSSEN & SCHNEIDER, 2005; SCHNEIDER ET AL., 2004A, 2006B, 2006A)

Taxon	Origin; Voucher	rbcL	rps4*	trnL-F
<b>drynarioids</b>				
<i>Aglaomorpha acuminata</i> (Willd.) Hovenkamp	cult. Bot. Gard. Heidelberg; no voucher	AY529147	AY529172	AY459176
<i>Aglaomorpha coronans</i> (Wall. ex Mett.) Copel.	cult. Bot. Gard. Heidelberg nr. 105656; no voucher	AF470349	AY459184	AY529463
<i>Aglaomorpha cornucopia</i> (Copel.) M. C. Roos	cult. Bot. Gard. München; <i>Janssen 2255</i> (GOET)	AY529148	AY529173	AY529464
<i>Aglaomorpha drynarioides</i> (Hook.) M. C. Roos	cult. Bot. Gard. Berlin nr. 239-27-90-33; <i>Janssen 2256</i> (GOET)	AY529149	AY529174	AY529465
<i>Aglaomorpha heraclea</i> (Kunze) Copel.	cult. Bot. Gard. Göttingen; <i>Janssen 2249</i> (GOET)	AY529150	AY529175	AY529466
<i>Aglaomorpha hieronymi</i> (Brause) Copel.	cult. Bot. Gard. Heidelberg nr. 100798; <i>Hagemann 2601</i> (HEID)	AY529151	AY529176	AY529467
<i>Aglaomorpha latipinna</i> (C. Chr.) M. C. Roos	Indonesia, Irian Jaya; <i>Mangen 2230</i> (L)	–	–	AY529468
<i>Aglaomorpha meyeniana</i> Schott	cult. Bot. Gard. Göttingen; <i>Janssen 2260</i> (GOET)	AY529153	AY459185	AY529470
<i>Aglaomorpha novoguineensis</i> (Brause) C. Chr.	cult. Bot. Gard. Berlin nr. 178-10-86-33; <i>Janssen 2254</i> (GOET)	AY529154	AY529178	AY529471
<i>Aglaomorpha parkinsonii</i> (Baker) Parris et M. C. Roos	cult. Bot. Gard. Göttingen; <i>Janssen 2259</i> (GOET)	AY529155	AY529179	AY529472
<i>Aglaomorpha pilosa</i> (J. Sm. ex Hook. et Bauer) Copel.	cult. Bot. Gard. Berlin nr. 239-09-90-33; <i>Janssen 2258</i> (GOET)	AY529156	AY529180	AY529473
<i>Aglaomorpha splendens</i> (J. Sm. ex Hook. et Bauer) Copel.	cult. Charles Alford Nursery; <i>A.R.Smith s.n.</i> (UC)	AY529157	AY529181	AY529474
<i>Drynaria bonii</i> H. Christ	cult. Bot. Gard. Berlin nr. 234-28-97-83; <i>Janssen 2248</i> (GOET)	AY529158	AY529182	AY529475
<i>Drynaria descensa</i> Copel.	cult. Bot. Gard. Heidelberg nr. 106187; <i>Schneider s.n.</i> (GOET)	AY529159	AY529183	AY529476
<i>Drynaria fortunei</i> (Kunze ex Mett.) J.Sm.	cult. Bot. Gard. Göttingen; <i>Janssen 2252</i> (GOET)	AY529160	AY529184	AY529477
<i>Drynaria laurentii</i> (Christ ex De Wild. & T. Durand) Hieron.	cult. Selby Bot. Gard. nr. 97-0378; <i>A.R.Smith s.n.</i> (UC)	AY529161	AY529185	AY529478
<i>Drynaria mollis</i> Bedd.	cult. Bot. Gard. Göttingen; <i>Janssen 2257</i> (GOET)	AY529162	AY529186	AY529479
<i>Drynaria quercifolia</i> (L.) J.Sm.	cult. Bot. Gard. Göttingen; <i>Janssen 2247</i> (GOET)	AY529165	AY529187	AY529480
<i>Drynaria rigidula</i> (Sw.) Bedd.	cult. Bot. Gard. Berlin nr. 082-04-97-50; <i>Janssen 2251</i> (GOET)	AY529166	AY529188	AY529481
<i>Drynaria sinica</i> Diels (1)	China, Xizang; <i>Miehe &amp; Wiendisch 94-155-28</i> (GOET)	AY529163	–	–
<i>Drynaria sinica</i> Diels (2)	China, Xizang; <i>Miehe 98-13402</i> (GOET)	AY529164	–	–
<i>Drynaria sparsisora</i> (Desv.) T. Moore	cult. Bot. Gard. Tübingen; <i>Janssen 2246</i> (GOET)	AY529167	AY529189	AY529482
<i>Drynaria volkensii</i> Hieron.	Tanzania, Kilimanjaro; <i>Hemp 3635</i> (UBT)	AY529168	AY529190	–
<i>Drynaria willdenowii</i> (Bory) T. Moore	cult. Bot. Gard. Berlin nr. 239-15-90-33; <i>Janssen 2250</i> (GOET)	AY529169	AY529191	AY529483
<i>Arthromeris lehmannii</i> (Mett.) Ching	Taiwan; <i>Cranfill TW-77</i> (UC)	AY096198	AY096216	AY459177
<i>Selliguea enervis</i> (Cav.) Ching	Java; <i>Wilson 2893</i> (UC)	AY096200	AY096218	AY459178
<i>Selliguea feei</i> Bory	Java; <i>Wilson 2862</i> (UC)	AY529170	AY529192	AY459179
<i>Selliguea heterocarpa</i> (Blume) Blume	Malaysia; <i>Jaman 5897</i> (UC)	AY459172	AY362619	AY459180
<i>Selliguea laciniata</i> (Bedd.) Hovenkamp	Malaysia; <i>Jaman 5894</i> (UC)	AY529171	AY529193	AY529484
<i>Selliguea lanceola</i> (Mett.) E. Fourn.	New Caledonia; <i>Munzinger et al. 1253</i> (P)	AY459173	AY459186	AY529481

(Continued)

APPENDIX  
(CONTINUED)

Taxon	Origin: Voucher	rbcl	tps4a	tml_F
<b>Loxogrammioids</b>				
<i>Dictyonia browniei</i> (Wikstr.) Copel.	cult. UC Bot. Gard. nr. 54.1240; <i>Werner 21</i> (UC)	DQ227292	DQ227295	DQ227298
<i>Dictyonia mackeei</i> Tindale	cult. Bot. Gard. Edinburgh nr. 19842659; <i>Schneider s.n.</i> (E)	DQ164441	DQ164472	DQ164504
<i>Loxogramme abyssinica</i> (Baker) M. G. Price (1)	Tanzania; <i>Hemp 3638</i> (DSM)	DQ164443	DQ164474	DQ164506
<i>Loxogramme abyssinica</i> (Baker) M. G. Price (2)	Grande Comore; <i>Rakotondrainibe 6711</i> (P)	DQ235157 / DQ235158 <sup>b</sup>	DQ235155	DQ235156
<i>Loxogramme avenia</i> (Blume) C. Presl	Malaysia; <i>Jaman 5866</i> (UC)	DQ227293	AY096215	DQ227299
<i>Loxogramme dicyopteris</i> (Mett.) Copel. [= <i>Anarthriopteris lanceolata</i> (J. Sm. ex Hook.f.) Pic.Serm.]	New Zealand; <i>Cranfill s.n.</i> (UC)	AY096107	AY096214	DQ227303
<i>Loxogramme graminifoliosa</i> (Baker) C. Chr.	Japan; <i>Hasebe 26661</i> (TI)	U05631	DQ227296	DQ227300
<i>Loxogramme mexicanica</i> (Fée) C. Chr.	Nicaragua; <i>Hall &amp; Bockus 7896</i> (UC)	—	—	DQ227301
<i>Loxogramme salicifolia</i> (Makino) Makino	cult. Bot. Gard. Edinburgh nr. 728/11; <i>Schneider s.n.</i> (E)	DQ227294	DQ227297	DQ227302
<b>Microgramma</b>				
<i>Microgramma bifrons</i> (Hook.) Lellinger	Peru; <i>van der Werff 18062</i> (MO)	AY362582	AY362654	<b>DQ642224</b>
<i>Microgramma bifrons</i> (Hook.) Lellinger	Ecuador; <i>Neill et al. 8309</i> (UC)	AY362573	AY362647	—
<i>Microgramma fuscopunctata</i> (Hook.) Vareschi	Ecuador; <i>Moran 6071</i> (NY)	AY362575	AY362649	—
<i>Microgramma lycopodioides</i> (L.) Copel.	Costa Rica; <i>Horich s.n.</i> (UC)	AY362577	<b>DQ642185</b>	<b>DQ642225</b>
<i>Microgramma mauritiana</i> (Willd.) Tardieu (1)	cult. Bot. Gard. Zürich (continental Africa); <i>Kreier s.n.</i> (GOET)	<b>DQ642148</b>	<b>DQ642186</b>	<b>DQ642226</b>
<i>Microgramma mauritiana</i> (Willd.) Tardieu (2)	cult. Bot. Gard. Zürich (continental Africa); <i>Kreier s.n.</i> (GOET)	AY362578	AY362650	—
<i>Microgramma megalophylla</i> (Desv.) de la Sota	cult. UC Bot. Gard. nr. 97.0025; <i>Smith s.n.</i> (UC)	<b>DQ642149</b>	<b>DQ642187</b>	<b>DQ164507</b>
<i>Microgramma perçuosa</i> (Cav.) de la Sota	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	<b>DQ642150</b>	<b>DQ642188</b>	<b>DQ642228</b>
<i>Microgramma squamulosa</i> (Kaulf.) de la Sota (1)	cult. Bot. Gard. Zürich; <i>Kreier s.n.</i> (GOET)	<b>DQ642150</b>	<b>DQ642188</b>	<b>DQ642229</b>
<i>Microgramma squamulosa</i> (Kaulf.) de la Sota (2)	cult. New York Bot. Gard. nr. 954/95A; <i>Collector unknown</i> (UC)	AY362579	AY362651	—
<i>Microgramma tecta</i> (Kaulf.) Alston	cult. Bot. Gard. Edinburgh nr. 19875234; <i>Schneider s.n.</i> (E)	AY362580	AY362652	<b>DQ642230</b>
<i>Microgramma tecta</i> (Kaulf.) Alston	Venezuela; <i>Smith 1543</i> (UC)	—	—	—
<i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel. (1)	cult. private garden; <i>Smith 2635</i> (UC)	AY362581	AY362653	—
<i>Microgramma vacciniifolia</i> (Langsd. & Fisch.) Copel. (2)	Charles Alford Nursery via Selby Botanic Gardens nr. 1981-0148; <i>Kreier s.n.</i> (GOET)	<b>DQ642151</b>	<b>DQ642189</b>	<b>DQ642231</b>
<i>Niphidium albobunctatissimum</i> Lellinger	Peru; <i>Hutchinson 1124</i> (UC)	AY362585	AY362658	—
<b>microsoroids</b>				
<i>Belvisia mucronata</i> (Fée) Copel.	cult. Bot. Gard. Zürich; <i>Kreier s.n.</i> (GOET)	AY362562	AY362629	<b>DQ642232</b>
<i>Belvisia mucronata</i> (Fée) Copel.	Malaysia; <i>Jaman 5891</i> (UC)	<b>DQ642152</b>	<b>DQ642190</b>	<b>DQ642233</b>
<i>Belvisia playrhynechos</i> (Kunze) Copel.	cult. Bot. Gard. Zürich; <i>Kreier s.n.</i> (GOET)	<b>DQ642153</b>	<b>DQ642191</b>	<b>DQ642234</b>
<i>Belvisia spicata</i> (L.f.) Mirb. ex Copel.	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	—	—	—

<i>Drymotaenium miyoshianum</i> (Makino) Makino	Taiwan; <i>Cranfill TW-087</i> (UC)	AY362563	AY362630	DQ179639
<i>Goniophlebium arguttum</i> (Wall.) J.Sm.	Taiwan; <i>Cranfill TW-075</i> (UC)	DQ164442	DQ164473	DQ164505
<i>Goniophlebium formosanum</i> (Baker) Rödl-Linder	Taiwan; <i>Cranfill TW-043</i> (UC)		AY096224	<b>DQ642235</b>
<i>Goniophlebium formosanum</i> (Baker) Rödl-Linder	source unknown; see Hirohara et al. (2000) Natural Medicines 54: 330–333.	AB043100		
<i>Goniophlebium percutissum</i> (Cav.) W. H. Wagner & Grether	Taiwan; <i>Cranfill TW-087</i> (UC)	AY362563	AY362630	DQ179639
<i>Goniophlebium subauriculatum</i> (Blume) C. Presl	cult. Bot. Gard. Bogor nr. 23A; <i>Smith et al. s.n.</i> (UC)	AY362561	AY362628	–
<i>Lecanopteris sinuosa</i> (Wall. ex Hook.) Copel.	cult. RBG Kew nr. 1980-1014; no voucher	AF470342	DQ168812	AY083645
<i>Lecanopteris sinuosa</i> (Wall. ex Hook.) Copel.	cult. Bot. Gard. Utrecht; <i>Hennipman 7821</i> (L)	AF470321	AY362634	AY083624
<i>Lemmaphyllum carnosum</i> C.Presl	cult. UC Bot. Gard. nr. 50.0326; A. R. <i>Smith s.n.</i> (UC)	AF470321	AY362631	AY083635
<i>Lepisorus clathratus</i> (C. B. Clarke) Ching	Tibet; <i>Dickoré 12430</i> (GOET)	<b>DQ642154</b>	<b>DQ642192</b>	<b>DQ642236</b>
<i>Lepisorus excavatus</i> (Willd.) Ching (1)	Tanzania; <i>Hemp 3561</i> (DSM)	<b>DQ642155</b>	<b>DQ642193</b>	<b>DQ642237</b>
<i>Lepisorus excavatus</i> (Willd.) Ching (2)	Grande Comore; <i>Rakotondrainibe et al. 6785</i> (P)	<b>DQ642156</b>	<b>DQ642194</b>	<b>DQ642238</b>
<i>Lepisorus longifolius</i> (Blume) Holttum	Malay Peninsula; <i>Cranfill BF012</i> (UC)	<b>DQ642157</b>	<b>DQ642195</b>	<b>DQ642239</b>
<i>Lepisorus megasorus</i> (C. Chr.) Ching	Taiwan; <i>Cranfill TW069</i> (UC)	<b>DQ642158</b>	<b>DQ642196</b>	<b>DQ642240</b>
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	cult. Bot. Gard. Zürich; <i>Kreier s.n.</i> (GOET)			<b>DQ642241</b>
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Taiwan; <i>Cranfill TW-115</i> (UC)	U05629	AY096226	
<i>Lepisorus thunbergianus</i> (Kaulf.) Ching	Japan; <i>Hasebe 512</i> (TI)	AY096203	AY096228	DQ179640
<i>Leptochilus decurrens</i> Blume	Java; <i>Douglas 28</i> (UC)			
<i>Leptochilus macrophyllus</i> (Blume) Noot. var. <i>wrightii</i> (Hook. & Baker) Noot.	Japan; <i>Craig s.n.</i> (UC)	AF470340	AY362639	AY083643
<i>Microsorium fortunei</i> (T. Moore) Ching	Taiwan; <i>Ranker 2087</i> (COLO)	<b>DQ642159</b>	<b>DQ642197</b>	<b>DQ642242</b>
<i>Microsorium grossum</i> (Langsd. & Fisch.) S. B. Andrews	French Polynesia; <i>Ranker 1941</i> (COLO)	<b>DQ179633</b>	<b>DQ179636</b>	<b>DQ179642</b>
<i>Microsorium linguiforme</i> (Mett.) Copel.	cult. Bot. Gard. Heidelberg nr. 106468; <i>Hagemann s.n.</i> (GOET)	AF470334	AY362635	AY083637
<i>Microsorium linguiforme</i> (Mett.) Copel.	New Guinea; <i>Ranker 1776</i> (UC)			
<i>Microsorium lucidum</i> (Roxb.) Copel.	cult. New York Bot. Gard.; A. R. <i>Smith s.n.</i> (UC1738194)	AF470335	AY096230	AY983638
<i>Microsorium lucidum</i> (Roxb.) Copel.	cult. Bot. Gard. Leiden nr. 3560; no voucher			
<i>Microsorium membranaceum</i> (D.Don) Ching	Taiwan; <i>Cranfill TW042</i> (UC)		<b>DQ642199</b>	<b>DQ642244</b>
<i>Microsorium membranaceum</i> (D.Don) Ching	source unknown; <i>Li et al. s.n.</i> (direct submission)	AY725054	<b>DQ642200</b>	<b>DQ642245</b>
<i>Microsorium membranifolium</i> (R. Br.) Ching	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	<b>DQ642161</b>	AY362636	AY083636
<i>Microsorium musifolium</i> (Copel.) Blume	cult. Bot. Gard. Heidelberg 105655; <i>Hagemann s.n.</i> (GOET)	AF470333		
<i>Microsorium musifolium</i> (Copel.) Blume	cult. UC Bot. Gard. nr. 58.0649; <i>Smith s.n.</i> (UC)	AF470336	–	AY083639
<i>Microsorium pappei</i> (Mett. ex Kuhn) Ching	cult. Bot. Gard. Leiden (Schelpe 44179 from Madagascar); no voucher			
<i>Microsorium papuanum</i> (Baker) Parris	cult. Bot. Gard. Berlin; <i>Schuettpelz 603</i> (GOET)	<b>DQ642162</b>	–	<b>DQ642246</b>
<i>Microsorium punctatum</i> (L.) Copel.	cult. Bot. Gard. Heidelberg 102934; <i>Schneider s.n.</i> (GOET)		DQ164475	DQ164508
<i>Microsorium punctatum</i> (L.) Copel.	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	DQ164444		
<i>Microsorium scolopendrium</i> (Burm.f.) Copel. (1)	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	<b>DQ642163</b>	<b>DQ642201</b>	<b>DQ642247</b>
<i>Microsorium scolopendrium</i> (Burm.f.) Copel. (2)	Mayotte; <i>Rakotondrainibe et al. 6601</i> (P)	<b>DQ642164</b>	<b>DQ642202</b>	<b>DQ642248</b>
<i>Microsorium varians</i> (Mett.) Hennipman & Hett.	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	AY362566	AY362638	DQ179643

(Continued)

APPENDIX  
(CONTINUED)

Taxon	Origin; Voucher	rbel.	rps4 <sup>a</sup>	tml-F
<i>Microsorium viellardi</i> (Mett.) Copel.	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	DQ179635	DQ179638	DQ179645
<i>Microsorium zippelii</i> (Blume) Ching	Indonesia; <i>Tsutsunoi IN112</i> (TI)	AB232411	<b>DQ642203</b>	<b>DQ642249</b>
<i>Neochlopteryx ensata</i> (Thunb.) Ching	Taiwan; <i>Cranfill TW-104</i> (UC)		AY096229	—
<i>Neochlopteryx ensata</i> (Thunb.) Ching	Japan; <i>Craig s.n.</i> (UC)	AY096204		—
<i>Neochlopteryx palmatopedata</i> (Baker) H. Christ	cult. Bot. Gard. Zürich; <i>Schneider s.n.</i> (GOET)	AY362567	AY362640	DQ212059
<i>Neochlopteryx superficialis</i> (Bedd.) Bosman	Taiwan; <i>Cranfill TW-073</i> (UC)	AY725055	AY725048	AY725049
<i>Thylacopteris papillosa</i> (Blume) Krause ex J. Sm.	Java; <i>Gravendeel et al.</i> 559 (L)	AY459175	AY459183	AY459188
<b>platycerioids</b>				
<i>Platynerium alticorne</i> Desv.	cult. Bot. Gard. Göttingen; <i>Kreier CG0401</i> (GOET)	DQ164445	DQ164478	DQ164511
<i>Platynerium andinum</i> Baker	cult. Bot. Gard. Göttingen; <i>Kreier CG0402</i> (GOET)	DQ164446	DQ164477	DQ164510
<i>Platynerium bifurcatum</i> (Cav.) C. Chr.	cult. Bot. Gard. Göttingen; <i>Kreier CG0403</i> (GOET)	DQ164447	DQ164478	DQ164511
<i>Platynerium coronarium</i> (J. König ex O. F. Müller) Desv.	cult. Bot. Gard. Göttingen; <i>Kreier CG0404</i> (GOET)	DQ164448	DQ164479	DQ164512
<i>Platynerium elephantois</i> Schweinf.	cult. Bot. Gard. Göttingen; <i>Kreier CG0405</i> (GOET)	DQ164449	DQ164480	DQ164513
<i>Platynerium ellisii</i> Baker	cult. Bot. Gard. Göttingen; <i>Kreier CG0406</i> (GOET)	DQ164450	DQ164481	DQ164514
<i>Platynerium grande</i> (Fée) Kunze	cult. Charles Alford Nursery; <i>Alford s.n.</i> (GOET)	DQ164451	DQ164482	DQ164515
<i>Platynerium hillii</i> T. Moore	cult. Bot. Gard. Göttingen; <i>Kreier CG0407</i> (GOET)	DQ164452	DQ164483	DQ164516
<i>Platynerium holtiumii</i> De Joch. & Hennipman	cult. Bot. Gard. Göttingen; <i>Alford s.n.</i> (GOET)	DQ164453	DQ164484	DQ164517
<i>Platynerium madagascariense</i> Baker	cult. Bot. Gard. Göttingen; <i>Kreier CG0408</i> (GOET)	DQ164454	DQ164485	DQ164518
<i>Platynerium quadridichotomum</i> (Bonap.) Tardieu	cult. Bot. Gard. Göttingen; <i>Alford s.n.</i> (GOET)	DQ164455	DQ164486	DQ164519
<i>Platynerium ridleyi</i> H. Christ	cult. Bot. Gard. Göttingen; <i>Kreier CG0409</i> (GOET)	DQ164456	DQ164487	DQ164520
<i>Platynerium stemaria</i> (Beauv.) Desv. var. <i>stemaria</i>	cult. Bot. Gard. Göttingen; <i>Kreier CG0410</i> (GOET)	DQ164457	DQ164488	DQ164521
<i>Platynerium stemaria</i> var. <i>laurentii</i> De Wild.	cult. Bot. Gard. Göttingen; <i>Kreier CG0411</i> (GOET)	DQ164458	DQ164489	DQ164522
<i>Platynerium superbum</i> De Joch. & Hennipman	cult. Bot. Gard. Göttingen; <i>Kreier CG0412</i> (GOET)	DQ164459	DQ164490	DQ164523
<i>Platynerium veitchii</i> (Underw.) C. Chr.	cult. Bot. Gard. Göttingen; <i>Kreier CG0413</i> (GOET)	DQ164460	DQ164491	DQ164524
<i>Platynerium wallichii</i> Hooker	cult. Charles Alford Nursery; <i>Alford s.n.</i> (GOET)	DQ164461	DQ164492	DQ164525
<i>Platynerium wandae</i> Racib.	cult. Bot. Gard. Göttingen; <i>Kreier CG0414</i> (GOET)	DQ164462	DQ164493	DQ164526
<i>Platynerium willinckii</i> (T. Moore) Domin	cult. Charles Alford Nursery; <i>Alford s.n.</i> (GOET)	DQ164463	DQ164494	DQ164527
<i>Pyrrhosia angustata</i> (Sw.) Ching	cult. Bot. Gard. Leiden nr. 970503; <i>Hovenkamp s.n.</i> (L)	<b>DQ642165</b>	<b>DQ642204</b>	<b>DQ642250</b>
<i>Pyrrhosia assmilis</i> (Baker) Ching	cult. Bot. Gard. Edinburgh nr. 728/12; Sino-Amer. Bot. Exped. 805 (E)	DQ164464	DQ164495	DQ164528
<i>Pyrrhosia christii</i> (Giesenh.) Ching	cult. Bot. Gard. Göttingen; <i>Schneider s.n.</i> (GOET)	DQ164465	DQ164496	DQ164529
<i>Pyrrhosia elegnifolia</i> (Bory) Hovenkamp	cult. Bot. Gard. Edinburgh nr. 19982312; <i>Schneider s.n.</i> (E)	<b>DQ642166</b>	<b>DQ642205</b>	<b>DQ642251</b>
<i>Pyrrhosia foveolata</i> (Alston) C. V. Morton	cult. Bot. Gard. Edinburgh nr. 19621476; <i>Schneider s.n.</i> (E)	<b>DQ642167</b>	<b>DQ642206</b>	<b>DQ642252</b>
<i>Pyrrhosia lanceolata</i> (L.) Farw.	Malaysia; <i>Cranfill BF10</i> (UC)	DQ164467	DQ164498	DQ164531
<i>Pyrrhosia liebuschii</i> (Hieron.) Schelpe	Tanzania; <i>Janssen et al.</i> 2624 (P)	—	—	<b>DQ642253</b>
<i>Pyrrhosia linearifolia</i> (Hook.) Ching	Taiwan; <i>Cranfill TW-101</i> (UC)	DQ164468	DQ164499	DQ164532
<i>Pyrrhosia lingua</i> (Thunbg.) Farw.	cult. Bot. Gard. Edinburgh nr. 19992206; <i>Schneider s.n.</i> (E)	AF470343	DQ164500	AY083646

<i>Pyrostia longifolia</i> (Burm.) C. V. Morton					DQ164501	DQ164533
<i>Pyrostia niphoboloides</i> (Baker) M. Price					<b>DQ642207</b>	<b>DQ642254</b>
<i>Pyrostia polydactyla</i> (Hance) Ching					DQ164470	DQ164534
<i>Pyrostia porosa</i> (C. Presl.) Hovenkamp					DQ164497	DQ164530
<i>Pyrostia rasamalae</i> (Racib.) K. H. Shing					<b>DQ642169</b>	<b>DQ642255</b>
<i>Pyrostia rupestris</i> (R.Br.) Ching					AY362558	<b>DQ991141</b>
<i>Pyrostia samarensis</i> (Mett.) Ching					<b>DQ642170</b>	<b>DQ642256</b>
<i>Pyrostia serpens</i> (G. Forst) Ching					DQ164471	DQ164535
<i>Pyrostia subfurfuracea</i> (Hook.) Ching					AY362559	<b>DQ642257</b>
<b>Pleopeltis</b>						
<i>Pleopeltis pseudoaureum</i> (Cav.) Lellinger					<b>DQ642171</b>	<b>DQ642258</b>
<i>Pleopeltis angusta</i> Humb. & Bonpl. ex Willd.					AY362590	AF159199
<i>Pleopeltis appressa</i> M. Kessler & A.R. Sm.					<b>DQ642172</b>	<b>DQ642259</b>
<i>Pleopeltis ballivianii</i> (Rosenst.) A.R. Sm.					<b>DQ642173</b>	<b>DQ642260</b>
<i>Pleopeltis bombayina</i> (Maxon) A.R. Sm.					<b>DQ642174</b>	<b>DQ642261</b>
<i>Pleopeltis bachtienii</i> (H. Christ & Rosenst.) A.R. Sm.					<b>DQ642175</b>	<b>DQ642262</b>
<i>Pleopeltis fraseri</i> (Kuhn) A.R. Sm.					<b>DQ642176</b>	<b>DQ642263</b>
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.					<b>DQ642177</b>	<b>DQ642264</b>
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.					<b>DQ642178</b>	<b>DQ642265</b>
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.					<b>DQ642179</b>	<b>DQ642266</b>
<i>Pleopeltis macrocarpa</i> (Bory ex Willd.) Kaulf.					-	<b>DQ642267</b>
<i>Pleopeltis polypodioides</i> (L.) E.G. Andrews & Windham					AY362592	AF159196
<i>Pleopeltis remota</i> (Desv.) A.R. Sm.					<b>DQ642180</b>	<b>DQ642268</b>
<i>Pleopeltis thysanolepis</i> (A.Braun ex Klotzsch) E.G. Andrews & Windham					<b>DQ642181</b>	<b>DQ642269</b>
<i>Pleopeltis tweediana</i> (Hook.) A.R. Sm.					<b>DQ642182</b>	<b>DQ642270</b>
<i>Polypodium furfuraceum</i> Schtdl. & Cham.					AY362610	<b>DQ642271</b>
<i>Polypodium furfuraceum</i> Schtdl. & Cham.					AY362606	AF159195
<i>Polypodium guttatum</i> Maxon					<b>DQ642183</b>	<b>DQ642272</b>
<i>Polypodium hirsutissimum</i> Raddi					<b>DQ642184</b>	<b>DQ642273</b>
<i>Polypodium macrolopis</i> Maxon					-	-
<i>Polypodium monosorum</i> Desv.					AY362604	-
<i>Polypodium myriolepis</i> H.Christ					AY362607	-
<i>Polypodium rosei</i> Maxon					AY362608	AF159197

<sup>a</sup> rps4 and the rps4-trnS IGS are submitted to GeneBank as a continuous sequence.

<sup>b</sup> Submitted to Genbank as 5' and 3' partial sequences.