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Towards a phylogenetic classification of the climbing fern genus *Arthropteris*

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Abstract We inferred the classification of the Paleotropical climbing fern genus *Arthropteris* and its close relative *Psammiosorus*, a monotypic genus endemic to Madagascar. The classification of these ferns has until now been poorly understood. To address this, we sampled more than half of the species diversity covering the whole range of the genus including the outlying occurrence at the Juan Fernández Islands. To reconstruct phylogenetic relationships, we obtained DNA sequences from up to six plastid genome regions, including coding and non-coding regions, for these two genera and representatives of all families of the eupolypod I clade, with an emphasis on the Tectariaceae. These data were analyzed using maximum parsimony, maximum likelihood, and Bayesian inference. We also obtained divergence time estimates. Three questions were addressed. (1) We established that *Arthropteris* and *Psammiosorus* form a well-supported clade representing a separate taxon based on their morphological distinctiveness, phylogenetic relationships, and separation since the Eocene from other accepted families of eupolypod ferns. (2) *Psammiosorus* was found to be nested within *Arthropteris*. (3) Our analyses supported recognition of a previously doubted species endemic to the karst regions of southern China and northern Vietnam. As a consequence of our results, we describe the new family Arthropteridaceae and introduce the new combination *Arthropteris paucivenia* for the Madagascan endemic previously treated under *Psammiosorus*.

Keywords *Arthropteris*; family classification; monotypic genera; natural classification; paraphyletic taxa; *Psammiosorus*; Tectariaceae

Supplementary Material Alignment is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

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■ INTRODUCTION

The genus *Arthropteris* J. Sm. ex Hook. f. comprises ten to twenty species of mainly climbing or scrambling ferns. It occurs throughout the Paleotropics, and extends to New Zealand, southern China and some eastern Pacific islands such as the Juan Fernández Islands (e.g., Holttum, 1966; Pichi Sermolli, 1966; Kramer, 1990; Lawalrée, 1990, 1991; Bell, 1998; Badré, 2008; Brownsey & Perrie, 2011). The phylogenetic relationships of species in this genus as well as the relationships of the genus to other derived fern genera are still poorly understood. The delimitation of some *Arthropteris* species is also still uncertain. Furthermore, little is known about the biogeographic history of *Arthropteris*. This study was principally designed to improve

understanding of the natural classification of these ferns, so that their taxonomy better reflects evolutionary history.

Arthropteris has been considered to have a close relationship to Davalliaceae and/or to the genus *Oleandra* Cav. (e.g., Liew, 1977; Kramer, 1990; Tryon & Lugardon, 1991), but recent phylogenetic analyses have supported a sister relationship of *Arthropteris* and the monotypic *Psammiosorus* (C. Chr.) C. Chr. to the clade comprising *Tectaria* Cav. and its relatives (Liu & al., 2007a; Schuettpelz & Pryer, 2007; Kuo & al., 2011). However, all studies considered this relationship as requiring further confirmation. The most recent fern classifications (Smith & al., 2006, 2008; Christenhusz & al., 2011) treated *Arthropteris* as a member of Tectariaceae. Notably, *Arthropteris* and *Psammiosorus* are distinct from Tectariaceae s.str. in

their predominantly climbing habit and the occurrence of leaves articulated to stipe-like phyllopodia. Besides *Arthropteris* and *Psammiosorus*, stipe-like phyllopodia are found only in the genus *Oleandra*, while articulated, rhizome-like phyllopodia are found in Davalliaceae and Polypodiaceae (Hovenkamp & Ho, 2012). These facts indicate the need to consider another family placement for *Arthropteris* and *Psammiosorus*.

Arthropteris has been regarded as closely related to the monotypic *Psammiosorus*, whose single species *P. paucivenius* (C. Chr.) C. Chr. is endemic to western Madagascar (Kramer, 1990; Schuettpelz & Pryer, 2007; Lehtonen, 2011). The two genera share the climbing habit but differ in leaf venation. Leaves of *Arthropteris* have free veins whereas *Psammiosorus* has irregularly but consistently anastomosing veins (Christensen, 1932; Kramer, 1990). However, leaf venation may be a homoplastic character in some groups of ferns and several genera include species with both free and netted veins (e.g., Hovenkamp, 1996; Schneider, 1996; Schneider & al., 2010). Previous phylogenetic studies (Schuettpelz & Pryer, 2007; Lehtonen, 2011) were unable to test the relationship of *Psammiosorus* to *Arthropteris* because of insufficient taxonomic sampling. Based on morphology, two hypotheses need to be considered: (1) *Psammiosorus* is sister to *Arthropteris* or (2) *Psammiosorus* is nested within *Arthropteris*.

The delimitation of species is the third unknown in the classification of *Arthropteris*. *Arthropteris* species vary in rhizome indument (shape and size of scales), leaf shape and dissection (pinnate or pinnate-pinnatifid to bipinnate), and sorus morphology (indusium present or absent). However, leaf shape is sufficiently variable in some species to obscure the distinctions among species, and the presence or absence of indusia may be unreliable as a taxonomic character (Holtum, 1966). This is reflected in different taxonomic treatments that consider *Arthropteris beckeri* (Hook.) Mett. and *A. repens* (Brack.) C. Chr. as separate from or part of *A. palisotii* (Desv.) Alston (Holtum, 1966; Bell, 1998; Wu & al., 2005; Brownsey & Perrie, 2011). This controversy also applies to *A. guinanensis* H.G. Zhou & Y.Y. Huang, a species based on specimens from Guangxi that are exindusiate and have flexuous pinnae margins (Zhou & al., 1996), but which is considered by some authors as a synonym of the widespread *A. palisotii* (Xing & al., 2012) or *A. repens* (Zhang, 2012). Uncertainty of species delimitation appears to be a widespread problem in climbing ferns (Moran, 2000; Hovenkamp & Ho, 2012). Here, we explore the capacity of DNA sequence data of the plastid genome to delimitate species of climbing ferns.

This study was designed to address these three issues using sequence data from up to six regions of the plastid genome. The datasets were assembled using previously published data available at GenBank and newly generated DNA sequences for up to 25 newly studied specimens including 11 species of *Arthropteris* plus the monotypic *Psammiosorus*. Phylogenetic inference was employed to address the family classification of *Arthropteris*, the generic classification of *Psammiosorus*, and the capacity of DNA sequences of the plastid genome to delimit species with emphasis on the distinctiveness of *A. guinanensis*. Finally, we used the recovered phylogenetic relationships to explore the biogeographic history of these ferns.

■ MATERIALS AND METHODS

Taxon sampling. — We assembled a dataset of 32 specimens of the *Arthropteris*-*Psammiosorus* clade, of which 25 were newly sequenced including the type of *Arthropteris*, *A. tenella* (G. Forst) J. Sm. ex Hook. f. The ingroup also included eight species of Tectariaceae s.str. (*Tectaria* s.l.), five species of Polypodiaceae, two species of Davalliaceae, one species of Oleandraceae, two species of Lomariopsidaceae, and one species of Nephrolepidaceae. This sampling was designed to be informative about the relationships of the *Arthropteris*-*Psammiosorus* clade as well as to test the two alternative hypotheses concerning the relationships of *Psammiosorus* and *Arthropteris*: *Psammiosorus* as sister to or nested within *Arthropteris*. The outgroup comprised eleven species of Dryopteridaceae and three species of Hypodematiaceae (Liu & al., 2007a, b; Schuettpelz & Pryer, 2007; Kuo & al., 2011; Lehtonen, 2011). Considering the uncertainty of generic classification in the Tectariaceae, all species of the *Tectaria* lineage were presented as species of *Tectaria* but alternative generic names such as *Ctenitopsis* and *Quercifilix* are given in parentheses in Fig. 1.

In the absence of a comprehensive taxonomic revision of *Arthropteris*, we followed species identifications as currently accepted in regional Floras such as *Flora of Australia* (Bell, 1998), *Flore des Mascareignes* (Badré, 2008), and the checklist of the Fijian ferns (Brownsey & Perrie, 2011). Thus, we accepted several species that have been treated as synonyms of other species by some authors. In total, we sampled up to eleven species of *Arthropteris*, with three from Afro-Madagascar and up to eight from the Asian-Australian-Pacific region. The poorly known *A. guinanensis* was represented by four specimens collected in Guangxi Province of China and one specimen collected in northern Vietnam (Appendix 1).

DNA extraction, PCR amplification, and sequencing. — DNA was extracted from silica-dried leaf fragments using either a modified CTAB approach (Doyle & Doyle, 1987) or the Plant Genomic DNA Kit (Tiangen Biotech Co., Beijing, China) following the manufacturer's protocol. DNA sequences of the chloroplast genome were amplified for up to six regions per specimen using established primers and protocols: *atpA* (Schuettpelz & Pryer, 2007), *atpB* (Liu & al., 2007b), *rbcL* (Chen & al., 1998), *rps4+rps4-trnS* intergenic spacer (Thomson & al., 2005), *trnL-F* region including the *trnL* intron and *trnL-trnF* intergenic spacer (Taberlet & al., 1991; Wang & al., 2003), and *trnG-R* intergenic spacer (Nagalingum & al., 2007). PCR products were cleaned using standard procedures. Sequences were generated by performing cycle-sequencing using either big dye chemistry and an ABI capillary sequencer of the Natural History Museum (London, U.K.) or by the Invitrogen Company (Guangzhou, China). Alignments were generated manually using Mesquite v.2.75 (Maddison & Maddison, 2011). Gaps were treated as missing data. We explored the non-coding markers for ambiguously aligned regions and inversions. None were identified.

Phylogenetic analyses. — Phylogenetic relationships were reconstructed using maximum parsimony (MP) as implemented in PAUP* v.4.0b10 (Swofford, 2002), maximum likelihood

(ML) as implemented in RAxML (Stamatakis & al., 2008) and PHYML (Guindon & Gascuel, 2003), and Bayesian inference (BI) of phylogeny as implemented in MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & al., 2012). jModeltest v.0.1.1 (Posada, 2008) was used to identify the optimal model of sequence evolution for ML and BI analyses. Akaike information criterion (AIC) was used to select the model for ML, whereas the Bayesian information criterion (BIC) was employed to select the model for BI. In the ML and BI analyses, we employed the optimal model but estimated the parameter values simultaneously with the tree search. Maximum parsimony analyses were performed using heuristic searches with 100 random-addition starting trees (RAS), TBR branch-swapping, and searches until completion. Strict consensus trees were calculated when more than one most parsimonious tree was found. Bootstrap values for MP (MP-BS) were obtained using 1000 bootstrap replicates, each with 10 RAS, and TBR. Maximum likelihood analyses were carried out using the default settings of RAxML. Trees were calculated with the data unpartitioned and partitioned into coding versus non-coding. Maximum likelihood bootstrap values (ML-BS) were obtained with 500 replicates and the default options. Bayesian inference analyses were conducted with both partitioning options and the optimal models implemented. Standard settings were employed in the BI analyses including the number of MCMC chains. Tracer v.1.5 (Rambaut & Drummond, 2009) was used to examine the results of the Bayesian analyses, particularly the convergence of the eight chains. The burn-in phase was determined using Tracer but we did not use the 10% default option. The TreeAnnotator tool of BEAST v.1.7.4 (Drummond & al., 2012) was used to summarize the trees obtained after the burn-in phase. Values given in the text correspond to the results of ML and BI analyses with the partitioning of coding versus non-coding regions. Evidence for the absence of conflict among genes regions was explored by visual comparison of the bootstrap consensus trees obtained in MP analyses of each region. We used the 70% criterion to identify evidence for incongruency (Mason-Gamer & Kellogg, 1996).

To explore the strength of the phylogenetic signal, we performed Neighbor-Net analyses (Bryant & Moulton, 2004) as implemented in SplitsTree v.4.10 (Huson & Bryant, 2006). We used LogDet distances (Lockhart & al., 1994) combined with filters including Least Square weighting and maximum dimensions set to four.

Morphological character reconstruction. — Selected morphological characters, e.g., growth habit and presence of leaf articulation, were plotted onto the phylogenetic hypothesis obtained from the ML analysis of the complete DNA sequence dataset. Character evolution was reconstructed using MP and ML as implemented in Mesquite v.2.75 (Maddison & Maddison, 2011). The ML reconstruction was carried out using the command to resolve zero branch length and the MK1 (Lewis, 2001) model of character evolution. Both ACCTRAN and DELTRAN character optimization were employed for MP analyses if applicable. The character leaf articulation was scored as presence of any kind of articulation including both phyllopodia with articulation and pinnae with articulation. A more

complex scoring was also employed in which these two types were distinguished but we show only the results of the simple presence/absence scoring. The growth habit of climbing versus non-climbing was scored rather restrictively. We employed a definition of climbing that required the taxon to have long-climbing rhizomes that originate from rhizomes rooted in the soil. This definition therefore excluded hemi-epiphytes. Furthermore, we scored taxa only as climbing when they regularly climb. For example, a climbing habit occurs in some species of Davalliaceae, Nephrolepidaceae, and Polypodiaceae, but it is unusual in these families.

Divergence time estimates. — Divergence time estimates were calculated using the lognormal relaxed molecular clock approach as implemented in BEAST v.1.7.4. The estimates were obtained using the three-gene dataset (*atpA*, *atpB*, *rbcL*) with each species reduced to a single representative. We only included specimens that had sequences for each of the three regions. The *Arthropteris palisotii* complex was reduced to one specimen of *A. submarginalis* Domin from Australia, one specimen of *A. repens* from Fiji, and one specimen of *A. palisotii* from China. The unpartitioned dataset was analysed with the GTR+I+G model implemented. The estimates were constrained using lognormal time constraints at three robust nodes: the root of the eupolypod I clade (mean age of 98.9 Ma), the age of the ingroup (mean age of 66.1 Ma), and the split of Oleandraceae from its sister clade Davalliaceae-Polypodiaceae (mean age of 63.6 Ma). The mean estimate for each of these nodes was obtained from Schuettpelz & Pryer (2009), who generated a framework of divergence time estimates for ferns using DNA sequence data of the three genes used here and the fossil record. Neither *Arthropteris* nor *Tectaria* are known from the fossil record and thus we could not add further fossil-based constraints. Reliability of the age estimates was controlled by checking carefully the convergence of all parameters calculated using Tracer v.1.5 with special emphasis on the distribution of the age estimates. In addition, two independent BEAST runs were compared.

■ RESULTS

Phylogenetic analyses. — All analyses recovered *Psammosorus* as nested within *Arthropteris* (Fig. 1; Table 1). The *Arthropteris* clade was recovered as sister to *Tectaria* s.l. (node 1 in Fig. 1 and Table 1) and this sister relationship was found in all analyses (node 1 in Table 1). Nevertheless, Neighbor-Net analyses indicated conflicting evidence concerning the relationships of the *Arthropteris* clade: Our data also contain phylogenetic signal that places the *Arthropteris* clade with the Davalliaceae, Polypodiaceae, Oleandraceae, and/or Lomariopsidaceae to the exclusion of *Tectaria* s.l. (Fig. 2).

The *Arthropteris* clade comprised two main clades (nodes 3 and 5 in Fig. 1 and Table 1). One consisted of the *A. orientalis* complex plus *A. articulata* (Brack.) C. Chr. The latter species was found to be sister to the *A. orientalis* complex, which consisted of the three sampled Afro-Madagascan species *A. monocarpa* (Cordem.) C. Chr., *A. orientalis* (J.F. Gmel.) Posth., and *A. parallela* C. Chr. Only one out of the six plastid

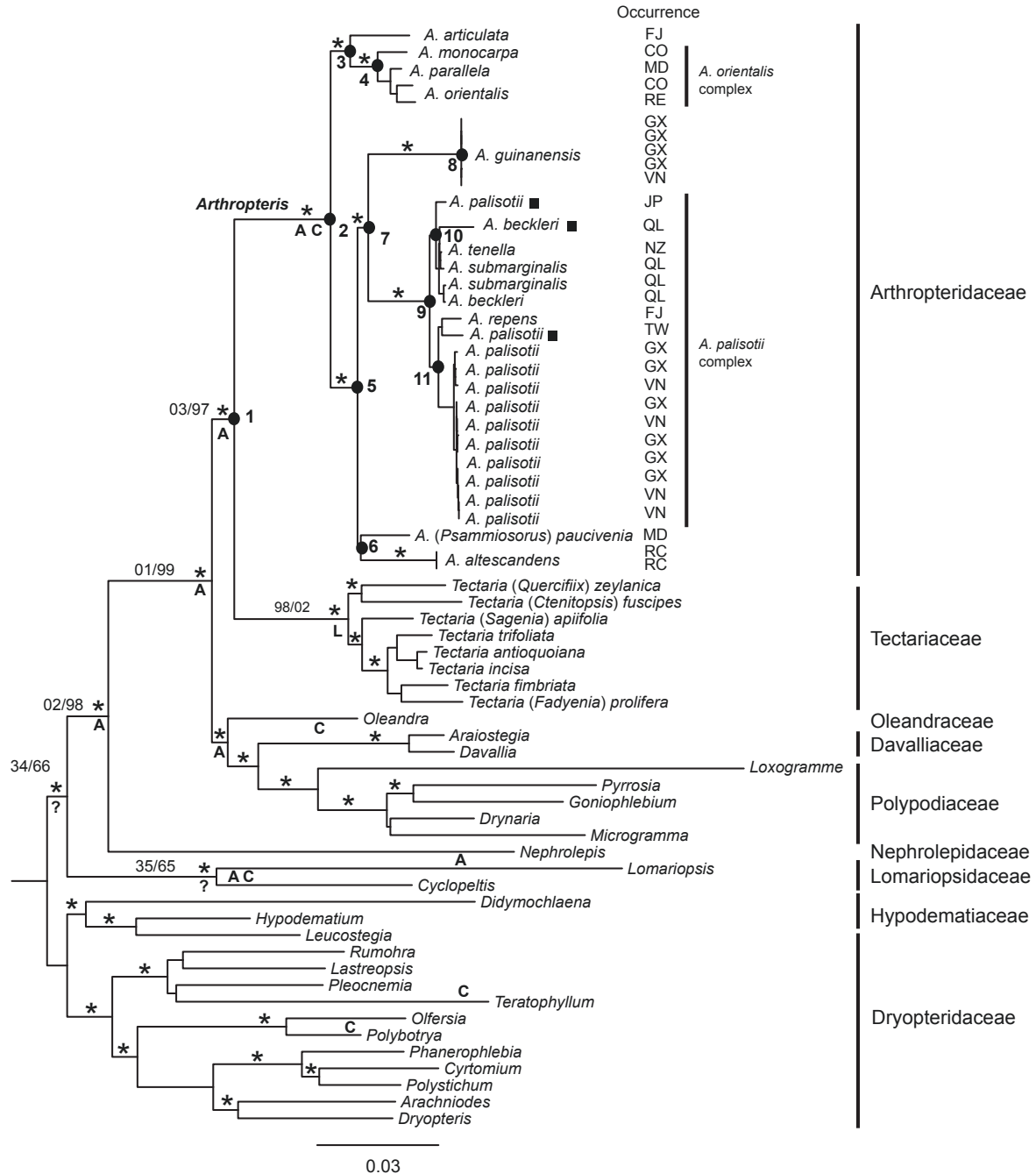


Fig. 1. Phylogenetic hypothesis obtained from the maximum likelihood analysis of the complete dataset (including all specimens and all regions). Dryopteridaceae and Hypodematiaceae were assigned to be the outgroups. Branch lengths correspond to the estimated number of substitutions. Family and genus names are given as used in the text. All species of Tectariaceae are recognized as *Tectaria* despite uncertainties about the generic classification of this lineage. Alternative generic names, such as *Ctenitopsis*, *Fadyenia*, *Psammiosorus*, *Quercifilix*, and *Sagenia*, are given in parentheses. The taxonomy of *Arthropteris* is based on current Floras with the exception of *A. guinanensis*. Occurrence data show localities of specimens of *Arthropteris*: CO = Grand Comoros, FJ = Fiji, GX = Guangxi Province, China, JP = Japan, MD = Madagascar, NZ = New Zealand, RC = Robinson Crusoe island (Juan Fernández Islands), RE = Réunion, QL = Queensland, Australia, TW = Taiwan, VN = northern provinces of Vietnam. Circles mark clades reported in Table 1 with the corresponding numbers 1 to 11 given either behind or below the circle. Squares indicate sequences of *A. beckeri* and *A. palisotii* that were obtained from GenBank (see Appendix 1). Stars indicate bootstrap values >95%. Capital letters above or below branches correspond to character reconstructions using maximum parsimony: A = clade with the ancestral character state of leaves with articulation either at the pinnae or petiole, C = clades/genera including climbing species, L = secondary loss of leaves with articulation in Tectariaceae; the question mark (?) = clades with equivocal reconstruction of the ancestral state of leaves without or with articulation. Numbers xx/xx indicate the percentage likelihood for the character states "leaves without articulation"/"leaves with articulation" using the maximum likelihood method in Mesquite. These maximum likelihood probabilities for character states are given only for nodes with probability values >99.2%.

Table 1. Summary of analyses to reconstruct the phylogeny of *Arthropteris*.

Dataset	Analysis	MPT	1	2	3	4	5	6	7	8	9	10	11	T/S	R/P*
<i>atpA</i>	ML	–	55	100	93	na	95	na	71	100	100	100	94	na	nr
<i>atpB</i>	ML	–	83	99	92	100	55	na	91	100	100	nr	88	nr	61
<i>rbcL</i>	ML	–	nr	99	al ^a	77	100	na	al ^b	100	99	nr	nr	nr	nr
<i>rps4</i>	ML	–	78	98	42	81	93	<50	<50	100	100	<50	91	nr	99
<i>trnL-F</i>	ML	–	56	100	82	98	97	na	63	100	100	99	99	nr	<50
<i>trnG-R</i>	ML	–	92	100	86	na	na	na	69	100	100	94	98	na	100
Total	ML	–	97	53	52	<50	58	<50	66	100	69	82	66	nr	nr
	BI	–	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	<0.95	nr	nr
3Genes	ML	–	79	100	93	na	100	na	85	100	100	99	84	na	<50
	MP	12	64	100	88	na	100	na	94	100	100	96	83	na	64
	BI	–	0.99	1.0	1.0	na	1.0	na	<0.95	1.0	1.0	1.0	1.0	na	1.0
3Genes+	ML	–	65	100	98	na	100	na	92	100	100	100	100	na	100
	MP	13	66	100	96	na	100	na	97	100	100	100	99	na	100
	BI	–	0.90	1.0	1.0	na	1.0	na	1.0	1.0	1.0	1.0	1.0	na	1.0

Columns correspond to datasets; kind of analysis (maximum likelihood, ML; maximum parsimony, MP; Bayesian inference, BI); number of most parsimonious trees (MPT); 1–11 are nodes marked in the phylogenetic hypothesis as shown in Fig. 1; T/S = differentiation of *A. tenella* versus *A. submarginalis*; R/P = differentiation of *A. repens* and *A. palisotii*. We present the results of ML, MP, and/or BI for each plastid region used (*atpA*, *atpB*, *rbcL*, *rps4* (= *rps4* + *rps4-trnS* IGS), *trnL-F* (= *trnL* intron + *trnL-trnF* IGS), *trnG-R* (= *trnG* intron + *trnG-trnR* IGS), and three combined analyses: Total corresponds to all data and all specimens (including specimens represented by a single region; see Fig. 1); 3Genes corresponds to a dataset including *atpA*, *atpB*, *rbcL* and exclusively specimens for which all three regions were obtained; 3Genes+ is the same dataset as 3Genes with respect to specimens but with the other genes added. The results for the nodes are presented as bootstrap values in case of the ML and MP analyses and as posterior *P*-values in case of BI; al = alternative relationships: al^a = *A. articulata* recovered as sister to clade 5 (ML-BS = 50%), al^b = *A. paucivenia* as sister to *A. guinanensis* (ML-BS = 83%); na = not applicable when one of the putative sister clades was not included; nr = not resolved when the clade collapsed in the most likely tree (ML) or consensus trees (MP, BI). * Datasets *atpB*, *rps4*, *trnL-F*, *trnG-R*, 3Genes, and 3Genes+ were restricted to Chinese samples of *A. palisotii*. Numbers considered to be of importance were printed in bold.

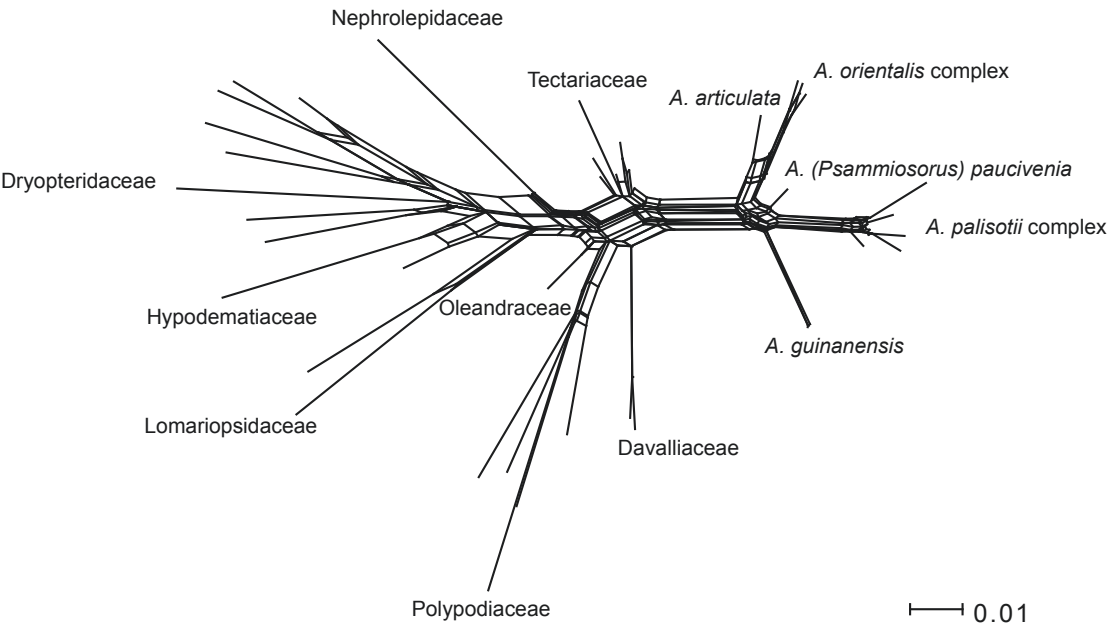


Fig. 2. Network of the combined dataset reconstructed using Neighbor-Net analyses and LogDet distances.

genome regions recovered an alternative in which *A. articulata* was sister to other main clade (nodes 3 and 4 in Fig. 1 and Table 1). The other main clade comprised the remaining species of *Arthropteris* as well as *Psammiosorus*. Four lineages were evident within this clade (Fig. 1). Three lineages each comprised a single species: *A. altescandens* J. Sm., *A. guianensis*, and *A. (Psammiosorus) paucivenia*. The fourth lineage comprised the *A. palisotii* complex including samples identified as *A. beckleri*, *A. palisotii*, *A. repens*, *A. submarginalis*, and *A. tenella*. The last species was found to be nested within the clade comprising specimens of *A. beckleri* and *A. submarginalis*. In turn this clade was closely related to a clade comprising specimens of *A. palisotii* and *A. repens*. The Japanese specimen of *A. palisotii* was found to be sister to the *A. beckleri*–*A. submarginalis*–*A. tenella* clade, whereas the Taiwanese specimen of *A. palisotii* was found to be the putative sister of *A. repens* from the Fiji islands (Fig. 1; Table 1). The relationships within the *A. palisotii* complex were ambiguous given the

low bootstrap values and posterior probability values obtained in most analyses (Fig. 1; Table 1).

Character reconstruction. — Maximum parsimony and maximum likelihood reconstructions supported the independent evolution of the climbing habit (defined as regularly climbing taxa with long-climbing rhizomes originating from rhizomes rooted in the soil) in three clades of the ingroup: *Arthropteris*, *Lomariopsis*, and *Oleandra*. Leaf articulation may have arisen in the common ancestor of the ingroup (MP equivocal, ML 66% probability) or in the common ancestor of the clade comprising all members of the ingroup with the exception of *Lomariopsidaceae* (MP origin of articulation, ML 98% probability). Articulation was found to be lost in the *Tectaria* clade as a result of an evolutionary reversal (MP loss of articulation, ML 98% probability).

Divergence time estimates. — Our estimates recovered a separation of *Arthropteris* and *Tectaria* s.l. dating to 59.6 (50.2 to 68.9) Ma (Fig. 3), which corresponds to the Late Cretaceous

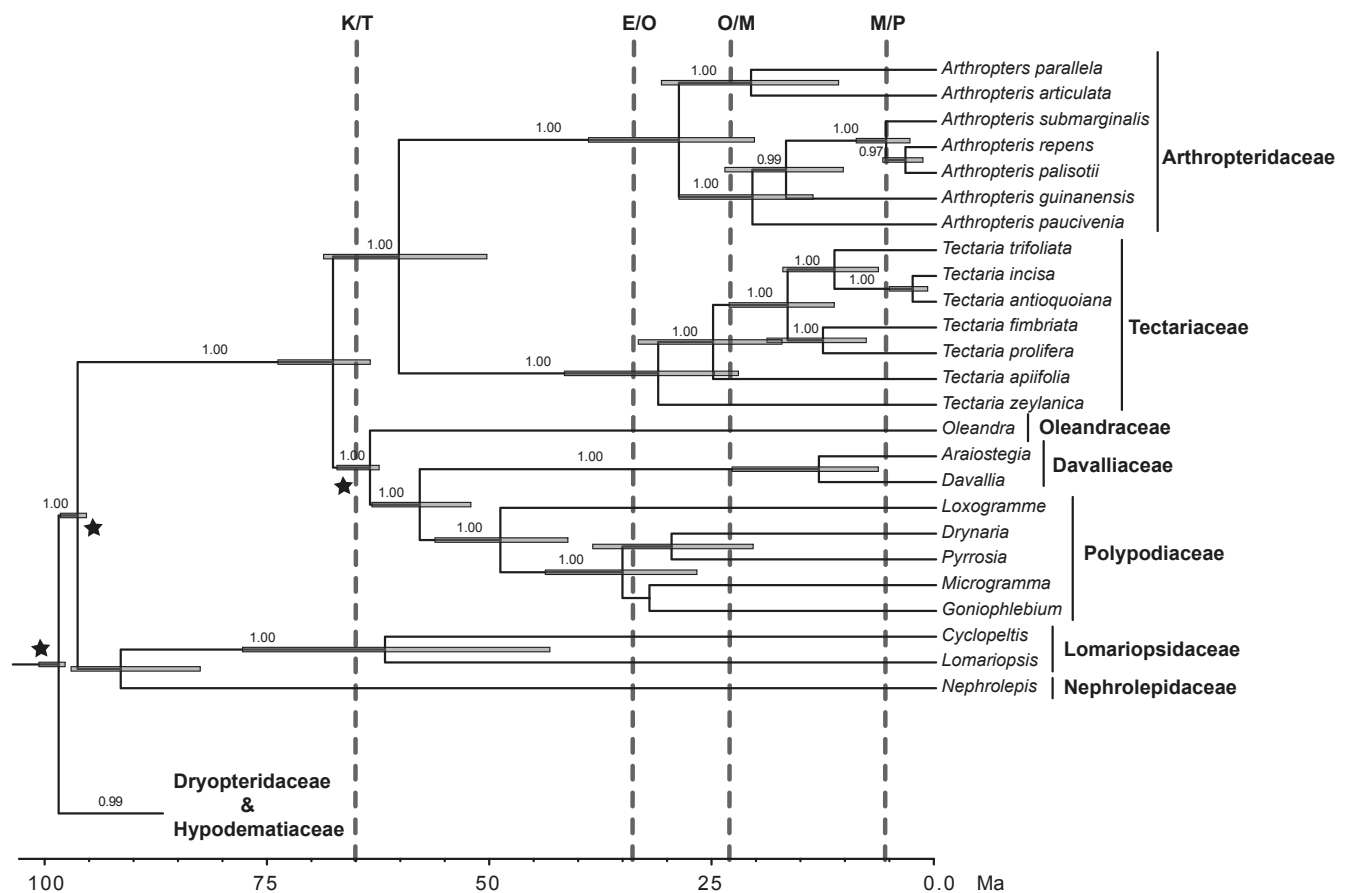


Fig. 3. Divergence time estimates based on lognormal relaxed molecular clock analyses of the 3Genes dataset using BEAST v1.7.4 (Drummond & al., 2012). Stars indicate nodes constrained using lognormal calibrations with mean age estimates obtained from Schuettpelz & Pryer (2009). Age estimates for the outgroup are not shown. Confidence intervals are shown as bars whereas mean age estimates are given by the chronogram. The time axis is formatted as millions of years before present (Ma). Posterior confidence values $P \geq 0.95$ are given above branches. Dashed lines indicate boundaries between geological epochs as defined by the International Chronostratigraphic Chart (www.stratigraphy.org): K/T = Cretaceous–Tertiary boundary; E/O = Eocene–Oligocene boundary; O/M = Oligocene–Miocene boundary; and M/P = Miocene–Pliocene boundary.

to Early Eocene radiation of derived ferns. The onset of the *Arthropteris* crown group diversification was estimated for the Late Oligocene (29.8 Ma with a confidence interval of 20.4 to 39.1 Ma). *Arthropteris* (*Psammiosorus*) *paucivenia* was found to be separated from its extant relatives since the Early Miocene (about 21.4 Ma with a confidence interval of 13.8 to 28.9), whereas *A. guinanensis* diverged about 17 Ma (10.4 to 23.7 Ma). The onset of the divergence of the *A. palisotii* complex was estimated as 6 Ma (2.9 to 8.9 Ma).

DISCUSSION

Towards a natural classification of *Arthropteris*. — Our results, with a much expanded sample of *Arthropteris*, are consistent with analyses reported previously (Liu & al., 2007a; Schuettpelz & Pryer, 2007; Kuo & al., 2011; Lehtonen, 2011). *Arthropteris*, when *Psammiosorus* is included in it, was found to form a distinct clade. For a decision on the taxonomic position of the *Arthropteris* clade, we consider four arguments to be relevant. (1) The node connecting *Arthropteris* and *Tectaria* s.l. generally obtained only moderate bootstrap and posterior probability values (see Table 1), and the branch subtending this clade was short in comparison to the branches subtending each of the *Arthropteris* and *Tectaria* s.l. clades. (2) The Neighbor-Net analyses recovered evidence for alternative relationships (Fig. 2). (3) Diversification time estimates provided evidence that the divergence of Davalliaceae, Oleandraceae, and Polypodiaceae happened around the same time period as the separation of the *Arthropteris* and the *Tectaria* s.l. clades. All families amongst this broader clade of derived ferns were established before the Eocene/Oligocene boundary (Fig. 3). (4) The morphology of *Arthropteris* is clearly distinct from that of the *Tectaria* s.l. clade. In our opinion, a strong morphological signal should only be overturned based on a very strong molecular phylogenetic signal, which was not reported in Schuettpelz & Pryer (2007), and which we also could not recover in our extended dataset. In conclusion, we consider all evidence to be best expressed by the recognition of two families: Tectariaceae s.str. and Arthropteridaceae.

The recognition of Arthropteridaceae as a separate family is consistent with recent classifications of eupolypods I and II, in which several species-poor families have been distinguished from related species-rich families because they are not nested within the species-rich family and because they are morphologically distinct (Smith & al., 2006, 2008; Christenhusz & al., 2011; Rothfels & al., 2012). For example, Onocleaceae are recognized as a separate family despite their sister relationship to Blechnaceae. The species-poor Onocleaceae is separated from the Blechnaceae by several distinct morphological features (see Smith & al., 2006).

As indicated above, *Arthropteris* is distinct from *Tectaria* s.l. in several morphological features including growth habit and the occurrence of articulation at the leaves. Character reconstruction, both in maximum parsimony and maximum likelihood analyses, recovered evidence that the presence of articulations is plesiomorphic in the eupolypod I clade comprising

Lomariopsidaceae, Nephrolepidaceae, Oleandraceae, Davalliaceae, Polypodiaceae, Arthropteridaceae, and Tectariaceae. Within this group, Lomariopsidaceae and Nephrolepidaceae have articulations between pinnae and rachis, while Arthropteridaceae, Davalliaceae, Oleandraceae, and Polypodiaceae have articulations between rhizome and stipe. In this scenario, Tectariaceae (= *Tectaria* s.l.) and part of Polypodiaceae have lost leaf articulation by evolutionary reversals. While we recognize the need of a phylogenetic investigation of Tectariaceae (Fig. 1), we think it is very unlikely that an increased sample of Tectariaceae would substantially alter its recovered relationship to *Arthropteris* or the reconstructions of the evolution of the characters we have discussed here.

The ingroup consists mainly of lineages showing predominantly three kinds of growth forms: climbing, hemi-epiphytism, or epiphytism. Tectariaceae are the principal exception because they usually are terrestrial or occasionally saxicolous. The loss of articulation in Tectariaceae thus coincides with a shift in ecological preference back to the ancestral terrestrial habit. This suggests that the presence of articulation of whatever kind may be linked to a climbing, hemi-epiphytic, and epiphytic growth form. These ecological and phylogenetic differences provide further arguments for the taxonomic separation of *Arthropteris* and Tectariaceae.

***Psammiosorus* is a synonym of *Arthropteris*.** — The Madagascar endemic *Psammiosorus* is nested within *Arthropteris* and thus the recognition of *Psammiosorus* renders the latter paraphyletic (Fig. 1; Table 1). This relationship is consistent with the shared growth form. Other characters considered to be informative are the absence of indusia and the netted venation. Most *Arthropteris* species have indusia but they are absent in *A. tenella* (type of the genus name), *A. altescandens*, and *A. guinanensis*, and the presence/absence of indusia does not seem a strong argument for keeping the two genera separated. Thus, only netted venation distinguishes *Psammiosorus* from the free-veined *Arthropteris*. However, netted venation has evolved independently many times in ferns and thus this character needs to be treated with care in the context of generic classifications (Schneider, 1996; Schneider & al., 2010). Our new treatment is also consistent with the spore characters described by Tryon & Lugardon (1991) who reported *Psammiosorus* as part of their description of *Arthropteris*.

We reject two alternative treatments: (1) The status quo with a paraphyletic *Arthropteris* is less informative (see Schmidt-Lebuhn, 2011) and, in emphasising a single morphological character, ignores the shared similarities and pattern of relationship. (2) Dissection of *Arthropteris* into multiple genera, each monophyletic, would create taxonomic instability, and require the introduction of new genera without clear morphological delimitations.

Species delimitation. — Our results recovered several well-distinguished species but also suggested the need for more extensive study of the *Arthropteris palisotii* complex. *Arthropteris guinanensis* was found to be distinct not only from sympatric samples of *A. palisotii* (Fig. 1; Table 1) but also from other members of the *A. palisotii* complex. In fact, *A. guinanensis* is supported as the sister clade of *A. palisotii*.

The two species are distinct in the absence/presence of indusia and the shape of the pinna margins (Fig. 4).

Arthropteris altescandens is found to be a similarly distinct species. It is endemic to the Juan Fernández Islands and its closest living relative may well be the Madagascan endemic *A. paucivenia*. This hypothesis is consistent with the absence of indusia in both species. In the presence of free veins and pinna

shape, *A. altescandens* shows greater similarity to *A. palisotii* and/or *A. articulata*, but these shared characters states are likely plesiomorphic.

Arthropteris articulata is found to be the sister of a clade composed of *A. monocarpa*, *A. parallela*, and *A. orientalis* (= Afro-Madagascan *A. orientalis* complex). This relationship is consistent with leaf morphology but not with geographic

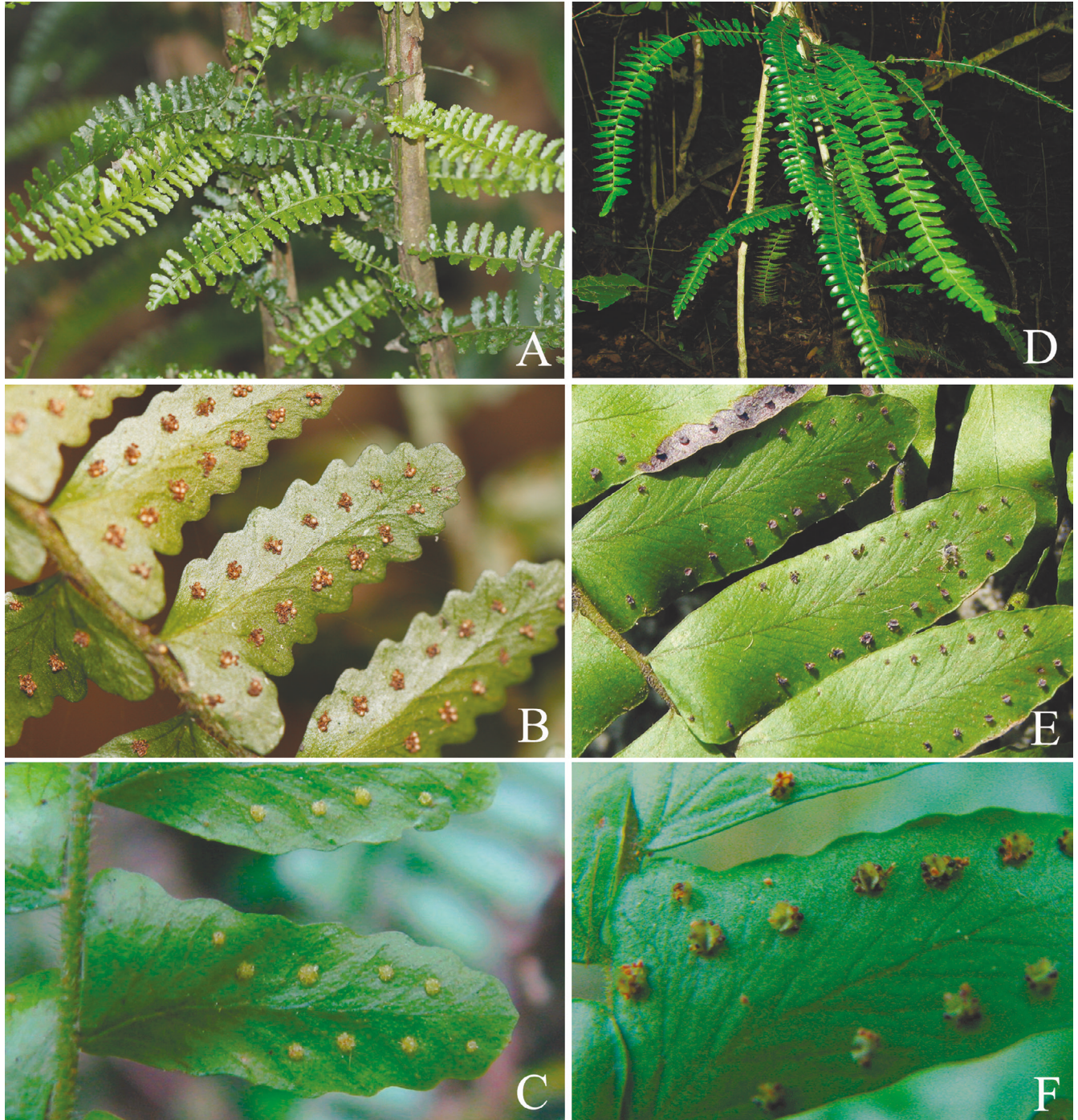


Fig. 4. Two species of *Arthropteris* occurring in Guangxi province/China. **A–C**, *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang: **A**, habit; **B**, shape of pinnae and sori position; **C**, exindusiate sori. **D–F**, *Arthropteris palisotii* (Desv.) Alston: **D**, habit; **E**, shape of pinnae and sori position; **F**, indusiate sori. — Photos by Ri-Hong Jiang.

distribution. *Arthropteris articulata* occurs in the Malay Archipelago (Moluccas, New Guinea) and Fiji islands (Brownlie, 1977; Hovenkamp & Leonardia, 2012) whereas the other taxa in this clade occur in the Afro-Madagascan region. *Arthropteris monocarpa* and *A. orientalis* are part of a complex of about ten named species occurring throughout tropical Africa and the islands in the Indian Ocean (e.g., Pichi Sermolli, 1966; Lawalrée, 1990, 1991; Badré, 2008), in which an increased sampling is clearly necessary to assess the taxonomy and species delimitation.

Our results are not conclusive regarding the taxonomy of the *A. palisotii* complex. Most of the included specimens identified as *A. palisotii* formed a distinct clade but this clade is exclusively composed of specimens from Guangxi Province, China, and the northern part of Vietnam. The specimens from Japan, Taiwan, and Fiji are not nested within this clade and the Taiwan specimen is sister to the Fijian specimen identified as *A. repens*. However, the delimitation of *A. repens* from *A. palisotii* is questionable (Brownsey & Perrie, 2011; Hovenkamp & Leonardia, 2012). Similarly, the distinction of *A. beckeri* is unclear.

Plastid DNA of *A. tenella* and *A. submarginalis* neither delimitates them from each other nor from *A. palisotii*. *Arthropteris submarginalis* is a localized endemic of Queensland, Australia, and shares some similarities in leaf shape with *A. tenella*, which occurs in coastal eastern Australia, New Zealand, Norfolk Islands, and Lord Howe Islands (Bell, 1998). However, *A. tenella* is clearly distinguished morphologically from other members of this clade by the absence of indusia and the presence of profuse large russet scales on the rhizome. The distinction of *A. beckeri* is also not resolved. Clearly, additional evidence is required to resolve the taxonomy of this complex.

In summary, our results resolve some issues regarding species delimitation within the genus, but not others. DNA sequences allowed us to unambiguously distinguish *A. guinanensis* from *A. palisotii*. To confirm this, we densely sampled both species in the Guangxi Province of China and areas of northern Vietnam. By doing so, we were able to record *A. guinanensis* for the first time in Vietnam. *Arthropteris guinanensis* appears to be restricted to the karst regions of southern China and northern Vietnam but this requires confirmation by further sampling in Indochina, which would also have to include specimens from northern Vietnam identified as *A. repens* (Wu & al., 2005). *Arthropteris palisotii* is ecologically more variable than *A. guinanensis* and has a wider distribution, but both species can be found in close proximity to each other. This makes species identification difficult but the absence or presence of indusia appears to provide reliable identification of specimens from southern China and perhaps also northern Vietnam.

The failure to resolve a species phylogeny for the *A. palisotii* complex could have been caused by several factors. (1) The DNA regions used here were insufficiently variable. Similar lack of variation has been recognized as a core problem for the DNA barcoding of plants (e.g., Hollingsworth & al., 2009). (2) Hybridization and/or introgression may result in deviation of the plastid phylogeny from the species phylogeny (Wang & al., 2012). (3) Speciation via polyploidization may have created

distinct species that cannot be differentiated using plastid DNA sequences alone. Taxonomic resolution of this complex will require a more extensive sampling and additional DNA sequence data.

Biogeography. — *Arthropteris* shows some intriguing distribution patterns including a centre of species diversity in the Afro-Madagascan region (Lawalrée, 1990, 1991; Badré, 2008). The two recognized clades show different ranges. The *A. orientalis* group is distributed in Afro-Madagascar with its sister *A. articulata* occurring in Malesia (Moluccas, New Guinea) and Fiji. The lack of denser sampling of African specimens renders the biogeographic pattern uncertain. The *A. palisotii* complex is distributed from Africa (not sampled here) to SE Asia and throughout Malesia and Australasia into the Pacific islands. Reports of this species from Madagascar need to be confirmed. In our results, the *A. palisotii* complex showed some internal geographical structuring with a China/Northern Vietnam clade distinguished from an Australian–New Zealand clade. However, this needs further investigation using a denser sampling, especially given the relationships recovered for *A. palisotii* s.l. from Fiji, Japan, and Taiwan (Fig. 1).

More intriguing are the distributions of the three phylogenetically isolated species: *A. guinanensis*, *A. paucivenia*, and *A. altescandens*. Each of these species has a well-defined and highly limited area of occurrence, and all three diverge relatively early in one of the two main clades of *Arthropteris* (Figs. 1, 3). Divergence time estimates (Fig. 3) indicate early- to mid-Miocene origins of these isolated taxa. It is tempting to consider their distributions as relictual.

Arthropteris guinanensis is found in karst areas in southern China and northern Vietnam. Southern China is well known for its relictual plants (Qian & Ricklefs, 1999; Wu & al., 2007), and thus *A. guinanensis* may be a further example. However, several questions remain to be addressed. (1) additional work is needed to confirm the range of this species in Vietnam. (2) *Arthropteris guinanensis* and *A. palisotii* occur sympatrically in this region, which raises questions concerning their ecological interactions, e.g., interspecific competition.

Two other putative relictual species are restricted to islands. *Arthropteris paucivenia* occurs in the lowland forests of western Madagascar. The western rainforest has been considered as a refugium that allowed the survival of southern Gondwanan elements in Madagascar (Vences & al., 2009). This part of Madagascar may have experienced less dramatic changes during the drift of this continental fragment since the break-up of Gondwana to its current position close to Africa. The distribution of *A. altescandens* is even more surprising. This fern is endemic to the Juan Fernández Islands in the Pacific Ocean, and is separated from other *Arthropteris* by several thousand kilometres. These islands are younger than 4 million years (Stuessy & al., 1984). Furthermore, these volcanic islands are known to house other putative relicts such as the tree fern *Thyrsopteris elegans* Kunze (Korall & al., 2006) and the basal angiosperm *Lactoris fernandeziana* Phil. (Crawford & al., 1994). These species may be relicts from the initial radiation of their genera in tropical forests on islands in the Indian and Pacific oceans. However, divergence time estimates (Schneider

& al., 2004, 2010; Schuettpelz & Pryer, 2009) suggest that the extant distribution of derived ferns is mainly shaped by events that are younger than the break-up of Gondwana. Our estimates of the divergence times of *Arthropteris* dated the initial radiation of the genus to the warm climates of the Early and Mid Miocene (Fig. 3). Thus, restricted ranges may be the result of the cooling of the global climate from the Late Miocene until today. However, this hypothesis cannot be further tested without fossil evidence. We can nevertheless reject a recent origin of *A. altescandens* from other species of this genus occurring in Malesia and Fiji.

In conclusion, *Arthropteris* shows some similarities to previously recorded biogeographic patterns in Paleotropical ferns. There is evidence for past exchange between the Asian and Afro-Madagascan tropics as reported previously for Polypodiaceae (Janssen & al., 2007; Hennequin & al., 2010; Schneider & al., 2010). However, an expanded sampling is required to obtain a comprehensive reconstruction of the biogeographic history of these ferns.

■ TAXONOMIC TREATMENT

Arthropteridaceae H.M. Liu, Hovenkamp & H. Schneid., **fam. nov.**

Description: Climbing or occasionally terrestrial ferns. Rhizomes slender, long-creeping/climbing; indument of peltate scales. Laminae pinnate to pinnate-pinnatifid (rarely bipinnate), monomorphic, stipes each articulated from a stipe-like phyllopodium; stipes and rachis grooved on the upper surface. Pinnae articulated to rachis, venation open, simple or forked or sparingly anastomosing. Sori superficial and circular in outline, indusia reniform to round or absent. Spores spherical to ellipsoid, monolete, surface with irregular wing-like folds. Chromosome number: $x = 41$ or $42?$ (Tindale & Roy, 2002).

One genus.

Arthropteris J. Sm. ex Hook. f., Fl. Nov.-Zel. 2: 43. 1854 – Type: *Arthropteris tenella* (G. Forst.) J. Sm. ex Hook. f., Fl. Nov.-Zel. 2: 43, t. 82. 1854 \equiv *Polypodium tenellum* G. Forst., Fl. Ins. Austr.: 81. 1786.

Arthropteris paucivenia (C. Chr.) H.M. Liu, Hovenkamp & H. Schneid., **comb. nov.** \equiv *Dryopteris paucivenia* C. Chr., Index Filic.: 283. 1905 \equiv *Psammiosorus paucivenius* (C. Chr.) C. Chr. in Dansk Bot. Ark. 7: 73, t.24. 1932 – **Lectotype (designated here)**: NW Madagascar, source of Sambirano River, Dec. 1890, *J.T. Last s.n.* (K No. K000435679!; isolecotypes: K No. K000435678!, BM [not yet mounted!]) [Type images available at: <http://plants.jstor.org/specimen/k000435679> and <http://plants.jstor.org/specimen/k000435678>].

Note. – Two sheets of *J.T. Last s.n.* in K are marked as holotype at <http://plants.jstor.org>. It is not known to us who has designated these specimens to be holotypes. We have selected the one with the most complete annotations in Baker's hand as the lectotype. The assignment is based on drawings and details given in the description of *Polypodium oligophlebium* Baker in

J. Bot. 29: 6. 1891 and *Dryopteris paucivenia* C. Chr. in Dansk Bot. Ark. 7: 73, t. 24. 1932. The later name is the homotypic replacement for the homonym *Polypodium oligophlebium* Baker as per Art. 7.42. Both publications are without doubt based on material collected by J.T. Last which is deposited at K and BM.

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Appendix 1. Voucher information and GenBank accession numbers for samples used in this study (* indicates newly sequenced data). Provenance (country, state with only the species collected from China) and voucher information only provided for species newly sequenced for this study. Herbaria of deposition were provided in parenthesis. For the sequences downloaded from GenBank, the publication information was also supplied.

Species, origin, voucher (collector, collection number) or publication information, GenBank number (in following order: ¹*rbcL*, ²*atpB*, ³*atpA*, ⁴*rps4* (= *rps4* + *rps4-trnS* IGS), ⁵*trnL-F* (= *trnL* intron + *trnL-trnF* IGS), ⁶*trnGR* (= *trnG* intron + *trnG-trnR* IGS).

INGROUP: ARTHROPTERIDACEAE: *Arthropteris altescandens* J. Sm., Masatierra, Cordo Salsipuedes, Crawford & al. 11126 (V), *KC977433*. *Arthropteris altescandens* J. Sm., Masatierra, Valle Villagra, Stuessy & al. 15379 (V), *KC977434*. *Arthropteris articulata* (Brack.) C. Chr., Fiji, Leon Perrie FJ11-50 (WELT), *KC977367*, *KC977348*, *KC977329*, *KC977437*, *KC977411*, *KC977402*. *Arthropteris beckeri* (Hook.) Mett., Australia, Queensland, Patrick J. Acock PA1025 (BM), *KC977361*. *Arthropteris beckeri* (Hook.) Mett., Hasebe & al. (1994), U05605. *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang, China, Guangxi, R.H. Jiang JRH 1506 (IBK), *KC977371*, *KC977341*, *KC977324*, *KC977446*, *KC977405*, *KC977398*. *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang, China, R.H. Jiang JRH 2794 (IBK), *KC977374*, *KC977353*, *KC977334*, *KC977442*, *KC977416*, *KC977400*. *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang, China, R.H. Jiang JRH 2802 (IBK), *KC977375*, *KC977354*, *KC977335*, *KC977443*, *KC977417*, *KC977401*. *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang, China, R.H. Jiang JRH H09939 (IBK), *KC977372*, *KC977340*, *KC977323*, *KC977445*, *KC977404*, *KC977397*. *Arthropteris guinanensis* H.G. Zhou & Y.Y. Huang, Vietnam, Schneider & al. 2011V018 (BM), *KC977364*, *KC977344*, *KC977326*, *KC977447*, *KC977407*, *KC977399*. *Arthropteris monocarpa* (Cordem.) C. Chr., Hennequin & al. (2010), HM748132. *Arthropteris orientalis* (J.F. Gmel.) Posth., France, Réunion, Hennequin SI56 (BM), *KC977378*, *KC977357*, *KC977435*, *KC977420*, *KC977403*. *Arthropteris orientalis* (J.F. Gmel.) Posth., Hennequin & al. (2010), HM748133. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, s.coll., s.n. (SZG), *KC977343*, *KC977325*, *KC977427*, *KC977406*, *KC977390*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, R.H. Jiang JRH1769 (IBK), *KC977365*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, R.H. Jiang JRH 2800 (IBK), *KC977376*, *KC977355*, *KC977336*, *KC977448*, *KC977419*, *KC977389*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, R.H. Jiang JRH 2803 (IBK), *KC977377*, *KC977356*, *KC977337*, *KC977449*, *KC977418*, *KC977385*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, R.H. Jiang H09936 (IBK), *KC977347*, *KC977432*, *KC977383*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, H.M. Liu GX009 (SZG), *KC977342*, *KC977429*, *KC977386*. *Arthropteris palisotii* (Desv.) Alston, Vietnam, (PE), *KC977352*, *KC977333*, *KC977436*, *KC977415*, *KC977387*. *Arthropteris palisotii* (Desv.) Alston, Vietnam, Schneider & al. 2011V005 (BM), *KC977369*, *KC977346*, *KC977328*, *KC977431*, *KC977409*, *KC977384*. *Arthropteris palisotii* (Desv.) Alston, Vietnam, Schneider & al. 2011V094 (BM), *KC977366*, *KC977345*, *KC977327*, *KC977428*, *KC977408*, *KC977391*. *Arthropteris palisotii* (Desv.) Alston, China, Guangxi, X.C. Zhang 4299 (PE), *KC977362*, *KC977351*, *KC977332*, *KC977440*, *KC977414*, *KC977392*. *Arthropteris palisotii* (Desv.) Alston, Ebiara & al. (2010), AB575230. *Arthropteris palisotii* (Desv.) Alston, Kuo & al. (2011), JF303977, JF304014. *Arthropteris palisotii* (Desv.) Alston, Australia, Queensland, Patrick J. Acock PA1033 (BM), *KC977358*, *KC977450*, *KC977421*, *KC977394*. *Arthropteris parallela* C. Chr., Schuettpelz & Pryer (2007), EF463266, EF463522, EF463862; cult. Old Bot. Garden Goettingen (origin Madagascar), Schuettpelz 524 (GOET), *KC977453*, *KC977425*. *Arthropteris repens* (Brack.) C. Chr., Fiji, Leon Perrie FJ11-191 (WELT), *KC977368*, *KC977349*, *KC977330*, *KC977438*, *KC977412*, *KC977393*. *Arthropteris submarginalis* Domin, Australia, Queensland, Patrick J. Acock PA1028 (BM), *KC977381*, *KC977360*, *KC977339*, *KC977452*, *KC977423*, *KC977395*. *Arthropteris submarginalis* Domin, Australia, Queensland, Patrick J. Acock PA1031 (BM), *KC977380*, *KC977359*, *KC977338*, *KC977451*, *KC977422*, *KC977396*. *Arthropteris tenella* (G. Forst.) J. Sm. ex Hook. f., New Zealand, Leon Perrie 6429 (BM), *KC977363*, *KF011547*, *KC977424*. *Arthropteris tenella* (G. Forst.) J. Sm. ex Hook. f., Australia, R. Coveny & P. Hind 10850 (PE), *KC977430*. *Psammiosorus paucivenius* (C. Chr.) C. Chr., Schuettpelz & Pryer (2007), EF463524.

Appendix 1. Continued.

³EF463864; Madagascar, *F. Rakotondrainibe* 6586 (P), ⁴KC977454*, ⁵KC977426*. **DAVALLIACEAE:** *Araiostegia hymenophylloides* (Blume) Copel., Schuettpelz & Pryer (2007), ³EF463648. *Araiostegia yunnanensis* (Christ) Copel., Kim & al. (unpub.), ¹JX103718, ²JX103676, ⁴JX103760, ⁵JX103802. *Davallia griffithiana* Hook., Schuettpelz & Pryer (2007), ¹EF463165, ²EF463371, ³EF463649. *Davallia tyermannii* (T. Moore) Baker, Kim & al. (unpub.), ⁴JX103761, ⁵JX103803. **LOMARIOPSIDIACEAE:** *Cyclopeltis crenata* (Fée) C. Chr., Liu & al. (2007b), ¹EF463119, ²EF450534; Kuo & al. (2011), ³JF304016; Liu & al. (2010), ⁴EF540718; Li & al. (2009), ⁵EU216747. *Lomariopsis pollicina* Mett. ex Kuhn, Schuettpelz & Pryer (2007), ¹EF463235, ²EF463481, ³EF463776; Hennequin & al. (2010), ⁴HM748162, ⁵HM748187; Rouhan (2007), ⁵DQ396588. **NEPHROLEPIDACEAE:** *Nephrolepis biserrata* (Sw.) Schott, Hennequin & al. (2010), ¹HM748143; Lehtonen & al. (2010), ³HQ157268, ⁵HQ157337; Hennequin & al. (2010), ⁴HM748169, ⁵HM748195. *Nephrolepis biserrata* var. *furcans* hort., ²DQ646105 / Qiu & al. (2006). **OLEANDRACEAE:** *Oleandra articulata* (Sw.) C. Presl, Schuettpelz & Pryer (2007), ¹EF463242, ²EF463487, ³EF463792. *Oleandra cumingii* J. Sm. ex C. Presl, Haufler & al. (2003), ⁵AY093596. **POLYPODIACEAE:** *Drynaria rigidula* (Sw.) Bedd., Schuettpelz & Pryer (2007), ¹EF463247, ²EF4634937, ³EF463811; Janssen & Schneider (2005), ⁴AY529188, ⁵AY529481. *Goniophlebium formosum* (Baker) Rodl-Linder, Schuettpelz & Pryer (2007), ¹EF463249, ²EF463495, ³EF463813; Schneider & al., (2002), ⁴AY096224; Janssen & al. (2006), ⁵DQ642235. *Loxogramme abyssinica* (Baker) M.G. Price, Schuettpelz & Pryer (2007), ¹EF463252, ²EF463498, ³EF463826; Schneider & al. (2006), ⁴DQ164474; Kreier & Schneider (2006), ⁵DQ235156. *Loxogramme salicifolia* (Makino) Makino, Sessa & al. (2012), ⁴JN189028. *Microgramma bifrons* (Hook.) Lellinger, Schneider & al. (2004), ⁵AY362582, ⁴AY362654; Schuettpelz & Pryer (2007), ²EF463499, ³EF463828; Janssen & al. (2006), ⁵DQ642224. *Pyrrosia serpens* (G. Forst.) Ching, Schuettpelz & Pryer (2007), ¹EF463260, ²EF463512, ³EF463845; Schneider & al. (2006), ⁴DQ164503, ⁵DQ164535. **TECTARIACEAE:** *Tectaria antioquiensis* (Baker) C. Chr., Schuettpelz & Pryer (2007), ¹EF463269, ²EF463525, ³EF463865. *Tectaria apiifolia* (Schkuhr) Copel., Schuettpelz & Pryer (2007), ¹EF463270, ²EF463526, ³EF463866. *Tectaria fimbriata* (Willd.) Proctor & Lourteig, Schuettpelz & Pryer (2007), ¹EF463271, ²EF463527, ³EF463867. *Tectaria fuscipes* (Wall. ex Bedd.) C. Chr., Liu & al. (2007a), ¹EF460680, ²EF450521; Li & Lu (2006), ⁵DQ514486. *Tectaria incisa* Cav., Schuettpelz & Pryer (2007), ¹EF463272, ²EF46252, ³EF463868; Lehtonen & al. (2010), ⁴HQ157325, ⁵HQ157340. *Tectaria prolifera* (Hook.) R.M. Tryon & A.F. Tryon, Schuettpelz & Pryer (2007), ¹EF463273, ²EF463529, ³EF463869. *Tectaria trifoliata* (L.) Cav, Schuettpelz & Pryer (2007), ¹EF463274, ²EF463530, ³EF463870. *Tectaria zeylanica* (Houtt.) Sledge, Liu & al. (2007a), ¹EF460688, ²EF450532; Rothfels & al. (2012), ³JF832143, ⁵JF832242. — OUTGROUP: **DRYOPTERIDACEAE:** *Arachniodes denticulata* (Sw.) Ching, Sessa & al. (2012), ¹JN189533, ⁴JN189207, ⁵JN189102, ⁵JN188997; Schuettpelz & Pryer (2007), ²EF463380, ³EF463664. *Cyrtomium falcatum* (L.f.) C. Presl, Schuettpelz & Pryer (2007), ¹EF463176, ²EF463387, ³EF463671; Li & al. (2008), ⁴EU106601; Lu & al. (2005), ⁵AY736332. *Dryopteris filix-mas* (L.) Schott, Schuettpelz & Pryer (2007), ¹EF463180, ²EF463391, ³EF463675; Sessa & al. (2012), ⁴JN189181, ⁵JN189075, ⁵JN188970. *Lastreopsis effusa* (Sw.) Tindale, D.P. Little & Barrington (2003), ¹AF537230; Schuettpelz & Pryer (2007), ²EF463422, ³EF463706; Moran & al. (2010), ⁴GU376689; Lu & Li (2006), ⁵DQ514503. *Olfersia cervina* (L.) Kunze, Schuettpelz & Pryer (2007), ¹EF463213, ²EF463431, ³EF463715; Sessa & al. (2012), ⁴JN189239, ⁵JN189026; Lu & Li (2006), ⁵DQ514508. *Phanerophlebia nobilis* (Schltdl. & Cham.) C. Presl, Schuettpelz & Pryer (2007), ¹EF463214, ²EF46343, ³EF463716; Sessa & al. (2012), ⁴JN189242, ⁵JN189134, ⁵JN189030. *Pleocnemia rufinervis* (Hayata) Nakai, Kuo & al. (2011), ³JF304012. *Pleocnemia winitii* Holttum, Liu & al. (2007a), ¹EF460686, ²EF450528. *Polybotrya alfredii* Brade, Schuettpelz & Pryer (2007), ¹EF463215, ²EF463433, ³EF463717; Sessa & al. (2012), ⁴JN189025. *Polybotrya caudata* Kunze, Sessa & al. (2012), ⁴JN189245. *Polystichum munitum* (Kaulf.) C. Presl, Sessa & al. (2012), ¹JN189508, ⁴JN189182, ⁵JN189076, ⁵JN188971; Schuettpelz & Pryer (2007), ²EF463438, ³EF463722. *Rumohra adiantiformis* (G. Forst.) Ching, Lu & Li (2006), ¹DQ508789, ⁵DQ514520; Schuettpelz & Pryer (2007), ²EF463443, ³EF463727; ⁴GU376712/Moran & al. (2010). *Teratophyllum ludens* (Fée) Holttum, Moran & al. (2007), ⁴GU376716, ⁵GU376567. *Teratophyllum wilkesianum* (Brack.) Holttum, Schuettpelz & Pryer (2007), ¹EF463223, ²EF463446, ³EF463730. **HYPODEMATIACEAE:** *Didymochlaena truncata* (Sw.) J. Sm., Smith & Cranfill (2002), ¹AF425105, ⁴AF425161; Schuettpelz & al. (2007), ²EF452030, ³EF452091; Lu & Li (2006), ⁵DQ514491; Rothfels & al. (2012), ⁵JF832210. *Hypodematium crenatum* (Forssk.) Kuhn, Schuettpelz & Pryer (2007), ¹EF463205, ²EF463421, ³EF463705; Smith & Cranfill (2002), ⁵AF425122. *Leucostegia pallida* (Mett.) Copel., Tsutsumi & Kato (2006), ¹AB232389; Schuettpelz & Pryer (2007), ²EF463425, ³EF463709.