

Phylogenetic relationships of Chinese *Adiantum* based on five plastid markers

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Received: 15 February 2011 / Accepted: 23 May 2011 / Published online: 3 August 2011
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Abstract *Adiantum* consists of about 150–200 species mostly with a pantropical distribution, yet the classifications of *Adiantum* have been based primarily on regional studies. Confounding the clarity of reconstructing the evolutionary history of *Adiantum* is that previous molecular phylogenetic studies suggest that a separate and distinctive clade, the vittarioids, may be derived from within *Adiantum*. Five plastid markers (*atpA*, *atpB*, *rbcL*, *trnL-F* and *rps4-trnS*) are employed to assess the monophyly of *Adiantum*, and construct the molecular phylogeny of Chinese *Adiantum*. Our analyses support the monophyly of *Adiantum*. All temperate *Adiantum* species form a clade nested within the pantropical grade, suggesting a tropical origin of *Adiantum*. Six main clades are supported within

Chinese *Adiantum*, which are only partially consistent with Lin's classification of the genus. Series *Caudata* is polyphyletic with series *Gravesiana* nested within one subgroup of series *Caudata*. The prolonged whip-like stolon at the apex of the fronds is the defining character for series *Caudata*, but it may have evolved multiple times. *Adiantum reniforme* with the simple fronds is sister to series *Venusta*, which has a decomposed lamina with many flabellate to cuneate segments. Series *Veneri-capilliformia* is not monophyletic, with *A. capillus-veneris* sister to series *Flabellulata* except for *A. diaphanum*, and *A. edentulum* sister to series *Pedata*. Series *Flabellulata* is biphyletic with *A. diaphanum* nested within the pantropical grade. The phylogeny suggests that convergent evolution in frond architecture has occurred in *Adiantum*.

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Keywords *Adiantum* · China · Diversification ·
Molecular phylogeny · Plastid markers · Pteridaceae

Introduction

Pteridaceae is a large and diverse family with a nearly worldwide distribution, although it is most diverse in the tropics. Tryon and Tryon (1982) recognized 35 genera in six tribes, and proposed that these tribes probably represent independent evolutionary lines or relicts from sources among now extinct relatives of the Schizaeaceae. Tryon et al. (1990) included 34 genera in the family Pteridaceae, and raised the tribes to the level of subfamilies. They suggested that Pteridaceae has no obvious close relationships with other living fern families except for Vittariaceae, and extinctions may have made it difficult to infer their evolutionary relationships. Smith et al. (2006) recognized about 50 genera and 950 species in Pteridaceae,

and treated Vittariaceae as a member of Pteridaceae. Several phylogenetic studies have been conducted on this large family (e.g., Gastony and Rollo 1995; Sánchez-Baracaldo 2004a, 2004b; Zhang et al. 2005, 2007; Kirkpatrick 2007; Prado et al. 2007; Schuettpelz and Pryer 2007; Schuettpelz et al. 2007; Ruhfel et al. 2008; Bouma et al. 2010). The view of an ancient and isolated Pteridaceae has been supported by recent molecular studies (Schneider et al. 2004; Schuettpelz and Pryer 2007; Schuettpelz et al. 2007), which supported five major clades within the family: the cryptogramroids (the CR clade), the ceratopteridoids (the CE clade), the pteridoids (the PT clade), the adiantoids (the AD clade), and the cheilanthoids (CH clade) (Schuettpelz and Pryer 2007; Schuettpelz et al. 2007).

Adiantum and the vittarioid ferns together form a well-supported AD clade (Schuettpelz and Pryer 2007; Schuettpelz et al. 2007). The close relationship among these ferns has been suggested in earlier studies (Hasebe et al. 1995; Pryer et al. 1995; Schneider et al. 2004). *Adiantum raddianum* was sister to the *Vittaria* group in the molecular phylogenetic study of Pteridaceae (Prado et al. 2007; Schuettpelz et al. 2007), suggesting that the vittarioids may be derived from *Adiantum*. The molecular phylogeny of New Zealand Pteridaceae using chloroplast *rbcL* sequences suggested that the monophyletic status of *Adiantum* remained unclear (Bouma et al. 2010). Additional data are required to assess the monophyly of *Adiantum* and infer its phylogeny.

Adiantum consists of about 150–200 species, with a worldwide distribution except in extremely cold or dry regions (Ching 1957; Tryon and Tryon 1982; Lin 1980, 1990; Tryon et al. 1990; Paris 1993; Hoshizaki and Moran 2001). Most species of this genus are in the tropical to subtropical regions, with the greatest diversity in the Neotropics (Huiet and Smith 2004). The classifications of *Adiantum* were, however, primarily based on regional studies (e.g., Jenman 1909; Scamman 1960; Nayar 1961; Tryon 1964; Tryon and Tryon 1982; Lin 1980) except for four earlier major treatments in the late 19th century and the early 20th century (Hooker and Baker 1874; Smith 1875; Christ 1897; Diels 1902). Tryon (1964) pointed out that most Peruvian *Adiantum* species fall into five rather well marked geographic groups. Cooper-Driver and Swain (1977) suggested that *Adiantum* may be divided into five sections on the basis of their flavonoid patterns. Tryon and Tryon (1982) presented a tentative classification of the genus into eight groups: the *A. capillus-veneris* group, the *A. patens* group, the *A. philippense* group, the *A. reniforme* group, the *A. pectinatum* group, the *A. tetraphyllum* group, the *A. platyphyllum* group, and the *A. phyllitidis* group. They pointed out that parallel or convergent evolution probably occurred in the frond architecture and other characters in *Adiantum*, which may have obscured the relationships among species (Tryon and Tryon 1982).

The Asian *Adiantum* species also were treated taxonomically on a regional basis. Holttum (1954) recorded seven *Adiantum* species in Malaya. Nayar (1961) recognized 15 *Adiantum* species in India, and classified them into four groups: the *Caudatum* group, the *Pedatum* group, the *Tenerum* group, and the *Capillus* group. There are eight *Adiantum* species in Japan (Iwatsuki et al. 1995), of which only one species (*A. ogasawarense* Tagawa) is endemic, and the remaining species also occur in China.

Ching (1957) recognized 34 *Adiantum* species from China and the neighboring regions. Based on morphology and habitat, Ching (1957) divided the genus into six series: *Gravesii*, *Radicans*, *Pedati*, *Flabellulati*, *Venusti*, and *Capillus-veneris* (Table 1). Lin (1980) published an additional series *Reniformia*, and classified the Chinese *Adiantum* species into seven series (Table 1). Lin (1990) recognized 31 species, six varieties, and four forms in China, with 23 species, varieties and forms endemic in China and southwestern China richest in taxon diversity.

Few molecular phylogenetic analyses have been conducted on *Adiantum*. Huiet and Smith (2004) used *rps4-trnS* sequences in their study of the genus and showed that the *A. philippense* group, the *A. tetraphyllum* group, and the *A. platyphyllum* group in the classification of Tryon and Tryon (1982) are each monophyletic, whereas the *A. patens* group, the *A. pectinatum* group, and the *A. capillus-veneris* group are each polyphyletic. The New Zealand *Adiantum* species are nested within a wide-ranging and principally southern hemisphere clade (Bouma et al. 2010).

In the present study, we sequenced five plastid markers (*atpA*, *atpB*, *rbcL*, *trnL-F* and *rps4-trnS*) and sampled 86 *Adiantum* taxa from Asia, Africa, the Americas, Australia, and Europe. Our objectives for this study are to (1) assess the monophyly of *Adiantum* and construct the molecular phylogeny of *Adiantum*, emphasizing the Chinese taxa; and (2) test the most recent classification of the genus by Lin (1980, 1990).

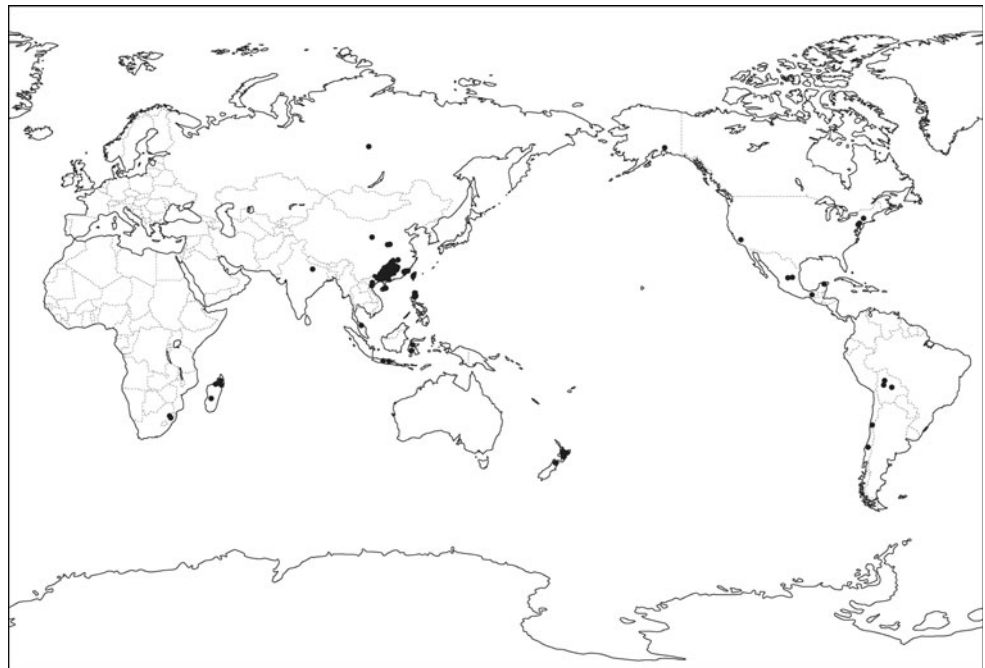
Materials and methods

Taxon sampling

We sequenced 44 species, varieties and forms representing the taxonomic and biogeographic diversity of Chinese *Adiantum*. Other 42 *Adiantum* samples (including 11 unidentified taxa) from Asia, Africa, the Americas, Australia and Europe, were sampled to broadly test the monophyly of the genus, and three plastid gene (*rbcL/atpA/atpB*) of 29 outgroup species were downloaded from GenBank. The locations of the samples that have been included in this study were indicated in Fig. 1. All taxa

Table 1 Classification of *Adiantum* by Ching (1957) and Lin (1980, 1990) and main characters of the series

Ching (1957)	Lin (1980, 1990)	Main characters
	Series <i>Reniformia</i>	Fronds simple and kidney-shaped with an entire margin, clustered from a short-creeping rhizome
Series <i>Gravesii</i>	Series <i>Gravesiana</i>	Fronde imparipinnate, pinnae entire, readily detached from the petiole upon drying; rachis always terminated by an end-pinna
Series <i>Radicans</i>	Series <i>Caudata</i>	Fronde once-pinnate, pinnae incised, herbaceous, rachis prolong into a leafless whip, rooting and viviparous at apex
Series <i>Pedati</i>	Series <i>Pedata</i>	Fronds pedately divided, generally with 4–6 once-pinnate, pinnae springing from the upper side of each of the 2 primary forking branches, rhizome creeping or oblique, temperate species
Series <i>Flabellulati</i>	Series <i>Flabellulata</i>	Fronds 2–3 times dichotomously divided or sometimes subdichotomously forked, tufted at the apex of short-erect rhizome; tropical or warm temperate species
Series <i>Venusti</i>	Series <i>Venusta</i>	Fronds fully 2–3-pinnate with several pairs of lateral pinnae, gradually shortened upwards; ultimate pinnules small, not lobed nor incised, flabellate or obdeltoid, cuneate and equally sided at base, temperate species
Series <i>Capillus-veneres</i>	Series <i>Veneri-capilliformia</i>	Fronds fully 2–3-pinnate with several pairs of lateral pinnae, ultimate pinnules larger (>1 cm long), dimidiate, base obliquely flabellate, subcuneate or cuneate, deeply 2–3-lobed; indusia transversely oblong or elongate

Fig. 1 The distribution of the samples that have been included in this study

included in this study, together with voucher information, collection sites, are listed in Appendix 1.

DNA extraction, PCR amplification and sequencing

Total DNAs were extracted from 15 mg of silica-gel-dried leaf material using Dneasy (QIAGEN) extraction kits. The *atpA* gene was amplified with primers “ESATPF412F” and “ESTRNR46F” and sequenced with “ESATPA535F” and “ESATPA877R” as well as “ESATPF412F” and “ESTRNR46F” (Schuettpelez et al. 2006). “ESATB172F” and “ESATPE45R” were used to amplify and sequence the *atpB*

gene (Schuettpelez and Pryer 2007). “1F” and “1379R” were used for amplifying and sequencing the *rbcL* gene (Little and Barrington 2003). The *trnL-F* region was amplified and sequenced with primers “c” and “f” or “p1” and “f” (Taberlet et al. 1991; Lu et al. 2005). Primers “trnS” (Shaw et al. 2005) and “rps4.5” (Souza-Chies et al. 1997) were used to amplify and sequence the *rps4-trnS* region.

All amplifications were performed in a 25 μ l reaction-mixture volume. The PCR reactions contained 1 U of *Taq* DNA polymerase (Biolone), 10X buffer, 0.25 mmol/L dNTP, Mg^{2+} , 0.5 mmol/L of each primer, BSA, and 25–60 ng sample DNA. For *atpA* and *atpB*, reactions were

incubated at 95 °C for 3 min, then cycled 35 times (95°C for 1 min, 50°C for 1 min, 72°C for 100 s), followed by a final extension for 10 min at 72°C. For *rbcL* and *trnL-F*, reactions were incubated at 95°C for 3 min, then cycled 35 times (95°C for 1 min, 51°C for 1 min, 72°C for 80 s), followed by a final extension for 10 min at 72°C. For *rps4-trnS*, reactions were incubated at 95°C for 3 min, then cycled 35 times (94°C for 30 s, 58°C for 45 s, 72°C for 80 s), followed by a final extension for 10 min at 72°C.

The PCR products were purified using the polyethylene glycol (PEG)/NaCl method of Kusakawa et al. (1990). Cycle sequencing was conducted using BigDye 3.1 reagents and the sequencing reactions were run on an ABI 3730 automated sequencer.

Phylogenetic analyses

The resulting sequences were assembled using Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, Michigan, USA). Sequences obtained in this study have been deposited in GenBank (Appendix 1). They were then aligned using ClustalX version 1.83 (Thompson et al. 1997), followed by manual adjustments using Se-AI (<http://tree.bio.ed.ac.uk/software/seal/>). All characters were equally weighted. Insertions and deletions were coded as missing data.

Phylogenetic trees were constructed using maximum parsimony and Bayesian methods. Maximum parsimony (MP) analysis was performed using PAUP 4.0b10 (Swofford 2001), treating gaps as missing data and using the heuristic search options with 1,000 random replications of stepwise data addition and TBR swapping and Multrees on no tree limit. Bootstrap analysis (Felsenstein 1985) was performed with 1,000 replicates to evaluate internal support, with one random taxon addition replicates saving all optimal trees at each step.

The optimal model of molecular evolution was determined by the Akaike Information Criterion (AIC) using Modeltest version 3.7 (Posada and Crandall 1998; Posada and Buckley 2004). Bayesian inferences were implemented in MrBayes 3.1 (Ronquist and Huelsenbeck 2003) with the model estimated above. We used four chains, with random initial trees. Trees were generated for 2000000 generations, with sampling every 100 generations. The first 4000 trees before stationarity were discarded as burn-in, and the remaining trees were used to construct majority-rule consensus trees using PAUP.

The combined 3-marker (*atpA/atpB/rbcL*) and the combined 5-marker (*atpA/atpB/rbcL/trnL-F/rps4-trnS*) data sets were analyzed phylogenetically. To assess the level of congruence between five separated data sets, we analyzed each data set separately to see if they produced similar topologies. Congruence between plastid data sets

was tested using the incongruence length difference (ILD) test (Farris et al. 1994), as implemented by the partition homogeneity test in PAUP for 100 replicates (heuristic search, simple addition, TBR branching swapping), each saving a maximum of 100 trees per replicate (Norup et al. 2006).

Results

Phylogenetic analyses

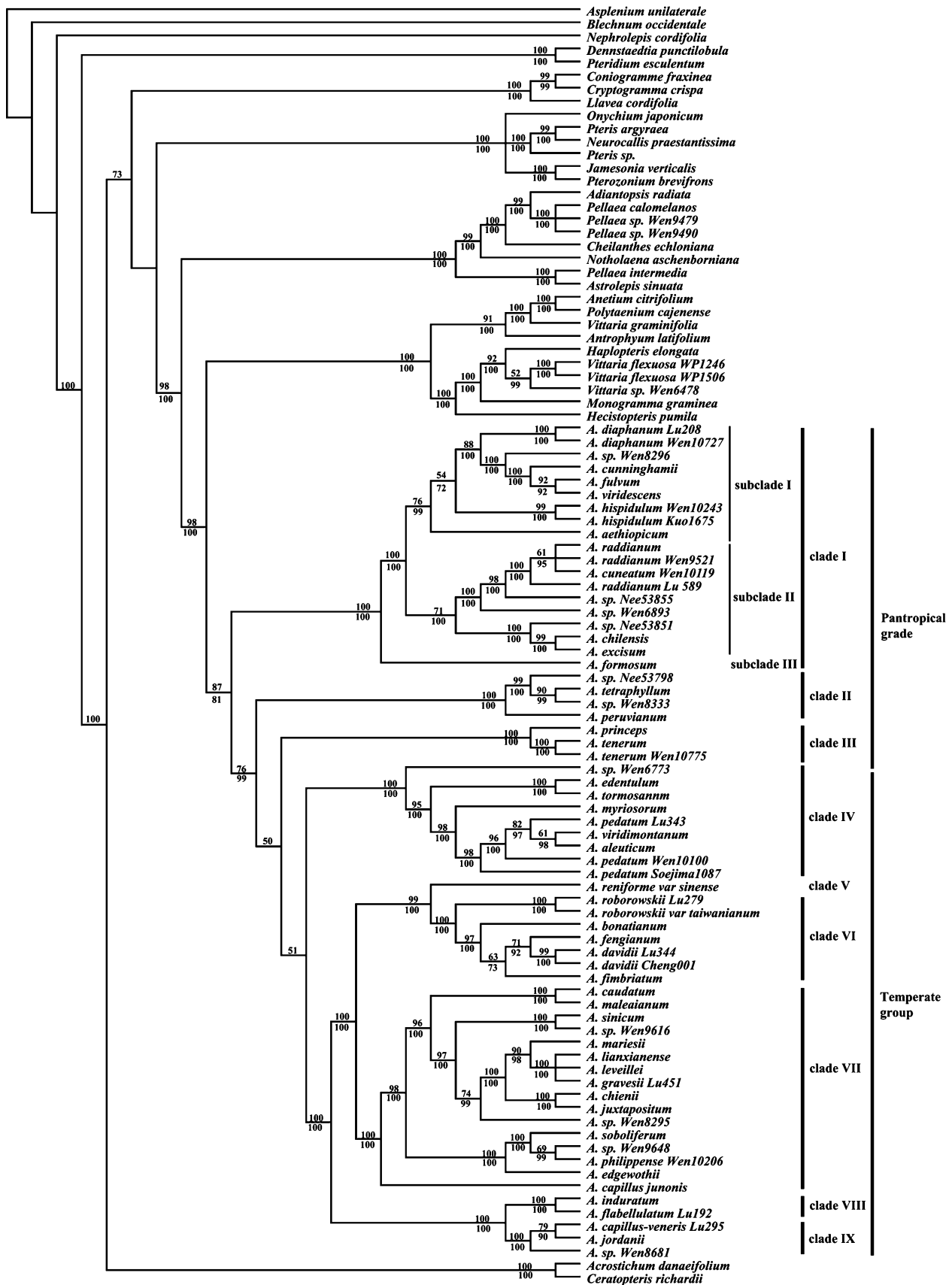
The alignment of the combined 3-marker (*atpA/atpB/rbcL*) in 98 taxa was 3,991 nucleotides in length. Sequences of 29 species were downloaded from GenBank. The data matrix contained 1688 variable sites (42.3%), of which 1,379 were phylogenetically informative (34.6%). The MP analysis of the 3-marker data set yielded two shortest trees of 7,332 steps, a consistency index (CI) of 0.336, and a retention index (RI) of 0.768.

The phylogenetic analysis strongly supported the monophyly of the adiantoid clade (i.e., the AD clade; BP = 98/PP = 100), and the monophyly of *Adiantum* was supported (87/81) (Fig. 2).

The *Adiantum* taxa from the temperate regions were nested within a large pantropical grade. The pantropical grade fell into four clades with clade I consisting of three subclades. Subclade I (76/99) of clade I included taxa from New Zealand, Australia, and tropical Asia (*A. hispidium*, *A. diaphanum* and another unidentified Asian sample), and subclade II (71/100) was primarily from Madagascar, Central America, and South America. *Adiantum formosum* from New Zealand and Australia was the sole member of subclade III, and was sister to the aggregate of subclades I and II. Clade II included four species from South America (100/100). Two species, *A. tenerum* and *A. princeps* from Mexico, constituted clade III (100/100). One *Adiantum* species from Central America was nested within clade IV along with the eastern Asian *A. edentulum* and *A. pedatum* complex.

Six main clades were identified in the temperate group (Fig. 2). The *A. pedatum* complex was nested within clade IV, along with the eastern Asian *A. edentulum* and one species from Central America (100/100). *A. reniforme* var. *sinense* was the sole member of clade V, which was sister to the venusta group (clade VI, 99/100). Series *Gravesiana* in Lin's classification was nested within series *Caudata* (clade VII, 100/100). Clade VIII was composed of the

Fig. 2 Strict consensus tree of two maximally parsimonious trees derived from the analysis of the plastid *atpA*, *atpB*, and *rbcL* sequences (tree length = 7,332 steps, CI = 0.336, and RI = 0.768). The bootstrap values for 1,000 replicates are shown above the lines, and the Bayesian posterior probabilities are shown below the lines



subtropical *A. flabellulatum* and *A. induratum*, and was sister to clade IX (100/100), which included *A. capillus-veneris* and *A. jordanii*.

The alignment of the combined 5-marker (*atpA/atpB/rbcL/trnL-F/rps4-trnS*) data of 81 species was 6,059 nucleotides in length. The data matrix contained 2,179 variable sites (36%), of which 1,912 sites were phylogenetically informative (31.6%). The MP analysis of the 5-marker data set yielded six shortest trees of 5,281 steps, a CI of 0.549, and an RI of 0.906.

The 5-marker analysis strongly supported the monophyly of *Adiantum* (100/100) (Fig. 3). The overall topology of the 5-marker trees was similar to that of the 3-marker trees concerning major clades, all of which had strong support. The close relationship between clade III and other temperate clades was supported by high bootstrap support (90); however, this relationship was not well supported by the Bayesian analyses (PP = 59).

Discussion

Monophyly of *Adiantum* and a tropical origin of the genus

Adiantum is supported to be monophyletic in our analyses using either five or three plastid markers (Figs. 2, 3). *Adiantum* has been considered an isolated genus within Pteridaceae (Tryon and Tryon 1982), although no fossil of *Adiantum* has been reported. The genus is defined by its shining black or chestnut-brown, and wiry stipe and the “false indusium” with sori borne along the apical part of veins on the underside of the sharply reflexed leaf margin. *Adiantum* and the vittarioid ferns together form a well-supported clade (98/100, Fig. 2) known as the AD clade as suggested by Schuettpelz and Pryer (2007). Yet the monophyly of *Adiantum* was not well resolved in previous studies (e.g., Prado et al. 2007; Schuettpelz and Pryer 2007; Schuettpelz et al. 2007; Bouma et al. 2010). *Adiantum raddianum* was suggested to be sister to the *Vittaria* group in the molecular phylogenetic study of Pteridaceae based on the combined *atpA/atpB/rbcL* analyses by Schuettpelz et al. (2007). The vittarioids were nested within *Adiantum* in the molecular phylogeny of the New Zealand Pteridaceae using *rbcL* (Bouma et al. 2010). In our analyses, the monophyly of *Adiantum* was supported with the bootstrap value of 87%, yet the PP value was only 81 in the Bayesian analysis (Fig. 2). Phylogenetic inferences for the AD clade are perhaps sensitive to taxon and marker sampling. Our taxon sampling is broader and we included more molecular characters as well. Nevertheless, it is necessary to further test the monophyly of *Adiantum* with a global sampling scheme.

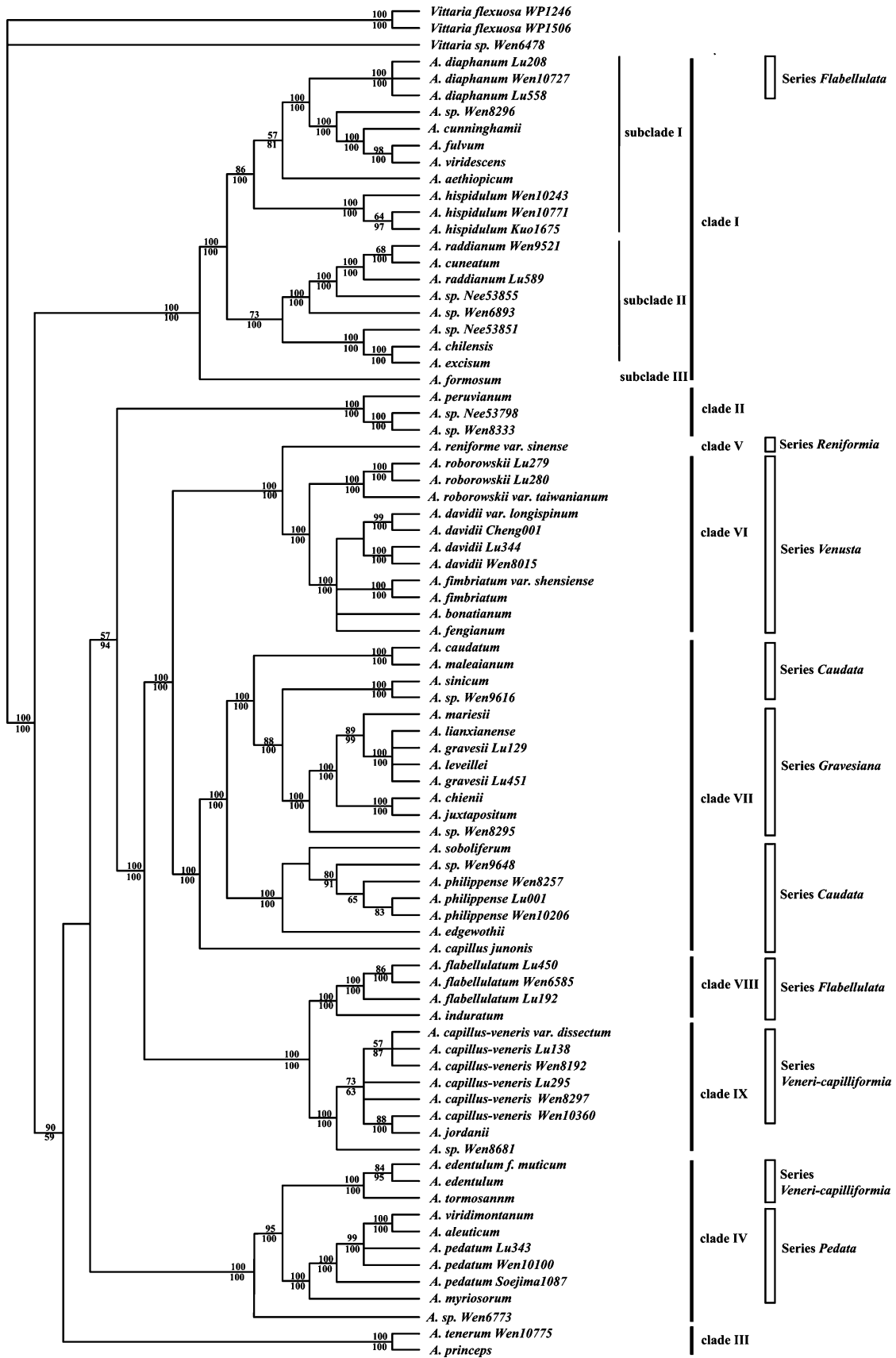
Our phylogenetic study supports a tropical origin of *Adiantum*. The closest sister of *Adiantum* is the tropical *Vittaria* and its allies. All temperate *Adiantum* species (including the species from Asia, Europe, and North America) form a clade, which is nested within the pantropical grade, suggesting a tropical origin of *Adiantum*. Most of the 150–200 species in *Adiantum* are distributed in tropical to subtropical regions, especially in the Neotropics (e.g., Tryon and Tryon 1982; Huiet and Smith 2004). *Adiantum* species of the Old World have a different flavonoid pattern from those species sampled from the New World (Cooper-Driver and Swain 1977). Based on the assumption of evolutionary trends in the chemistry of flavonoids and cinnamic esters of *Adiantum*, Cooper-Driver and Swain (1977) regarded the Old World species of *Adiantum* in section 1 (mainly the *Caudatum* group) as the most primitive and the New World species in sections 3 and 4 as the most advanced. They concluded that the Old World species represent the more primitive stocks. They placed most temperate species in the Old World in section 1 and most tropical species in the Old World in section 2 with some exceptions (e.g., tropical *A. aethiopicum* was assigned in section 1, and *A. soboliferum* was put in section 5 (Cooper-Driver and Swain 1977).

Almost all sampled Asian species fell into one temperate group except for *A. diaphanum* and *A. hispidum*. *Adiantum diaphanum* is distributed in southern China, Vietnam, Malaysia, Indonesia, Australia, and New Zealand, and *A. hispidum* is distributed in southern India, eastern Africa, and the Pacific islands. There are some hispid hairs on the petioles and the adaxial leaf surface in *A. diaphanum* and *A. hispidum*. It is possible that the two species have a tropical origin, and migrated northward to eastern Asia. The long hairs can be found in the petioles and rachises of a few temperate to subtropical Asian *Adiantum* species. These species (e.g., *A. induratum*, *A. caudatum* and *A. malesianum*) can extend to tropical Asia.

Main clades of Chinese *Adiantum* and evaluation of Lin's classification

Ching (1957) divided the Chinese *Adiantum* species into six series. Lin (1980) added an additional series *Reniformia*. We sampled over 80% of the species, varieties, and forms of Chinese *Adiantum* in this study. Six main clades are resolved within Chinese *Adiantum* (Figs. 2, 3) and the

Fig. 3 Strict consensus tree of six maximally parsimonious trees derived from the analysis of *atpA*, *atpB*, *rbcL*, *trnL-F*, and *rps4-trnS* sequences (tree length = 6,059 steps, CI = 0.549, and RI = 0.906). The bootstrap values for 1,000 replicates are shown above the lines, and the Bayesian posterior probabilities are shown below the lines. The series of Lin's (1980) classification was labeled in column



phylogenetic results show some incongruence with Lin's classification of the genus.

Series *Caudata* is polyphyletic with series *Gravesiana* nested within one subgroup of series *Caudata* in clade VII. *A. reniforme* with the simple fronds is sister to series *Venusta* which has a decomposed lamina with many flabellate to cuneate segments. Series *Veneri-capilliformia* is not monophyletic, with *A. capillus-veneris* sister to series *Flabellulata* except for *A. diaphanum*, and *A. edentulum* is nested within clade IV, along with the *A. pedatum* complex. Series *Flabellulata* is biphyletic with *A. diaphanum* nested within the pantropical grade while the two species (*A. flabellulatum* and *A. induratum*) nested within clade VIII.

Series *Caudata* is characterized by the herbaceous texture of fronds with the rachis prolonged into a whip, while series *Gravesiana* has coriaceous fronds with the pinnae readily detached by articulation from the petiole upon drying, and the rachis always terminated by an end-pinna, never prolonged into a whip nor rooting at the apex. Morphologically, the two series can be easily distinguished from each other although series *Gravesiana* is nested within series *Caudata* in the present analyses. *Adiantum lianxianense* and *A. leveillei* are nested within *A. gravesii*, suggesting a close relationship among the three limestone species and the need to evaluate their species limits. The major morphological differences among the three species are the plant size and the pinna size. Lin (1980) treated *A. leveillei* as a synonym of *A. gravesii* and published a new species *A. lianxianense*. Both the molecular phylogeny and morphology suggest that *A. lianxianense* may be treated as a synonym of *A. gravesii*. Furthermore, *Adiantum juxtositum* may be a synonym of *A. chienii* as there are few differences in DNA sequences and morphological characters. The major diagnostic character between the two Danxia landform species, *Adiantum juxtositum* and *A. chienii*, is the number of false indusia. The former was described to have 3–4 indusia while the latter has one (occasionally 2). However, we noted in the field that there are a few plants with 3–4 indusia in the one-indusium population in Mt. Guanzhi, Fujian.

Series *Veneri-capilliformia* is not monophyletic. *A. capillus-veneris* is sister to series *Flabellulata* (*A. flabellulatum* and *A. induratum*) except for *A. diaphanum*; while the other species of series *Veneri-capilliformia*, *A. edentulum*, is sister to series *Pedata*. *A. capillus-veneris* is one of the most widely distributed fern species, occurring primarily in warm-temperate to subtropical areas. However, it is a species with little morphological homogeneity in *Adiantum*. The fronds of *A. capillus-veneris* are bipinnate, tripinnate or occasionally quadripinnate; the ultimate pinnules are variable in size and shape, roughly cuneate at base; the outer margin is deeply incised, incised or lobed,

with 1–5 sori occurring per pinnule on the margins of the lobes. However, all sampled *A. capillus-veneris* from Asia, Europe and the New World grouped together, which is consistent with the analysis of phenolic chemotaxonomy of *Adiantum* (Cooper-Driver and Swain 1977). The morphological heterogeneity of this species may owe to its widespread distribution and broad ecological range. Furthermore, Cooper-Driver and Swain (1977) suggested that *A. capillus-veneris* has probably spread relatively recently. Huiet and Smith (2004) reported that *A. capillus-veneris* is sister to the clade of all other members of *Adiantum*. Our analyses indicate that *A. capillus-veneris* is not the first diverged species in this genus. On the contrary, the evidence from the coherence in DNA sequences in all sampled *A. capillus-veneris*, the biogeographic analyses, and the Bayesian dating (Lu et al. unpublished) all support the presumption of a recent geographic migration for *A. capillus-veneris* (Cooper-Driver and Swain 1977).

Series *Reniformia* is sister to series *Venusta*. *A. reniforme* has the simplest frond form and is regarded as a highly derived species (Tryon et al. 1990) in *Adiantum*. The species has three varieties in Madeira and the Canary islands (Atlantic, *A. reniforme*), southern Africa and Madagascar (*A. reniforme* var. *asariforme* (Willd.) Sim.), and China (*A. reniforme* var. *sinense*). *A. reniforme* var. *sinense* is sister to series *Venusta* which has a decomposed lamina with many flabellate to cuneate segments. Parallel or convergent evolution did occur in the frond architecture in *Adiantum*. There is no evidence to indicate that *A. reniforme* is either highly derived or the most primitive taxon in *Adiantum*.

Series *Flabellulata* is biphyletic. *A. flabellulatum* and *A. induratum* form a well-supported clade sister to *A. capillus-veneris*, while *A. diaphanum* is nested within a pantropical grade. There are some hispid hairs on petioles and the adaxial leaf surface in *A. diaphanum*. The hispid hairs are heterogeneous in Chinese *Adiantum* species and only can be found in *A. diaphanum*.

Series *Pedata* is sister to *A. edentulum*, even though series *Pedata* is more similar to *A. flabellulatum* and *A. hispidulum* in frond architecture. Series *Pedata* is distributed in the north temperate zone while *A. hispidum* and *A. flabellatum* are in tropical and subtropical Asia (Lin 1990; Paris 1993). Their similarities in frond architecture seem to represent convergent evolution. *Adiantum myriosorum*, the earliest divergent member in series *Pedata*, is distributed in southwestern China, overlapping with *A. edentulum*.

The molecular phylogenetic study using *rps4-trnS* showed that the *A. patens* group, the *A. pectinatum* group, and the *A. capillus-veneris* group in the classification of Tryon and Tryon (1982) are each polyphyletic (Huiet and Smith 2004). Our results support that the *A. patens* group,

and the *A. capillus-veneris* group of Tryon et al. (1990) are each polyphyletic (see Huiet and Smith 2004).

About 60 species of *Adiantum* are native to Asia. There is an endemic *Gravesiana* group in limestone areas and the Danxia landforms in China and northern Vietnam. Series *Gravesiana* can be easily distinguished from series *Caudata* in morphology; thus it was unexpected to discover series *Gravesiana* nested within series *Caudata* in our analyses. It is possible the characteristic of the prolonged whip-like stolon at the apex is lost in series *Gravesiana* in limestone areas and Danxia landforms. The water availability is low in limestone areas and Danxia landforms so that it may not be possible to provide enough water to prolong the whip-like stolon and rooting.

Tryon and Tryon (1982) proposed that parallel and convergent evolution probably occurred in leaf architecture in *Adiantum*. The species with a simpler lamina was thought to be more specialized while the species which have a decomposed lamina with many flabellate to cuneate segments are least derived (Tryon and Tryon 1982). Huiet and Smith (2004) suggested that the frond morphology as in *A. capillus-veneris* occurs in at least three clades. Bouma (2008) pointed out *A. raddianum* and *A. aethiopicum* in the *A. capillus-veneris* group of Tryon and Tryon (1982) were quite distantly related to *A. capillus-veneris* based on their concatenated analysis of four chloroplast loci. Our phylogeny also supported convergent evolution of frond architecture in *Adiantum*.

Acknowledgments We thank Xiao Cheng, Yu-xiao Zhang, Li-Yaung Kuo, Akiko Soejima and Tom Heutte for sample collection, and Elizabeth Zimmer for providing primers. The study was supported by the National Natural Science Foundation of China (Grant no. 31070199, 30800063), the Project of Knowledge Innovation Program of the Chinese Academy of Sciences (Grant no.: 2010KIBA02), the Research Fund for the Large-scale Scientific Facilities of the Chinese Academy of Sciences (Grant no. 2009-LSF-GBOWS-01), and the John D. and Catherine T. MacArthur Foundation (to J. Wen, R. Ree and G. Mueller).

Appendix 1

Voucher information and GenBank accession numbers for taxa used in the phylogenetic study on *Adiantum*. Taxon, voucher specimen (herbarium), collection locality, and GenBank accession number in the order of *rbcL*, *atpB*, *atpA*, *trnL-F*, and *rps4-trnS*.

Adiantum aethiopicum L.; *J. Wen 10780* (US); New Zealand; JF935350; JF935432; JF937305; JF980695; JF980616.

Adiantum aleuticum (Rupr.) C.A. Paris; *Heutte s.n.* (US); Alaska, USA; JF935362; JF935447; JF937320; JF980709; JF980631.

Adiantum bonatianum Brause; *J.-M. Lu 216* (KUN); Yunnan, China; JF935294; JF935371; JF937247; JF980639; JF980556.

Adiantum capillus-junonis Rupr.; *J.-M. Lu 111* (KUN); Guangxi, China; JF935314; JF935395; JF937269; JF980662; JF980578.

Adiantum capillus-veneris L.; *J. Wen 10360* (US); Russia; JF935345; JF935427; JF937300; JF980690; JF980611.

Adiantum capillus-veneris; *J.-M. Lu 138* (KUN); Guangxi, China; JF935320; JF935401; JF937274; JF980666; JF980584.

Adiantum capillus-veneris; *J.-M. Lu 295* (KUN); Chongqing, China; JF935322; JF935403; JF937276; JF980667; JF980586.

Adiantum capillus-veneris; *J. Wen 8192* (US); Chongqing, China; JF935332; JF935413; JF937286; JF980676; JF980597.

Adiantum capillus-veneris; *J. Wen 8297* (US); Luzon, the Philippines; JF935334; JF935415; JF937288; JF980678; JF980599.

Adiantum capillus-veneris var. *dissectum* (Mart. Et Galeot.) Ching; *J.-M. Lu 118* (KUN); Guangxi, China; JF935318; JF935399; JF937273; JF980665; JF980582.

Adiantum caudatum L.; *J.-M. Lu 209* (KUN); Hainan, China; JF935296; JF935373; JF937249; JF980641; JF980558.

Adiantum chienii Ching; *J.-M. Lu 568* (KUN); Fujian, China; JF935303; JF935381; JF937256; JF980649; JF980565.

Adiantum chilense Kaulf.; *J. Wen 7313* (US); Nuble, Chile; JF935336; JF935418; JF937291; JF980681; JF980602.

Adiantum cuneatum Langsd & Fisch.; *J. Wen 10119* (US); West Java, Indonesia; JF935339; JF935421; JF937294; JF980684; JF980605.

Adiantum cunninghamii Hook.; *J. Wen 10782* (US); New Zealand; JF935351; JF935433; JF937306; JF980696; JF980617.

Adiantum davidii Franch.; *J.-M. Lu 344* (KUN); Shanxi, China; JF935310; JF935391; JF937265; JF980659; JF980574.

Adiantum davidii; *J. Wen 8015* (US); Gansu, China; JF935319; JF935400; —; —; JF980583;

Adiantum davidii; *X. Cheng 001* (KUN); Yunnan, China; JF935316; JF935397; JF937271; —; JF980580.

Adiantum davidii var. *longispinum* Ching; *J.-M. Lu 247* (KUN); Yunnan, China; JF935292; JF935369; JF937245; JF980638; JF980554.

Adiantum diaphanum Blume; *J.-M. Lu 208* (KUN); Hainan, China; JF935301; JF935379; JF937254; JF980647; JF980563.

- Adiantum diaphanum*; J.-M. Lu 558 (KUN); Fujian, China; JF935304; JF935382; JF937257; JF980650; JF980566.
- Adiantum diaphanum*; J. Wen 10727 (US); Indonesia; —; JF935439; JF937312; JF980702; JF980623.
- Adiantum edentulum* H. Christ; J.-M. Lu 222 (KUN); Yunnan, China; JF935291; JF935368; JF937244; JF980637; JF980553.
- Adiantum edentulum* f. *muticum* (Ching) Y. X. Lin; J.-M. Lu 226 (KUN); Yunnan, China; JF935290; JF935367; JF937243; JF980636; JF980552.
- Adiantum edgeworthii* Hook.; J.-M. Lu 114 (KUN); Guangxi, China; JF935311; JF935392; JF937266; JF980660; JF980575.
- Adiantum excisum* Kunze; J. Wen 7326 (US); Concepcion, Chile; JF935337; JF935419; JF937292; JF980682; JF980603.
- Adiantum fengianum* Ching; J.-M. Lu 228 (KUN); Yunnan, China; JF935308; JF935388; JF937262; JF980656; JF980571.
- Adiantum fimbriatum* Christ; J.-M. Lu 215 (KUN); Yunnan, China; JF935321; JF935402; JF937275; —; JF980585.
- Adiantum fimbriatum* var. *shensiense* (Ching) Ching; J.-M. Lu 227 (KUN); Yunnan, China; JF935293; JF935370; JF937246; —; JF980555.
- Adiantum flabellulatum* L.; J.-M. Lu 192 (KUN); Guizhou, China; JF935315; JF935396; JF937270; JF980663; JF980579.
- Adiantum flabellulatum*; J.-M. Lu 450 (KUN); Guangdong, China; JF935295; JF935372; JF937248; JF980640; JF980557.
- Adiantum flabellulatum*; J. Wen 6585 (US); Hainan, China; JF935325; JF935406; JF937279; JF980670; JF980589.
- Adiantum formosanum* Tagawa; L.-Y. Kuo 430 (TAIF); Taiwan, China; —; JF935384; —; JF980652; JF980568.
- Adiantum formosum* R. Br.; J. Wen 10779 (US); New Zealand; JF935352; JF935434; JF937307; JF980697; JF980618.
- Adiantum fulvum* Raoul; J. Wen 10781 (US); New Zealand; JF935353; JF935435; JF937308; JF980698; JF980619.
- Adiantum gravesii* Hance; J.-M. Lu 129 (KUN); Guangxi, China; JF935312; JF935393; JF937267; —; JF980576.
- Adiantum gravesii*; J.-M. Lu 451 (KUN); Guangdong, China; JF935317; JF935398; JF937272; JF980664; JF980581.
- Adiantum hispidulum* Sw.; J. Wen 10243 (US); Sulawesi, Indonesia; JF935341; JF935423; JF937296; JF980686; JF980607.
- Adiantum hispidulum*; J. Wen 10771 (US); Virginia cultivated, USA; JF935349; JF935431; JF937304; JF980694; JF980615.
- Adiantum hispidulum*; L.-Y. Kuo 1675 (TAIF); Taiwan, China; —; JF935377; —; JF980645; —.
- Adiantum induratum* H. Christ; J.-M. Lu 210 (KUN); Hainan, China; JF935309; JF935389; JF937263; JF980657; JF980572.
- Adiantum jordanii* C.H. Mull.; J. Wen 10778 (US); California, USA; JF935348; JF935430; JF937303; JF980693; JF980614.
- Adiantum juxtapositum* Ching; J.-M. Lu 575 (KUN); Fujian, China; JF935305; JF935383; JF937258; JF980651; JF980567.
- Adiantum leveillei* H. Christ; J.-M. Lu 163 (KUN); Guangxi, China; JF935313; JF935394; JF937268; JF980661; JF980577.
- Adiantum lianxianense* Ching and Y.X. Lin; J.-M. Lu 441 (KUN); Guangdong, China; JF935306; JF935385; JF937259; JF980653; JF980569.
- Adiantum malesianum* Ghatak; J.-M. Lu 050 (KUN); Yunnan, China; JF935297; JF935374; JF937250; JF980642; JF980559.
- Adiantum mariesii* Baker; J.-M. Lu 120 (KUN); Guangxi, China; JF935302; JF935380; JF937255; JF980648; JF980564.
- Adiantum myriosorum* Baker; J.-M. Lu 297 (KUN); Chongqing, China; JF935359; JF935444; JF937317; JF980706; JF980628.
- Adiantum pedatum* L.; J. Wen 10100 (US); Maryland, USA; JF935361; JF935446; JF937319; JF980708; JF980630.
- Adiantum pedatum*; J.-M. Lu 343 (KUN); Shanxi, China; JF935360; JF935445; JF937318; JF980707; JF980629.
- Adiantum pedatum*; A. Soejima 1087 (US); Osaka, Japan; JF935363; JF935448; JF937321; JF980710; JF980632.
- Adiantum peruvianum* Klotzsch; J.-M. Lu 338 (KUN); India; JF935288; JF935365; JF937241; JF980634; JF980550.
- Adiantum philippense* L.; J.-M. Lu 001 (KUN); Yunnan, China; JF935331; —; —; —; JF980596.
- Adiantum philippense*; J. Wen 8257 (US); Luzon, the Philippines; JF935330; JF935412; JF937285; JF980675; JF980595.
- Adiantum philippense*; J. Wen 10206 (US); Indonesia; JF935340; JF935422; JF937295; JF980685; JF980606.
- Adiantum princeps* T. Moore; J. Wen 10777 (US); Yucatan, Mexico; JF935356; JF935438; JF937311; JF980701; JF980622.
- Adiantum raddianum* C. Presl; J. Wen 9521 (US); Antsiranana, Madagascar; JF935323; JF935404; JF937277; JF980668; JF980587.

Adiantum raddianum; *J.-M. Lu 589* (KUN); Shenzhen cultivated, China; JF935307; JF935387; JF937261; JF980655; JF980570.

Adiantum reniforme var. *sinense* Y.X. Lin; *J.-M. Lu 238* (KUN); Hubei, China; JF935287; JF935364; JF937240; JF980633; JF980549.

Adiantum roborowskii Maxim.; *J.-M. Lu 279* (KUN); Chongqing, China; JF935289; JF935366; JF937242; JF980635; JF980551.

Adiantum roborowskii; *J.-M. Lu 280* (KUN); Chongqing, China; JF935298; JF935375; JF937251; JF980643; JF980560.

Adiantum roborowskii var. *taiwanianum* (Tagawa) Shieh; *Wade 909* (TAIF); Taiwan, China; —; JF935386; JF937260; JF980654; —.

Adiantum sinicum Ching; *J.-M. Lu 269* (KUN); Yunnan, China; JF935300; JF935378; JF937253; JF980646; JF980562.

Adiantum soboliferum Wall.; *Y.-X. Zhang 009* (KUN); Yunnan, China; JF935299; JF935376; JF937252; JF980644; JF980561.

Adiantum sp.; *J. Wen 6773* (US); Costa Rica; —; JF935440; JF937313; —; JF980624.

Adiantum sp.; *J. Wen 6893* (US); Cartago, Costa Rica; —; JF935417; JF937290; JF980680; JF980601.

Adiantum sp.; *J. Wen 8295* (US); Luzon, the Philippines; JF935329; JF935411; JF937284; JF980674; JF980594.

Adiantum sp.; *J. Wen 8296* (US); Luzon, the Philippines; —; JF935410; JF937283; —; JF980593.

Adiantum sp.; *J. Wen 8333* (US); Malaysia; JF935344; JF935426; JF937299; JF980689; JF980610.

Adiantum sp.; *J. Wen 8681* (US); Oaxaca, Mexico; JF935338; JF935420; JF937293; JF980683; JF980604.

Adiantum sp.; *J. Wen 9616* (US); Antsiranana, Madagascar; JF935326; JF935407; JF937280; JF980671; JF980590.

Adiantum sp.; *J. Wen 9648* (US); Antsiranana, Madagascar; JF935327; JF935408; JF937281; JF980672; JF980591.

Adiantum sp.; *Nee and Wen 53798* (US); Bolivia; —; JF935390; JF937264; JF980658; JF980573.

Adiantum sp.; *Nee and Wen 53851* (US); Bolivia; JF935333; JF935414; JF937287; JF980677; JF980598.

Adiantum sp.; *Nee and Wen 53885* (US); Bolivia; JF935335; JF935416; JF937289; JF980679; JF980600.

Adiantum tenerum Sw.; *J. Wen 10775* (US); Yucatan, Mexico; JF935355; JF935437; JF937310; JF980700; JF980621.

Adiantum viridescens Colenso; *J. Wen 10783* (US); New Zealand; JF935354; JF935436; JF937309; JF980699; JF980620.

Adiantum viridimontanum C.A. Paris; *Paris 856* (US); Vermont, USA; JF935347; JF935429; JF937302; JF980692; JF980613.

Cheilanthes eckloniana Mett.; *J. Wen 10088* (US); Kwazulu Natal, South Africa; JF935343; JF935425; JF937298; JF980688; JF980609.

Pellaea sp.; *J. Wen 9479* (US); Ihoisy, Madagascar; JF935324; JF935405; JF937278; JF980669; JF980588.

Pellaea sp.; *J. Wen 9490* (US); Toamasina, Madagascar; JF935328; JF935409; JF937282; JF980673; JF980592.

Pellaea calomelanos (Sw.) Link; *J. Wen 10082* (US); Kwazulu Natal, South Africa; JF935346; JF935428; JF937301; JF980691; JF980612.

Peteri sp.; *J. Wen 10179* (US); Indonesia; JF935342; JF935424; JF937297; JF980687; JF980608.

Vittaria flexuosa Fée; *WP1246* (KUN); Vietnam; JF935357; JF935441; JF937314; JF980703; JF980625.

Vittaria flexuosa; *WP1506* (KUN); Vietnam; —; JF935442; JF937315; JF980704; JF980626.

Vittaria sp.; *J. Wen 6478* (US); Yunnan, China; JF935358; JF935443; JF937316; JF980705; JF980627.

Appendix 2

Samples included in the 3-marker analyses of *Adiantum*.

Taxon: *rbcL* GenBank accessions, *atpB* GenBank accessions, *atpA* GenBank accessions.

Acrostichum danaeifolium: EF452129, EF452008, EF452065;

Adiantopsis radiata: EF452131, EF452010, EF452067;

Adiantum raddianum: U05906, U93840, EF452071;

Adiantum tenerum: EF452134, EF452014, EF452072;

Adiantum tetraphyllum: EF452135, EF452015, EF452073;

Anetium citrifolium: U21284, EF452017, EF452075;

Antrophyum latifolium: EF452138; EF452018, EF452076;

Asplenium unilaterale: EF452140, EF452020, EF452078;

Astrolepis sinuata: EF452141, EF452021, EF452079;

Blechnum occidentale: U05909, U93838, EF452080;

Ceratopteris richardii: AB059585, AY612691, EF452082;

Coniogramme fraxinea: AM177359, AY612693, AM176470;

Cryptogramma crista: EF452148, EF452027, EF452087;

Dennstaedtia punctilobula: U05918, U93836, EF452090;

Haplopteris elongata: EF452153, EF452035, EF452096;

Hecistopteris pumila: U21286, EF452036, EF452097;

Jamesonia verticalis: EF452155, EF452038, EF452099;

Llavea cordifolia: U27726, EF452039, EF452100;

Monogramma graminea: EF452157, EF452040, EF452102;
Nephrolepis cordifolia: U05933, EF452041, EF452103;
Neurocallis praestantissima: EF452158, EF452042, EF452104;
Notholaena aschenborniana: EF452159, EF452043, EF452105;
Onychium japonicum: U05641, EF452045, EF452107;
Pellaea intermedia: EF452163, EF452047, EF452109;
Polytaenium cajenense: U20934, EF452052, EF452114;
Pteridium esculentum: U05940, U93834, EF452115;
Pteris argyraea: EF452169, EF452054, EF452117;
Pterozonium brevifrons: EF452175, EF452061, EF452124;
Vittaria graminifolia: U21295, EF452064, EF452128.

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