

PHYLOGENY AND BIOGEOGRAPHY OF THE STAGHORN FERN GENUS *PLATYCERIUM* (POLYPODIACEAE, POLYPODIIDAE)¹

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The genus *Platyserium* is one of the few pantropical epiphytic fern genera with six species in Afro-Madagascar, 8–11 Australasian species, and a single species in tropical South America. Nucleotide sequences of four chloroplast DNA markers are employed to reconstruct the phylogeny of these ferns and to explore their historical biogeography. The data set was designed to resolve conflicting hypotheses on the relationships within the genus that were based on previous phylogenetic studies exploring morphological evidence. Our results suggest a basal split of *Platyserium* into two well-supported clades. One clade comprises species occurring in Africa, Madagascar, and South America, whereas the second clade contains exclusively Australasian species. The latter clade is further divided into a clade corresponding to *P. bifurcatum* and its putative segregates and a clade of seven species occurring from Indochina throughout the Malesian region to New Guinea and Australia. The Afro-Madagascan clade includes a clade of two species found in tropical Africa and a clade of four species that includes three species endemic to Madagascar. The single neotropical species of this genus, *P. andinum*, is nested within the Afro-Madagascan clade but is not closely related to any extant species.

Key words: Africa; historical biogeography; Madagascar; Malesia; phylogeny; polygrammoid ferns; Polypodiaceae; South America.

In several recent studies, the evolution of epiphytic ferns was explored with phylogenetic approaches using nucleotide sequence data (e.g., Schneider et al., 2002, 2004a, c; Haufler et al., 2003; Janssen and Schneider, 2005). This approach provided new insights in the relationships of these ferns, biogeography, and morphological evolution. In this context, a similar study on the staghorn fern genus, *Platyserium* Desv., is of particular interest because we may solve a longstanding controversy about the relationships within this genus and its biogeographic history (Hoshizaki, 1972; Hennipman and Roos, 1982; Hoshizaki and Price, 1990; Hoshizaki and Moran, 2001).

The staghorn fern genus, *Platyserium* Desv., stands out among ferns as one of the most commonly grown ornamental ferns (Hoshizaki and Moran, 2001; Poremski and Biedinger, 2001; Darnaedi and Praptosuwiryo, 2003). Both the economic value and the accessibility of living plants is reflected in the frequent use of these ferns in studies on cytological, developmental, and physiological features of vascular plants (e.g., Camloh and Gogala, 1992; Kwa et al., 1995; Ong et al., 1995; Brumme et al., 1998; Camloh et al., 1999; Holtum and Winter, 1999; Abrozoic-Dolinsek et al., 2002). These attractive plants are distinct from other ferns by the presence of stellate hairs (shared with *Pyrrosia* Mirbel) on the leaf lamina, the differentiation of the leaves into litter collectors—often called mantle leaves or base fronds—and dichotomously forked trophosporophylls with coenosoroid to acrosoroid patches of sporangia (Hoshizaki, 1970, 1972; Hennipman and Roos, 1982; Lee, 1989; Hoshizaki and Price, 1990; Hoshizaki and

Moran, 2001). The genus consists of 15 to 18 species growing predominantly as epiphytes or sometimes on rocks in subtropical to tropical lowland forests. They are among the most frequent vascular plant epiphytes in those forests and predominantly grow in relatively open conditions (Boyer, 1964; Hoshizaki, 1972; Kornas, 1979; Hennipman and Roos, 1982; Benzing, 1990; Gardette, 1996; Leon and Young, 1996; Hoshizaki and Moran, 2001; Zotz and Hietz, 2001). Occurrence of crassulacean-acid-metabolism (CAM) and formation of water-storage tissue are further conspicuous characters suggesting adaptation to open conditions in dry, semideciduous forests (e.g., Hennipman and Roos, 1982; Benzing, 1990; Burrows, 1990; Ong et al., 1995; Zotz and Hietz, 2001).

Platyserium is one of the few genera of polygrammoid ferns with a pantropical distribution although only a single species, *P. andinum* Baker, is found in tropical South America (Hoshizaki, 1972; Hennipman and Roos, 1982; Hoshizaki and Price, 1990; Hoshizaki and Moran, 2001). Roughly one half (six species) of all species occurs in Africa and Madagascar, while 8–11 species are found in subtropical to tropical Asia, Malesia, and Australia. None of these species occurs in all three regions distinguished here, and the species diversity in the Afro-Madagascan region is notable because all other genera of polygrammoid ferns show a much lower rate of species diversity in Africa when compared to either the neotropics or the Australasian region.

Two studies explored the relationships among the species of *Platyserium* using morphological evidence and a cladistic approach to analyze these data (Hoshizaki, 1972; Hennipman and Roos, 1982), but both analyses generated strongly divergent hypotheses. They disagree in the proposed relationships of several species, although their data sets are based on more or less the same morphological characters. They differ mainly in the homology assessment of some characters and by differently weighing the information of other characters (Hennipman and Roos, 1982; Hoshizaki and Price, 1990). In

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contrast to Hennipman and Roos (1982), the phylogenetic hypothesis of Hoshizaki (Hoshizaki, 1972; Hoshizaki and Price, 1990) suggested a strong correlation between clade differentiation and geographical distribution. The Afro-Madagascan species together with the neotropical taxa form one clade, whereas the Australasian species form its sister clade. This second clade was divided into two putative natural groups in which one corresponds to the *P. bifurcatum* (Cav.) C. Chr. complex consisting of either a single species with four varieties or of four morphological quite similar species with partly overlapping distributions (Hoshizaki, 1972; Hennipman and Roos, 1982; Bostock and Spokes, 1998; Hoshizaki and Moran, 2001). The phylogenetic hypothesis of Hoshizaki (1972) suggests an early split of *Platynerium* into an African clade and an Asiatic clade, whereas Hennipman and Roos (1982) hypothesize a more complex pattern created by repeated long-distance dispersal and/or extinction events. So far, the phylogeny of staghorn ferns has not been explored using DNA sequence data, which may provide new evidence in the ongoing controversy.

The introduction of phylogenetic studies based on cpDNA sequence data has strongly improved our understanding of the evolution of polygrammoid ferns (Schneider et al., 2002, 2004a, c; Ranker et al., 2004). These studies have confirmed some of the proposed relationships but challenged other generally accepted or controversial hypotheses of natural relationships. Whereas most of these studies focused on global relationships, some data sets were designed to explore the relationships in particular lineages/genera of polygrammoid ferns, such as the grammitid fern *Adenophorus* (Ranker et al., 2003), the ant-fern *Lecanopteris* (Haufler et al., 2003), the non-natural genus *Polypodium* and its relatives (Haufler and Ranker, 1995; Haufler et al., 2000; Schneider et al., in press), and the drynarioid ferns (Janssen and Schneider, 2005). The study on drynarioids is of particular interest for the study of *Platynerium* because both lineages were studied with a cladistic approach using morphological evidence and share the occurrence of a single, well-studied sister lineage. The cpDNA data supported most of the relationships suggested by morphological evidence (Roos, 1985), improved our understanding of their evolution based on the clearly defined sister clade, and increased information about the phylogenetic distance among species (Janssen and Schneider, 2005; H. Schneider and T. Janssen, in preparation). The sister lineage of *Platynerium*, the genus *Pyrrhosia*, was studied in a comprehensive monographic study using morphological evidence (Hovenkamp, 1986). The relationships of both genera were assumed based on the shared character of stellate hairs on the lamina, which was subsequently supported in global phylogenetic studies of polygrammoids (Schneider et al., 2002, 2004c).

In this study, we explore the phylogeny of *Platynerium* using sequences of four cpDNA regions for all currently accepted species. Using this evidence, we want to infer the hypotheses of Hoshizaki (1972) and Hennipman and Roos (1982) as well as reconstruct the biogeographic history of this fern lineage. It has been proposed that the neotropical species *P. andinum* is closely related to the Madagascan *P. quadridichotomum* (Bonap.) Tardieu (Hoshizaki, 1972; Hennipman and Roos, 1982; Hoshizaki and Price, 1990; Moran and Smith, 2001), and this putative species pair was included in a list of possible vicariance events between South America and Africa (Moran and Smith, 2001). However, neither the fossil record (van

Uffelen, 1991; Collinson, 2001) nor divergence time estimates (Schneider et al., 2004b) support an origin of these ferns before the breakup of Gondwana, which is required in the vicariance hypothesis. In general, historical biogeography of these ferns may provide unique insights into the evolution of epiphytic vegetation in extant subtropical and tropical forests.

MATERIALS AND METHODS

Samples of leaf material were collected of all currently accepted species of *Platynerium* from the Old Botanical Garden of the University of Göttingen and from the garden of Charles Alford (Florida). At least a single representative was collected of each species including representatives of all four putative segregates of the *P. bifurcatum* complex, both variations of *P. stemaria* (Beauv.) Desv., and three collections of *P. alcorni* Desv. Sequences of other polygrammoid ferns were predominantly used in previous studies (Schneider et al., 2002, 2004a, c; Janssen and Schneider 2005; Schneider et al., in press), but some additional sequences, especially for *Pyrrhosia*, were added in this study. Voucher specimens were deposited at the herbarium of the University Göttingen (GOET), whereas all new sequence data were submitted to GenBank (see Appendix for voucher information and GenBank accession numbers).

Genomic DNA was extracted using Invisorb Plant Mini kit (Invitex, Berlin, Germany). Sequences of four chloroplast regions, *rbcL*, *rps4*, *rps4-trnS* intergenic spacer (IGS), and *trnL-F* IGS, were generated using PCR primers and protocols identical to those in previous studies (Haufler et al., 2003; Schneider et al., 2004a, c; Janssen and Schneider, 2005). PCR products were prepared for sequencing with a BigDye Terminator Cycle Sequencing kit, version 3.1 (ABI Prism, Applied Biosystems, Foster Coty, California, USA) and sequenced using an ABI capillary sequencer 3100 (Applied Biosystems). All sequences were assembled and manually aligned using BioEdit (<http://www.mbio.ncsu.edu/BioEdit/bioedit.html>), and the final alignment was adjusted manually in MacClade 4.0 (Maddison and Maddison, 2000). Ambiguously aligned regions were excluded from all analyses. Taxonomically informative indels were identified visually.

Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed with PAUP* version 4.0b10 (Swofford, 2000). Model and parameters were selected using the hierarchical likelihood ratio test and the Akaike information criterion as implemented in Modeltest (Posada and Crandall, 1998). MP and ML analyses were calculated using the heuristic mode with 1000 respectively 100 random-addition-sequence replicates, tree-bisection-reconnection (TBR) branch swapping to completion, and MULTIPARS on. Bootstrap support values were estimated by calculating 100 or 1000 respectively 100 bootstrap replicates, each with 10 random-addition-sequence replicates, TBR branch swapping, and MULTIPARS on. NeighborNet (Bryant and Moulton, 2004) and split decomposition analyses (Huson, 1998), based on a distance matrix calculated using the general-time-reversible (GTR) model, were applied to estimate alternative relationships within *Platynerium*, indicated by subset of characters.

The distribution ranges of ancestral nodes were inferred using the software DIVA (Ronquist, 1997), which allows us to estimate ancestral distributions by taking dispersal and vicariance events into account. In addition, a maximum parsimony approach was applied to reconstruct ancestral distributions with both ACCTRAN and DELTRAN optimization of character state changes as implemented in MacClade 4.0. Likelihood estimates of ancestral area estimates were calculated using the one-parameter Markov K-state model (Lewis, 2001) as implemented in the ancestral state reconstruction packages for Mesquite 9.0 (Maddison and Maddison, 2003; website, <http://mesquiteproject.org>). This approach maximizes the probability of arriving at the distribution of terminal taxa, given a stochastic model of evolution (Schluter et al., 1997; Pagel, 1999). Information about species distributions was obtained from herbarium specimens and literature (Hennipman and Roos, 1982; Johns, 1991; Bostock, 1998; Roux, 2001; Fernandez, 2003). The influence of the hypothetical basal lineage of African *Pyrrhosia*, as suggested in a phylogenetic analysis of this genus (Hovenkamp, 1986), was inferred by generating a hypothetical phylogeny in which such a lineage is placed as the sister to all other lineages within *Pyrrhosia*. Patterns of character evolution were reconstructed using MacClade 4.0 by plotting the character matrices of previous studies (Hoshizaki, 1972; Hennipman and Roos, 1982) onto the phylogeny recovered using the combined cpDNA data set.

RESULTS

Phylogeny of *Platynerium*—Maximum parsimony and maximum likelihood analyses of the combined data sets found the same general topology (Figs. 1, 2). The maximum parsimony analyses resulted in 36 most parsimonious trees of a length 3729 steps (consistency index [CI] = 0.421, homoplasy index [HI] = 0.579, retention index [RI] = 0.727, rescaled consistency index [RC] = 0.364), whereas the maximum likelihood found a single tree with a $-\ln = 24\,041.06$ using the GTR model with the parameters based on a base-pair distribution of A = 0.3035, C = 0.1863, G = 0.2087, T = 0.3017, rate of invariable sites I = 0.3067, and a gamma distribution of $\Gamma = 1.200$. *Pyrrosia* was found to be sister to a monophyletic genus *Platynerium*, which consists of three lineages with 100% bootstrap support in maximum parsimony and maximum likelihood analyses. These clades correspond to the Afro-American group, Javan-Australian group, and Malayan-Asian group proposed by Hoshizaki (1972). All analyses recovered with considerable support the Afro-Madagascan-neotropical clade as sister to the other two clades. Analyses of the single-gene data sets did not give any evidence for conflicting information among the four cpDNA data sets.

The Afro-American clade showed an internal split into a tropical African clade comprising *P. elephantotis* Schweinf. and *P. stemaria* (Beauv.) Desv. and a Madagascan clade including all species occurring in Madagascar. Sister to three exclusively Madagascan species (*P. ellisii* Baker, *P. madagascariense* Baker, *P. quadridichotomum* (Bonap.) Tardieu) is *P. alcicorne* Desv., which is the only species occurring in Madagascar and along the coast of East Africa. Samples of *P. alcicorne* from East Africa and Madagascar possessed 100% identical *trnL-F* IGS sequences. The sole New World species, *P. andinum* Baker, comes out as sister to the Madagascan subclade but without bootstrap support. Neither the single cpDNA marker data sets nor the combined data set found evidence for the hypothesis of *P. andinum* being sister species to *P. quadridichotomum*.

The Javan-Australian clade is synonymous to the *P. bifurcatum* complex, which occurs throughout the Sunda Islands and eastern Australia. The four cpDNA markers were more or less identical in the four samples that correspond to one representative of each putative species [*P. bifurcatum* (Cav.) C. Chr., *P. hillii* T. Moore, *P. veitchii* (Underw.) C. Chr., *P. willinckii* T. Moore].

Among the seven species of the Malayan-Asian clade, *P. coronarium* (J. König ex O.F. Müll.) Desv. and *P. ridleyi* forms a strongly supported subclade. These two species occur more or less sympatric in western Malesia (Malay Peninsula, Sumatra, Java, Borneo), the Philippines, and the southern part of Indochina (only *P. coronarium*). The remaining five species are also grouped in a strongly supported clade, but their internal relationships were poorly resolved. Two species pairs were found without bootstrap support, *P. grande* (Fée) Kunze + *P. holtumii* de Jonch. & Hennipman, *P. superbum* de Jonch. & Hennipman + *P. wandae* Racib., leaving *P. wallichii* Hook. as an isolated taxon.

The neighborNet and split-decomposition analyses found no alternatives to the strongly supported clades but indicate that the current data set is insufficient to distinguish between alternative relationships among the *P. wallichii* group and the clade comprising three species endemic to Madagascar.

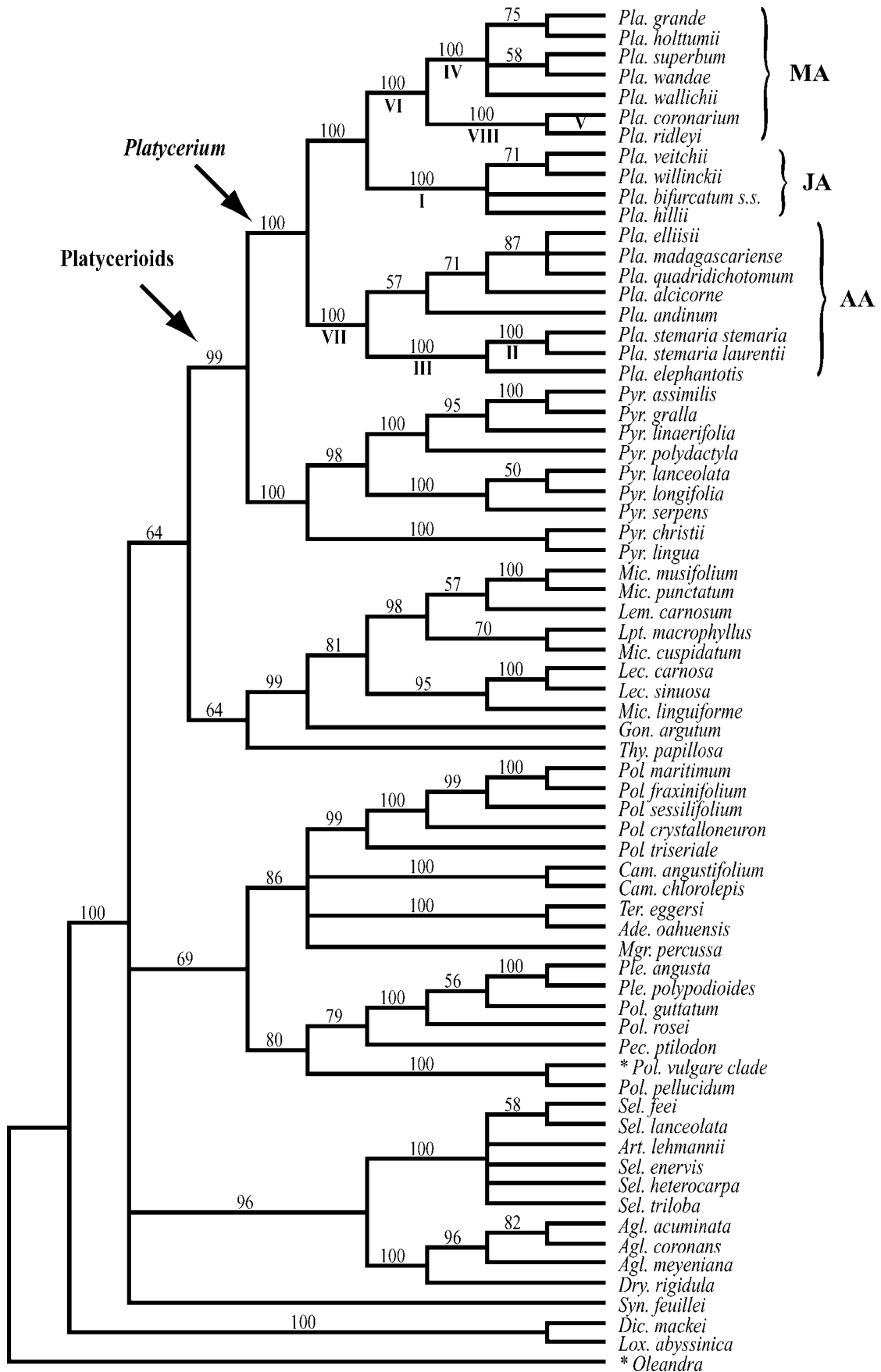
Several clades of *Platynerium* possess clade-specific deletion or insertion with a length of more than two base pairs in the

two studied chloroplast spacer regions. None of the clades showed more than one indel. These signatures allow us to recognize the major phylogenetic groups using these two IGS regions.

Phylogenetic biogeography of *Platynerium*—The phylogeny suggests an early split into an Afro-Madagascan lineage and an Australasian lineage (Fig. 3). The first one splits into a tropical African lineage with two species and an East African-Madagascan lineage with four species of which three are endemic to Madagascar. *Platynerium alcicorne* is sister to an exclusively Madagascan clade and its occurrence in both East Africa and Madagascar may indicate a dispersal from East Africa to Madagascar. However, likelihood reconstruction allows us to suggest an origin of this species in Madagascar with a subsequent expansion of its distribution to East Africa, the Comoros, and Mascarenes. The ancestor of the neotropical *P. andinum* likely occurred in the Afro-Madagascan region, but the exact pattern is ambiguous. The Australasian sister lineage of the Afro-Madagascan clade may have originated either in Australia or SE Asia as indicated by likelihood and maximum parsimony reconstructions of ancestral distributions. The Javan-Australian lineage may have originated in Australia and expanded its distribution towards Java. The alternative concept of an origin in Java and migration to Australia cannot be excluded based on current data. Its sister lineage, the Australasian clade, may have its ancestral distribution either in Australia or Indochina + western Malesia, but likelihood estimates gave slightly higher probabilities for the second hypothesis. The ancestors of the clade containing *P. superbum* and *P. wandae* were growing in central or western Malesia, whereas the alternative hypothesis of origin in eastern Malesia to Australia is less likely, according to the phylogenetic reconstructions. The clade comprising *P. coronarium* and *P. ridleyi* is more or less restricted to western Malesia + Philippines. Likewise, *P. wallichii* occurs in Thailand, Burma, and northern India. The other two putative species pairs may be the result of disruptions of their ancestral distribution. *Platynerium grande* from the Philippines is sister to *P. holtumii* occurring in Indochina, whereas *P. superbum* from eastern Australia is sister to *P. wandae* occurring in New Guinea. In general, the ancestral distributions for many basal nodes are poorly resolved.

DISCUSSION

Hypotheses for *Platynerium* phylogeny—The Malayan-Asian clade of *Platynerium* is easily recognized by the soral patches, of which there are only one or two per frond. In the sister species *P. coronarium* and *P. ridleyi*, these patches are localized at specialized lobes of the lamina, whereas in the other five species of this lineage these patches are on conspicuously broadened sinuses (Hoshizaki, 1972; Hoshizaki and Price, 1990). Hennipman and Roos (1982) did not accept the homology of the soral patches and found those taxa nested in different clades. Their cpDNA data support the homology assessment of Hoshizaki (1972) by providing evidence for a putative transformation of the sorus location at broadened sinuses to specialized lobes of the lamina. The two species with the specialized lobes, *P. coronarium* and *P. ridleyi*, were found to be sister species, and their position as sister to the other species with soral patches leaves it unclear if this condition evolved from those patches as found in the *P. wallichii* clade.



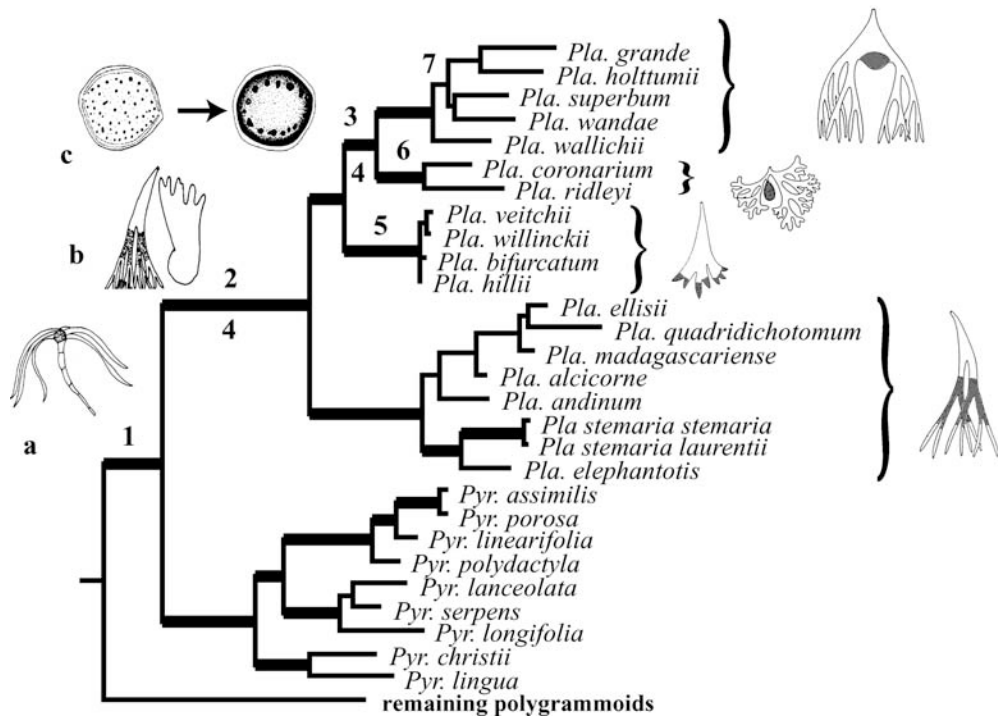


Fig. 2. Phylogram of the maximum likelihood (ML) analyses of the combined data set. Only platyceriods are shown. Length of branches corresponds to the like number of substitutions. Thick branches indicate support of $\geq 95\%$ in ML bootstrap analyses. Sketches of fertile leaves illustrate the typical position of the coenosori (gray areas) in the major lineages of *Platycerium*. The sketches are based on Hoshizaki (1972). Numbers above or below branches correspond to putative synapomorphic character states. Unambiguous reconstructions are given above branches, whereas those characters with alternative optimization of character reconstructions under ACCTRAN and DELTRAN are given below branches. 1 = presence of stellate hairs on the lamina (a); 2 = differentiation of mantle leaves (b, trophosporophyll on the left, mantle leaf on the right); 3 = one to two soral patches that are localized relatively basally on the fertile frond + dark sclerenchymatous cells in the cortex of the stipe (illustrated c); 4 = root buds present or absent (present in all species of *Platycerium* except the members of the clade including *P. ridleyi* to *P. grande*); 5 = scales pseudopeltate to peltate; 6 = sporangia located on a stalked lobe of the lamina + only eight spores per sporangium + sporangium reduced + large scales with flabelloid margin; 7 = large scales without flabelloid margin.

The sister pair *P. coronarium* and *P. ridleyi* share several unique morphological characters, such as reduced sporangia containing only eight spores instead of sixty-four, the shape of the paraphyses, and the ornamentation of the spores (Hoshizaki, 1972; Hennipman and Roos, 1982). The relationships among the remaining taxa of the Malayan-Asian clade are still not fully discovered. *Platycerium wallichii* is isolated morphologically by several autapomorphic character states such as the lack of marginal scale indument. Reduction of one main branch in the foliage frond, horizontally exposed soral patches, and the long paraphyses rays have been interpreted as character states that suggest relationships to the African *P. elephantotis*. These homology assessments were criticized

because the character states are too variable in this fern genus (Hoshizaki and Price, 1990). The structure of the stipe cortex and the soral patches indicates the alternative relationships with members of the Malayan-Asian clade that are strongly supported by cpDNA evidence. In contrast to conflicting hypotheses concerning *P. wallichii*, close relationships among the remaining four species of this lineage were undisputed, based on the presence of more or less sinuate base frond margin with a conspicuous fringe and the very dense set of hairs on the rhizome scales (Hoshizaki, 1972; Hennipman and Roos, 1982; Hoshizaki and Price, 1990).

The Javan-Australian clade is easily recognized by the occurrence of subpeltate to peltate rhizome scales. The

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Fig. 1. Bootstrap consensus tree obtained in a maximum parsimony analyses of the combined data set. Numbers above branches correspond to bootstrap values. The three major clades, Afro-American (AA), Javan-Australian (JA), and Malayan-Asian (MA), are indicated with parentheses. The other abbreviations indicate taxa occurring at least predominantly in: AU = Australia, IN = Indochina, MD = Madagascar; ME = Madagascar and east Africa; TA = tropical Africa, NG = New Guinea; NT = neotropics; PH = Philippines; and WM = western Malesia. Genera are abbreviated as follows: *Ade.* = *Adenophorus*, *Agl.* = *Aglomorpha*, *Art.* = *Arthromeris*, *Cam.* = *Campyloneurum*, *Dic.* = *Dictymia*, *Dry.* = *Drynaria*, *Gon.* = *Goniophlebium*, *Lec.* = *Lecanopteris*, *Lem.* = *Lemmaphyllum*, *Lpt.* = *Leptochilus*, *Lox.* = *Loxogramme*, *Mic.* = *Microsorium*, *Mgr.* = *Microgramma*, *P.* = *Platycerium*, *Ple.* = *Pleopetis*, *Pol.* = *Polypodium*, *Pyr.* = *Pyrrosia*, *Sel.* = *Selliguea*, *Ter.* = *Terpsichore*; *Thy.* = *Thylacopteris*. Taxa marked with a star are composed of sequences from different species of the same genus. The Latin numbers below the branches indicate the presence of clade-specific insertions-deletions of more than two base pairs. I = insertion in the *trnL-F* IGS of TTTATTTAACCCCA; II = insertion in the *trnL-F* IGS of TTCTCA; III = deletion in the *rps4-trnS* IGS of ATTTATGC; IV = deletion in the *rps4-trnS* IGS of AAAAGACTTAG; V = deletion in the *rps4-trnS* IGS of CTTGTTCATT; VI = insertion in the *rps4-trnS* IGS of CAAATT(GA)A; VII = deletion in the *rps4-trnS* IGS.

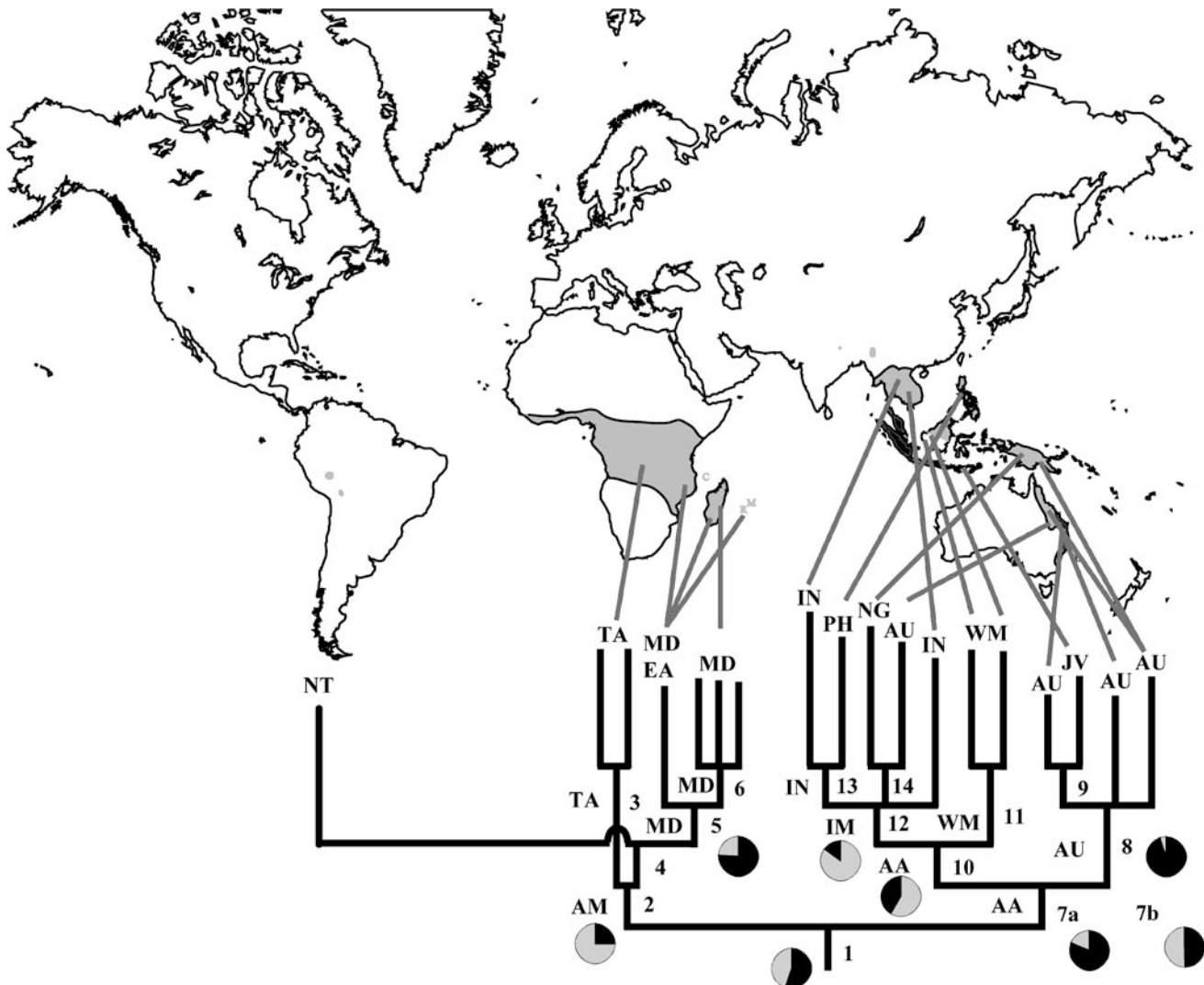


Fig. 3. Distribution and phylogeny of the genus *Platycerium* including reconstructed distribution of each ancestor. Gray areas indicate current distribution of the genus. Reconstructed ancestral areas are given to each node: AA = Australasian, AM = Afro-Madagascan region, AU = Australia, EA = east Africa, IN = Indochina, IM = Indochina + Western and Central Malesia; JV = Java, MD = Madagascar, ME = Madagascar + East Africa, NG = New Guinea, PH = Philippines, SA = South America, NA = New Guinea + Australia, NT = neotropics, TA = tropical Africa, WA = western Malesia. Probability of ancestral areas was calculated using likelihood approaches for nodes 1 to 14, but pie charts are only given for 1, 2, 5, 6, 7, 8, 10, and 12. Two versions are given for node 7 marks as 7a and 7b. Pie chart node 1, 2, 7a: gray = Afro-Madagascan, black = Australasian. Pie chart node 5: gray = tropical Africa or neotropics, black = Madagascan. Pie chart node 7b, 8, 11, 12: gray = Indochina, western and central Malesia, Black = Australia and eastern Malesia.

presented data does not provide further insights into the differentiation of this clade because sampling is insufficient (only four specimens), and the markers are not variable enough to resolve the internal phylogeny of this clade.

The Afro-American clade is characterized by the presence of well-developed central meristemes in the stipes and by the ability to proliferate through root buds, although root buds are also found in *P. bifurcatum* s.s. Hoshizaki (1972) regards *P. andinum* as a lineage apart within the Afro-American clade sharing only plesiomorphic traits with the others, especially *P. quadridichotomum*. Our results strongly support the lack of any morphological synapomorphic character state distinguishing *P. andinum* and *P. quadridichotomum*. Characters such as brown, mature base fronds and the position of the fertile fronds and

soral patches are either homoplastic or plesiomorphic. The two tropical African species, *P. elephantotis* and *P. stemaria*, are characterized by the occurrence of mixed sporangia (intermingling of sporangia of different maturity in the same sporangia patch) and distantly inserted receptacles (0.6–0.9 mm apart), but these features occur also in some Asiatic taxa (Hoshizaki, 1972).

Inference of *Platycerium* phylogeny using morphological characters is difficult because of the variability of some features and the absence of many critical characters in the sister clade *Pyrrhosia* (Hovenkamp, 1986). Denser sampling is not likely to smooth out this gap because none of the extant species of *Pyrrhosia* resembles closely the morphology of *Platycerium*. Hovenkamp (1986) stressed out the occurrence of asymmetric leaves in *Pyrrhosia africana* (Kunze) F. Ballard as a single

character suggesting close relationships between this species and the *Platynerium* lineage, but we did not have access to DNA from this species. Some putatively interesting traits, such as the evolution of CAM, are impossible to investigate based on the paucity of observations (Ong et al., 1995; Holtum and Winter, 1999; Zotz and Hietz, 2001).

A further issue is the limitation of available DNA sequence data to the chloroplast genome, which is likely inherited maternally in these ferns (Vogel et al., 1998). These data make it impossible to detect misleading information that is caused by introgression and/or hybrid speciation (Linder and Rieseberg, 2004). However, the few hybrids reported for these ferns are only known to arise only in cultivation (Hoshizaki, 1975; Hoshizaki and Price, 1990; Hoshizaki and Moran, 2001), and no hybrids were ever reported to occur in the wild. This is similar to other groups of polygrammoid ferns in which nearly all known natural hybrids are members of the temperate *Polypodium* s.s. lineage. Based on a study of the epiphytic polygrammoid fern genus *Pleopeltis* in Mexico, Hafler et al. (2000) suggested different speciation mechanisms in *Pleopeltis* vs. temperate *Polypodium*. Similar results were found for the epiphytic asplenoid fern, *Asplenium nidus*, in Australasia (Yatabe et al., 2001). This hypothesis implies that hybridization and introgression are rare or at least less common in tropical epiphytic ferns.

Scenarios of historical biogeography—The reconstruction of the history of *Platynerium* is hindered by the absence of fossils allowing us to estimate the distribution of this genus in space and time. Inference of divergence times is problematic for the whole lineage of polygrammoid ferns due to their poor fossil record and equivocal assignment of these few fossils to extant lineages (van Uffelen, 1991; Collinson, 2001; Kvacek et al., 2004). However, the current fossil record of derived ferns and existing divergence time estimates indicate that this genus did not originate before the Eocene (Schneider et al., 2004b). The observed split into an Afro-American and Australasian lineage is unlikely to be the result of the breakup of Gondwana. Similar, the proposed vicariance between *P. andinum* and other members of the Afro-American clade does not fit in with the time of the Gondwana break-up. Long-distance dispersal with subsequent speciation events is therefore the preferred explanation for the observed origin of the Southern American species from Afro-Madagascan ancestors. A similar problem arises with the separation of the Afro-Madagascan and Australasian clades of *Platynerium*. The sister clade, *Pyrrosia*, also occurs in both regions but has a considerably higher species diversity in Australasia than in the Afro-Madagascan region. Unfortunately, current sampling of *Pyrrosia* is insufficient to test the hypothesis of an African clade as sister to the remaining clades of *Pyrrosia*, as suggested by Hovenkamp (1986). To test the putative influence of this putative sister clade to the remaining species of *Pyrrosia* missing in this study, we reconstructed ancestral areas using DIVA, MP, and ML analyses with and without inclusion of this putative clade. However, both analyses failed to provide unambiguous support for either an Afro-Madagascan or Australasian origin. The pattern recovered within the Afro-Madagascan clade fits best with the hypothesis of a colonization of Madagascar by species occurring in Africa followed by a subsequent speciation event(s). The three species endemic to Madagascar occur mainly in the northern habitats that may have evolved since the Eocene/Oligocene (Wells, 2003). The diversification of these ferns in the Australasian region is mysterious, but a few

conclusions seem to be possible. This region evolved as a result of the collision between Southeast Asia and the Australian croton in the Miocene (Hall, 2002). In a recent study on drynarioid ferns, evidence was found for a correlation of the distribution pattern and species diversity of these ferns with the formation of the Malesian region in the Miocene (H. Schneider and T. Janssen, unpublished manuscript). Whereas drynarioid ferns often grow in wet rainforests dominating the core of Malesia, *Platynerium* occurs predominantly in seasonally dry forests found in Indochina, the Sunda Islands, and eastern Australia (Hoshizaki, 1972; Hennipman and Roos, 1982). The phylogenetic patterns may, therefore, reflect the unfolding of these habitats since the drift of Australia from the southern Pacific towards SE Asia. Long distance dispersal events may have been an important factor, but we also need to consider the transformation of the vegetation in Malesia during and after the Pleistocene glaciations. Currently available information is insufficient to fully explore these hypotheses.

In summary, the current distribution of *Platynerium* appears to be created by the combination of long-distance dispersals and subsequent speciation(s) in Madagascar and Australasia.

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APPENDIX. Voucher specimens and GenBank accession numbers. A dash indicates that the region was not sampled. Collected material was obtained either from field collections or more often from cultivated material from one of the following Botanical Gardens: BGG = Old Botanical Garden of the University of Göttingen, Germany; BGH = Botanical Garden of the University of Heidelberg, Germany; CAN = Charles Alford Plant Nursery, Vero Beach, Florida, USA; RBGE = Royal Botanic Garden Edinburgh, UK. Country of origin is given for material from field collections. Voucher specimens are deposited in one of the following herbaria: DSM = University of Dar es Salaam, E = Royal Botanic Garden Edinburgh, GOET = Herbarium of the University of Göttingen, LPB = Herbario Nacional de Bolivia, Bolivia, UC = University herbarium, University of California.

(A) Voucher information for newly generated sequences

Taxon; GenBank accession: *rbcl*, *rps4* + *rps4-trnS*, *trnL-F*; **Source;** Voucher specimen.

- Dictydia mckeei* Tindale; DQ164441, DQ164462, DQ164504; Cult. RBGE, Coll. Nr. 19842659 (E).
Goniophlebium argutum (Hook.) J. Sm.; DQ16442, DQ164473, DQ164505; Taiwan, Cranfill TW075 (UC).
Loxogramme abyssinica (Baker) M. G. Price; DQ164443, DQ164474, DQ164506; Tanzania, Hemp 3638 (DSM).
Microgramma percussa (Cav.) de la Sota; —, —, DQ164507; Cult. BGG, Schneider s.n. (GOET). *Microsorium punctatum* (L.) Copel.; DQ164444, DQ164474, DQ164508; cult. BGH, Schneider s.n. (GOET).
Platycerium alaicorne Desv.; DQ164445, DQ164476, DQ164509; Cult. BGG, Kreier CG0401 (GOET). *P. andinum* Baker; DQ164446, DQ164477, DQ164510; Cult. BGG, Kreier CG0402 (GOET). *P. bifurcatum* (Cav.) C. Chr.; DQ16447, DQ164478; DQ164511; Cult. BGG, Kreier CG0403 (GOET). *P. coronarium* (J. König ex O. F. Müller) Desv.; DQ164448, DQ164479, DQ164512; Cult. Bot. Gard. Göttingen, Kreier CG0404 (GOET). *P. elephantotis* Schweinf.; DQ164449, DQ164480, DQ164513; Cult. BGG, Kreier CG0405 (GOET). *P. ellisii* Baker; DQ164450, DQ164481, DQ164514; Cult. BGG, Kreier CG0406 (GOET). *P. grande* (Fée) Kunze; DQ164451, DQ164482, DQ164515; Cult. CAN, Alford s.n. (GOET). *P. hillii* T. Moore; DQ164452, DQ164483, DQ164516; Cult. BGG, Kreier CG0407 (GOET). *P. holttumii* De Jonch. & Hennipman; DQ164453, DQ164484, DQ164517; Cult. CAN, Alford s.n. (GOET). *P. madagascariense* Baker; DQ164454, DQ164485, DQ164518; cult. Bot. Gard. Göttingen, Kreier CG0408 (GOET). *P. quadridichotomum* (Bonap.) Tardieu; DQ164455, DQ164486, DQ164519; Cult. CAN, Alford s.n. (GOET).
Platycerium ridleyi Christ; DQ164456; DQ164487; DQ164520; Cult. BGG, Kreier CG0409 (GOET).
P. stemaria (Beauv.) Desv.; DQ164457, DQ164488, DQ164521; Cult. BGG, Kreier CG0410 (GOET). *P. stemaria* var. *laurentii* De Wild.; DQ164458, DQ164489, DQ164522; Cult. BGG, Kreier CG0411 (GOET). *P. superbum* De Jonch. & Hennipman; DQ164459, DQ164490, DQ164523; Cult. BGG, Kreier CG0412 (GOET). *P. veitchii* (Underw.) C. Chr.; DQ164490, DQ164491, DQ164524; Cult. BGG, Kreier CG0413 (GOET). *P. wallichii* Hooker; DQ164461, DQ164492, DQ164525; Cult. CAN, Alford s.n. (GOET). *P. wandae* Racib.; DQ164462, DQ164493, DQ164426; Cult. BGG, Kreier CG0414 (GOET). *P. willinckii* (T. Moore) Domin; DQ164463, DQ164494, DQ164527; Cult. CAN, Alford s.n. (GOET).
Pyrrosia assimilis (Baker) Ching; DQ164464, DQ164495, DQ164528; Cult. RBGE, Coll. Nr. 728/12, Sino-Amer. Bot. Exped. 805 (E). *P. christii* (Giesenh.) Ching; DQ164465, DQ164496, DQ164529; Cult. BGG, Schneider s.n. (GOET). *P. porosa* (Pers.) Hovenkamp; DQ164466, DQ164497, DQ164430; Taiwan, Cranfill TW094 (UC). *P. lanceolata* (L.) Farw.; DQ164467, DQ164498, DQ164431; Malay Peninsula, Cranfill BF10 (UC). *P. linaerifolia* (Hooker) Ching; DQ164468; DQ164499; DQ164532; Taiwan, Cranfill TW101 (UC). *P. lingua* (Thunbg.) Farw.; —, DQ164500, —; Cult. RBGE, Coll. Nr. 19992206 (E). *P. longifolia* (Burm.) Morton; DQ164469, DQ164501, DQ164533; Cult. BGG, Schneider s.n. (GOET). *P. polydactyla* (Hance) Ching; DQ164470, DQ164502, DQ164534; Cult. BGG, Schneider s.n. (GOET). *P. serpens* (G. Forst) Ching; DQ164471; DQ164503, DQ164535; Cult. RBGE, Coll. Nr. 19734551 (E).
Polypodium crystalloneuron Rosenst.; DQ151907, DQ151932, DQ151959; Bolivia, Jimenez 1176 (LPB). *P. fraxinifolium* Jacq.; DQ151909, DQ151934, DQ151961; Bolivia, Jimenez 1035 (LPB). *P. maritimum* Hieron.; DQ151918, DQ151943, DQ151970; Cult. CAN, Alford s.n. (UC). *P. sessilifolium* Desv.; DQ151923, DQ151948, DQ151975; Bolivia, Jimenez 755 (LPB). *P. triseriale* Sw.; DQ151926, DQ151953, DQ151980; Bolivia, Jimenez 1994 (LPB).
Synammia feuillei (Bertero) Copel.; DQ168808, DQ168813, DQ168819; Chile, Juan Fernandez Islands, Danton and Perrier s.n. (UC).

(B) Genbank accession numbers of sequences used in previous studies (Haulfer and Ranker, 1995; Schneider et al., 2002, 2004a, c; Haulfer et al., 2003; Ranker et al., 2003, 2004; Janssen and Schneider, 2005)

Taxon; GenBank accession: *rbcl*, *rps4* + *rps4-trnS*, *trnL-F*.

- Adenophorus oahuensis* (Copel.) L. E. Bishop; AY057382, AY096236, AF469789. *Aglaomorpha acuminata* (Willd.) Hovenkamp; AY529147, AY529172, AY459176. *A. coronans* (Wall. ex Mett.) Copel.; AF470349, AY459184, AY529463. *A. meyeniana* Schott; AY529153, AY459185, AY529470. *Arthromeris lehmannii* (Mett.) Ching; AY096216, AY096198, AY459177.
Campyloneurum angustifolium (Sw.) Fée; AF470344, AY362645, AY083648. *C. chlorolepis* Alston; AF470345, AY362646, AY093647.
Drynaria rigidula (Sw.) Bedd.; AY529166, AY529188, AY529481.
Lecanopteris carnosa (Reinw.) Blume; AF470322, AY362634, AY083625. *L. sinuosa* (Wall. ex Hook.) Copel.; AF470321, AY096227, AY083624. *Lemmaphyllum carnosum* C. Presl; AF470332, AY362631, AY083635. *Leptochilus macrophyllum* (Blume) Noot.; AF470340, AY362639, AY083643.
Microgramma percussa (Cav.) de la Sota; AY362574, AY362648, —. *Microsorium lucidum* (Roxb.) Copel.; AF470335, AY096230, AY083638. *M. musifolium* (Copel.) Blume; AF470333, AY362636, AY083636.
Oleandra Cav. (*O. cumingii* J. Sm. + *O. pistillaris* (Sw.) C. Chr.); AY093597, AY096209, AY093596.
Pecluma pilodon (Kunze) M. G. Price; AY362588, AY362661, AF159193. *Pleopeltis angusta* Humb. & Bonpl. ex Willd.; AY362590, AY362664, AF159199. *P. polypodioides* (L.) E. G. Andrews & Windham; AY362592, AY362665, AF159196. *Polypodium guttatum* Maxon; AY362606, AY362678, AF159195. *P. pellucidum* Kaulf.; U21149, AY096234, AF159190. *P. rosei* Maxon; AY362608, AY362680, AF159197. *P. vulgare* L. s.l. (*P. glycyrrhiza* D.C. + Eaton, *P. vulgare* L.); U21146, X84137, AF159188. *Pyrrosia lingua* (Thunbg.) Farw.; AF470343; —; AY083646.
Selliguea enervis (Cav.) Ching; AY096200, AY096218, AY459178. *S. feei* Bory; AY459179, AY529192, AY459179.
S. heterocarpa (Blume) Blume; AY362619, AY459180, AY459172. *S. lanceolata* (Mett.) E. Fourn.; AY459186, AY459173, AY459181. *S. triloba* (Houtt.) M. G. Price; AY459174, AY459187, AY459182.
Terpsichore eggersii (Baker ex Hook.) A. R. Sm.; AF468209, AY362694, AF469798. *Thylacopteris papillosa* (Blume) Kunze ex J. Sm.; AY459175, AY459188, AY459183.