

**Phylogeny and diversification of Chinese Araliaceae based
on nuclear and plastid DNA sequences data**

Running title: phylogeny and diversification of Chinese Araliaceae

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Abstract Chinese Araliaceae consist of 20 genera and 173 species. To assess the evolutionary relationships of Araliaceae and their biogeographic diversification in China, the phylogeny of Chinese Araliaceae was constructed by sampling 96 accessions representing 20 genera and 50 species of Chinese Araliaceae and 45 closely related taxa using sequences of the nuclear ribosomal internal transcribed spacer (ITS) region and six plastid regions (the *ndhF* gene, the *trnL-trnF* region, the *rps16* intron, the *atpB-rbcL* intergenic spacer, the *rpl16* intron, and the *psbA-trnH* intergenic spacer). Phylogenetic analyses of the combined plastid and ITS data supported the results of the previously studies that the Chinese members of Araliaceae were scattered within the Asian Palmate group and the *Aralia-Panax* group with *Osmoxylon* at the base of core Araliaceae. The generic status of *Pentapanax* and *Tupidanthus* is not supported. Our analysis clearly places them in *Aralia* and Asian *Schefflera*, respectively. In a broader phylogenetic framework of Araliaceae, based on the fossil-calibrated Bayesian dating, Chinese Araliaceae was inferred to have originated in Asia and underwent a rapid radiation in its evolutionary history. Its diversification is hypothesized to have been driven largely by the orogenies in Asia during the Cenozoic.

Key words *Aralia-Panax* group, Asian Palmate group, Chinese Araliaceae, diversification, phylogeny.

Araliaceae (the ginseng family) consist of approximately 45 genera and 1,500 species with a wide distribution in tropical and subtropical Asia, the Pacific and the Indian Ocean basin, and the neotropics, with a few well-known genera from the north and south temperate zones (Wen et al., 2001; Plunkett et al., 2004). Members of Araliaceae are characterized by mostly woody habit and relatively conserved floral morphology, i.e., mostly 5-merous flowers with inferior ovaries, inflorescences commonly a compound umbel (rarely a raceme or head), and fruit a drupe with 2-5 (rarely to many) seeds, yet highly variable leaf morphology (simple, palmately compound, to variously pinnately compound) (Philipson, 1970; Wen et al., 2001; Yi et al., 2004). Phylogenetic studies of the Araliaceae based on analyses of sequence data from nuclear ribosomal DNA and chloroplast DNA have circumscribed four major monophyletic groups (the Asian Palmate group, the *Polyscias-Pseudopanax* group, the *Aralia-Panax* group, and the greater *Raukaua* group) placed in a basal polytomy together with a group of poorly resolved minor lineages (Wen et al., 2001; Plunkett et al., 2004; Mitchell et al., 2012).

In total, 20 genera and 173 species of Araliaceae have been recognized in China (Table 1). Of these taxa, two genera and 82 species are endemic (Shang & Lowry, 2007). Since Li (1942), taxonomic treatments for Chinese Araliaceae have been published, such as Hoo & Tseng (1965, 1978) and Shang & Lowry (2007). Tseng & Hoo (1982) divided Araliaceae into five tribes (Plerandreae Benth., Tetraplasandreae Hoo & Tseng, Mackinlayae Benth., Aralieae Benth., and Panaceae Benth.) based on petal aestivation and leaf morphology. In their classification system, the Chinese members of Araliaceae were placed in four tribes (Plerandreae, Tetraplasandreae, Aralieae, and Panaceae) (Table 1). Recent molecular phylogenetic studies (Wen et al., 2001; Mitchell & Wen, 2004; Plunkett et al., 2004) revealed that the Chinese members of Araliaceae are scattered within two major lineages of the family (the Asian Palmate group and the *Aralia-Panax* group), with *Osmoxylon* Miq. at the base of core Araliaceae (Table 1). Even so, the phylogenetic relationships among the genera within each major group have been poorly resolved in the early studies, although most genera are well circumscribed by molecular data. With the Chinese

Araliaceae accounting for nearly half of the total number of genera in the family, a phylogenetic analysis of Araliaceae from China using additional markers and expanding the sampling scheme is indispensable to facilitate a better understanding of the evolutionary diversification and classification of this family.

China harbors a broad geographical area (about 9.6 million km² and a span for more than 50° latitude), with enormous variations in geographical and topographical features, from mostly plateaus and mountains in the west to lower lands in the east (Wu & Wang, 1983). The diverse habitats and rich biodiversity in China have long intrigued biologists (Axelrod et al., 1998; Qian & Ricklefs, 1999; Wang et al., 2012). The past climate fluctuations and correlated change in the distribution of land and sea, plate tectonic activities, and the Quaternary glacial periods are seen as major contributors to the present distribution of plants and animals in this region (Shi et al., 1998; An et al., 2001). However, only a few phylogenetic studies with a biogeographic context in this region have focused on plants (e.g., Fan et al., 2009; Yu et al., 2011; Zhou et al., 2013). To better understand the biogeographic diversification of plants in this region, we need to evaluate the phylogenetic relationships and estimate divergence times in many lineages. The Chinese Araliaceae provide a good opportunity to examine the biogeographic pattern in this region because the family is distributed throughout China except Xinjing province.

In this study, we use a taxon sampling scheme throughout the range of the family, expanding the Chinese sampling used in previous studies up to 50 current recognized species in Flora of China. The main goals of the present study are to: (1) test the phylogenetic relationships of Araliaceae in China, with a particular emphasis on the generic status of *Pentapanax* Seem., which was merged into *Aralia* L. by Wen (2002), but recognized by Shang & Lowry (2007), and *Tupidanthus* J. D. Hooker & Thomson, which was included in Asian *Schefflera* (Frodin & Govaerts, 2003; Li & Wen, 2014), but recognized by Shang & Lowry (2007); and (2) elucidate the biogeographic diversification history of the Chinese Araliaceae. We have herein sequenced the nuclear internal transcribed spacer (ITS) regions of ribosomal DNA and six coding or non-coding plastid regions (the *ndhF* gene, the *trnL-trnF* intergenic

spacer, the *rps16* intron, the *atpB-rbcL* intergenic spacer, the *rpl16* intron, and the *psbA-trnH* intergenic spacer), because these sequences have been shown to be useful for inferring relationships at the generic and specific levels of Araliaceae (e.g., Wen et al., 2008; Mitchell et al., 2012; Li & Wen, 2013, 2014; Valcárcel et al., 2014). We also used the “relaxed clock” analyses and fossil calibrations (Drummond et al., 2006) to obtain age estimates of the main clades of Chinese Araliaceae.

1 Materials and methods

1.1 Taxon sampling

Ninety-six plant accessions used in this study were sequenced for the nuclear ribosomal ITS regions, and the plastid *ndhF* gene, the *trnL-trnF* intergenic spacer, the *rps16* intron, the *atpB-rbcL* intergenic spacer, the *rpl16* intron, and the *psbA-trnH* intergenic spacer (Table 2). The sampling included 50 accessions representing 20 genera and 50 species of Chinese Araliaceae, which covers the morphological and geographic diversity of Chinese Araliaceae. We included 45 various taxa in the following genera within the core Araliaceae (Wen et al., 2001; Plunkett et al., 2004): *Arthrophyllum* Blume, *Astrotricha* DC., *Cussonia* Thunb., *Gastonia* Comm. & Lam., *Harmsiopanax* Warb., *Meryta* J. R. Forst. & G. Forst., *Oreopanax* Decne. & Planch., *Plerandra* A. Gray, *Polyscias* J. R. Forst. & G. Forst., *Pseudopanax* K. Koch, *Raukaua* Seem., and *Tetraplasandra* A. Gray. Because a close relationship of Pittosporaceae and Araliaceae has been shown (e.g., in Plunkett et al., 1996), *Pittosporum illicioides* Makino of Pittosporaceae was included as an outgroup taxon. The wide range of multiple taxa was selected to further test the evolutionary relationships of Chinese Araliaceae and to infer the biogeographic diversification with a broader phylogenetic framework.

1.2 DNA extraction, amplification and sequencing

Total DNA was extracted from about 15 mg silica-gel dried leaf material using the DNeasy plant mini kits (Qiagen, Mississauga, Canada) following the

manufacturer's protocol or the modified CTAB extraction method (Doyle & Doyle, 1987).

The ITS region was amplified and sequenced using primers ITS4 and ITS5 (White et al., 1990). When amplification of the ITS region was unsuccessful, two other primers Nnc18S10 and C26A were used (Wen & Zimmer, 1996). The gene *ndhF* was amplified and sequenced in three segments with the following primer pairs: 1F and 972R, 803F and 1603R, 1318F and 2110R or 1995R (Olmstead & Sweere, 1994; Wen et al., 2003). The *trnL-trnF* region was amplified and sequenced using primers c and f (Taberlet et al., 1991). The *rps16* intron was amplified and sequenced using primers F and R2 (Oxelmann et al., 1997). The *atpB-rbcL* region was amplified and sequenced following Manen et al. (1994). The *rpl16* intron was amplified and sequenced using primers *rpl16*-F and R (Asmussen, 1999). The *psbA-trnH* region was amplified and sequenced using primers *psbA* and *trnH* (Sang et al., 1997). Polymerase chain reaction (PCR) amplifications were carried out in a 25 μ L volume containing 1.5 mmol/L MgCl₂, 0.2 mmol/L of each dNTP, 0.4 mmol/L of each primer, 1 U of *Taq* polymerase (Bioline, Taunton, MA, USA), and approximately 10-50 ng of DNA template under the following conditions: 3 min at 95°C, followed by 37 cycles of 20 s at 94°C, 30 s at 50°C, and 40 s at 72°C, and then a final 5 min extension at 72°C.

The PCR products were purified using the polyethylene glycol precipitation procedure following the protocol of Sambrook et al. (1989). Cycle sequencing was carried out using BigDye 3.1 reagents using the following profile: 35 cycles of 97°C for 15 s, 50°C for 5 s, and 60°C for 4 min. The products of cycle-sequencing reactions were cleaned using the Sephadex columns (Amersham Pharmacia Biotech, Piscataway, NJ, USA). The sequences were generated on an ABI prism 3730XL capillary sequencer (Applied Biosystems, Foster City, CA, USA).

1.3 Sequence alignment and phylogenetic analyses

The program Sequencher 4.8 (Gene Codes, Ann Arbor, MI, USA) was used to evaluate chromatograms for base confirmation and to edit contiguous sequences. Sequences were initially aligned with ClustalX version 1.83 (Thompson et al., 1997),

followed by manual adjustments on Se-AI v2.0a11 (Rambaut, 2007).

Following the previous studies using the same DNA markers (Mitchell et al., 2012; Li & Wen, 2013, 2014), we combined the plastid (*ndhF*, *trnL-trnF*, *rps16*, *atpB-rbcL*, *rpl16*, and *psbA-trnH*) and the ITS data sets for phylogenetic analyses, because the resulting tree obtained from the combined data was better resolved and generally better supported.

Phylogenetic trees were constructed using maximum parsimony (MP) and Bayesian methods (Fig. 1). The MP analyses was conducted using PAUP* version 4.0b10 (Swofford, 2002). All characters were weighted equally and gaps were treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1,000 replicates with random stepwise sequence addition, tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, multiple tree option in effect, saving 100 trees from each random sequence addition. Parsimony bootstrap values (PB) for the clades (Felsenstein, 1985) revealed in the maximally parsimonious trees (MPTs) were calculated with 500 bootstrap replicates. In each replicate, we carried out 100 random sequences addition replicates following by tree bisection-reconnection (TBR) swapping algorithm and keeping no more than 10 trees per replicate. Tree statistics including consistency index (CI) and the retention index (RI) were calculated using PAUP*.

Modeltest 3.7 (Posada & Buckley, 2004) was used to determine the optimal model of molecular evolution and gamma rate heterogeneity using the Akaike Information Criterion (AIC). Bayesian inference was implemented with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) using a mixed model Bayesian analysis strategy. We assigned model parameters for each gene partitions identified by AIC in Modeltest (Table 3). The Markov chain Monte Carlo (MCMC) algorithm was run for 4,000,000 generations with one cold and three heated chains, starting from random trees and sampling one out of every 100 generations. Runs were repeated twice. The resulting log-likelihood and number of generations were plotted to determine the point after which the log-likelihoods had stabilized. After discarding the trees saved prior to this point as burn-in, the remaining trees were imported into PAUP* and a

50% majority-rule consensus tree was produced to obtain posterior probabilities (PP) of the clades. Internodes with posterior probabilities ≥ 0.95 in the consensus trees were considered statistically significant.

1.4 Estimation of divergence times

To estimate divergence times within Chinese Araliaceae, the combined plastid and ITS data set was used with gaps treated as missing data. The Bayesian dating method with a relaxed molecular clock was implemented with the program BEAST 1.5.3 (Drummond & Rambaut, 2007) using the strategy of different nucleotide substitution models for each gene region suggested by Modeltest (Table 3). The Yule process for the tree prior model was employed using uncorrelated rates drawn from a lognormal distribution (Drummond et al., 2006). A normal distribution was specified for the priors. Posterior distributions of parameters were approximated using two independent MCMC analyses of 40,000,000 generations with 10% burn-in. Results were checked using the program Tracer 1.5 (Rambaut & Drummond, 2007) to ensure that plots of the two analyses were converging on the same area and the value of the effective sample size for each statistic was above 100.

We constrained the ages of two nodes in the phylogeny of Chinese Araliaceae and its close relatives (Fig. 2). First, the stem lineage of *Metapanax* was constrained to be 44 mya old (node A in Fig. 2) based on the fruit fossil of *Paleopanax oregonensis* Manchester from the Nut Beds flora of the Clarno Formation (north-central Oregon in the middle Eocene). This fossil was comparable to the Asian “*Pseudopanax*” (= *Metapanax*) (Manchester, 1994). Secondly, the crown age of Araliaceae was constrained to be 84 mya old (node B in Fig. 2) based on the estimates by Mitchell et al. (2012).

2 Results

2.1 DNA sequences data and phylogenetic relationships

We excluded the poly A, poly T or poly A/T regions from the data sets (*trnL-F*,

5 bp between 716 and 720; *rps16*, 21 bp between 744 and 764; *atpB-rbcL*, 7 bp between 611 and 617 and 13 bp between 626 and 638; *rpl16*, 9 bp between 764 and 772 and 4 bp between 846 and 849; and *psbA-trnH*, 6 bp between 61 and 66, 13 bp between 341 and 353, and 3 bp between 560 and 562). The statistics of the plastid and ITS data sets are shown in Table 3. Treating gaps as missing data, the maximum parsimony analysis based on the combined plastid and ITS data produced 30,814 MPTs of 3,457 steps, with a CI of 0.61, a CI excluding uninformative characters of 0.45, a RI of 0.70, and a RC of 0.42. The 50% majority-rule consensus tree resulting from the Bayesian analysis was largely congruent with the trees of the parsimony analysis except that the genera *Oreopanax*, *Sinopanax*, and *Fatsia* formed a clade with the posterior probability (PP) value of 0.98; *Raukaua anomalus*, *Schefflera digitata*, *Pseudopanax laetevirens*, and *P. valdiviensis* formed a monophyletic group (PP = 1.0). The Bayesian tree with parsimony bootstrap (PB) and posterior probability (PP) support is shown in Fig. 1.

The combined plastid and ITS data strongly supported the previously identified four groups (Wen et al., 2001; Plunkett et al., 2004; Mitchell et al., 2012): the Asian Palmate group (PB = 96%, PP = 1.0), the *Polyscias-Pseudopanax* group (PB = 98%, PP = 1.0), the *Aralia-Panax* group (PB = 100%, PP = 1.0), and the greater *Raukaua* group (PB < 50%, PP = 1.0) (Fig. 1). The Chinese members (19 genera) of Araliaceae were scattered within the Asian Palmate group and the *Aralia-Panax* group except the placement of *Osmoxylon* remains unclear (Fig. 1). The Asian Palmate group includes *Dendropanax*, *Macropanax*, *Metapanax*, *Kalopanax*, *Trevesia*, *Brassaiopsis*, *Eleutherococcus*, *Merrilliopanax*, *Sinopanax*, *Hedera*, *Chengiopanax*, *Fatsia*, *Gamblea*, Asian *Schefflera*, *Heteropanax*, *Tetrapanax*, and *Oplopanax*. The *Aralia-Panax* group comprises *Aralia* and *Panax*.

2.2 Molecular dating

The chronogram and results of divergence time estimation based on the combined plastid and ITS data set from the Bayesian approach are shown in Fig. 2. The crown of the Asian Palmate group was dated to be at 60.16 Mya (95% HPD:

50.24–70.33 Mya; node 1 in Fig. 2). The crown *Aralia*–*Panax* group was estimated at 57.49 Mya (95% HPD: 44.18–69.18 Mya; node 2 in Fig. 2).

3 Discussion

3.1 Phylogenetic relationships in Chinese Araliaceae

Comparison of the findings of our molecular data to the classification of Chinese Araliaceae reveals little agreement (Table 1). The closely related genera *Aralia* and *Panax* were placed in two distinct tribes (Aralieae and Panaceae) in Tseng & Hoo's (1982) system. Also, the members from tribe Tetraplasandreae (e.g., *Heteropanax*) and tribe Plerandreae (e.g., *Dendropanax*, *Oplopanax*) in Tseng & Hoo's (1982) system form a group together with Neotropical representatives (e.g., *Oreopanax*, *Schefflera angulata*) in the molecular tree (Fig. 1). Those showed that the morphological characters (petal aestivation and leaf morphology) employed to delimit infrafamilial taxa within Chinese Araliaceae are highly homoplastic and have little utility at the intergeneric level.

3.2 Generic evaluation of Chinese Araliaceae

The *Aralia*–*Panax* group. The close relationship between *Aralia* and *Panax* was strongly supported (PB = 100%, PP = 1.0) in the present study (Fig. 1). Overall, *Aralia* and *Panax* share many features, including imbricate floral aestivation, uniform endosperm, similar pollen morphology and ultrastructure, and similar floral vasculature (Eyde & Tseng, 1971; Wen, 1993; Wen & Nowicke, 1999). The current definition of *Aralia* recognized the following morphological synapomorphies: pinnately compound leaf architecture, presence of stipules, 5-12-locular ovaries, smooth seed surface, and flattened seeds (Wen, 1993, 2011). In contrast, its closest relative, the genus *Panax* possesses palmately compound leaves, 2-4-locular ovaries, rough seed surfaces, and non-flattened seeds (Wen & Zimmer, 1996; Wen, 2001a, b; Zuo et al., 2011, 2015). Historically, the phylogenetic position of *Panax* has long been controversial, Decaisne & Planchon (1854) and Clarke (1879) placed *Panax* within

Aralia. Furthermore, Harms (1896) and Hoo (1961) regarded *Panax* as derived from an herbaceous member of *Aralia*.

Aralia stellata, *A. castanopsisicola*, and *A. leschenaultii*, included in this study, were previously classified as species of *Pentapanax* (Seemann, 1864), which was established primarily based on undivided styles, pinnately compound leaves with 3-5 leaflets, and racemose to umbellate inflorescence units. Based on the minor morphological character variation (leaf architecture and styles structure) between *Pentapanax* and *Aralia*, Wen (1993) treated *Pentapanax* as a section of *Aralia* (also see Wen, 2002, 2004, 2011). Our phylogenetic analysis supported the merge of *Pentapanax* into *Aralia* (Wen, 1993), because the taxa of *Pentapanax* were nested within *Aralia* (Fig. 1).

Asian *Schefflera* + *Heteropanax* + *Tetrapanax* clade. Chinese members of *Schefflera* belong to the Asian *Schefflera*. The monophyly of Asian *Schefflera* + *Heteropanax* + *Tetrapanax* is supported (PB = 84%, PP = 1.0) by our analysis. Our phylogenetic study confirmed the earlier finding (Li & Wen, 2014) that the sister of Asian *Schefflera* is *Heteropanax*. The Asian *Schefflera*–*Heteropanax* subclade is then sister to the Asian monotypic *Tetrapanax* (Fig. 1). Asian *Schefflera* is similar to *Heteropanax* and *Tetrapanax* in habit, lack of prickles, lack of pedicle articulations, inflorescence architecture, and valvate aestivation. Their close relationships were also recognized by Harms (1894), because he assigned those three taxa to his broadly defined tribe Schefflereae based on the identical character of valvate petals. However, Asian *Schefflera* can be easily distinguished from *Heteropanax* by its palmately compound or rarely simple to double digitately compound leaves, stipules united within the base of petiole and extending into a ligular appendage, ovaries with 5 or more locules, and styles united into a column or absent, rare base united and free apically. On the contrary, *Heteropanax* possesses 2–5-pinnately compound leaves, inconspicuous stipules, 2-locular ovaries, and styles free or united to middle. *Tetrapanax* has simple and palmately lobed leaves, cone-shaped stipules, 2-locular ovaries, and free styles.

Historically, *Schefflera pueckleri* was treated as a member of the distinct genus

Tupidanthus Hook. f. & Thomson (1856), which was established based on its very high numbers of stamens and locules in the ovary. However, the evolution of polymery in Araliaceae has been shown to have occurred independently multiple times (Wen et al., 2001; Plunkett et al., 2004). In the present study, *Tupidanthus* is clearly nested within the Asian *Schefflera* clade, supporting its transfer to *Schefflera* by Frodin (Stone, 1978), which also shares the character of the absence of styles like its close relatives.

Macropanax + *Metapanax* + *Kalopanax* clade. The close relationship between *Macropanax* and *Metapanax* recognized by the present and previous studies (Wen et al., 2001; Plunkett et al., 2004) is supported by the shared presence of evergreen leaves, mostly dentate leaflet margins, articulated pedicels, and bicarpellate ovaries. However, the two genera can be distinguished by their different endosperm types (ruminant in *Macropanax*, smooth in *Metapanax*), the division of styles (undivided in *Macropanax*, divided in *Metapanax*), and fruit shape (subglobose or ovoid in *Macropanax*, somewhat flattened in *Metapanax*) (Shang, 1985). Our phylogeny presented here suggests that the sister of the *Macropanax*–*Metapanax* subclade is *Kalopanax* (PB = 72%, PP = 1.0) (Fig. 1). These three genera are similar in both inflorescence structure (terminal panicle with the umbels as the basic inflorescence units) and floral morphology (hermaphrodite flowers), but they may also be clearly differentiated: *Kalopanax* is deciduous and generally have prickles on the stem, whereas *Macropanax* and *Metapanax* are evergreen and unarmed.

Brassaiopsis and *Trevesia*. The close relationship between *Brassaiopsis* and *Trevesia* (PB = 100%, PP = 1.0) (Fig. 1) was found in the present phylogeny and previous molecular analyses (Wen et al., 2001; Plunkett et al., 2004). Previous workers (e.g., Harms, 1894; Li, 1942; Hoo & Tseng, 1978) regarded the two genera as distantly related, placing emphasis on differences in the number of locules in the ovary. However, Jebb (1998) discussed the morphological similarities between *Brassaiopsis* and *Trevesia*, both of which contain species with more or less prickly stems, non-articulated pedicels, semi-inferior ovaries, undivided styles, and projected floral disks. Both genera can be distinguished by their different numbers of floral

parts (2 or rarely 3-5 in *Brassaiopsis*, 6-12 in *Trevesia*) and endosperm types (ruminant in *Brassaiopsis*, smooth in *Trevesia*).

Hedera and its putative relationship to *Dendropanax* or *Merrilliopanax*. The sister-groups of *Hedera* remain unclear because the origin of the *Hedera* lineage may fit in a temperate niche conservatism scenario where the combination of the radiation with lineage admixtures prevents us from discovering its relatives (Valcárcel et al., 2014). However, several workers (e.g., Hutchinson, 1967; Tseng & Hoo, 1982; Shang & Callen, 1988) regarded *Dendropanax* as closely related to *Hedera*, and this close relationship was supported by the ITS phylogeny of Araliaceae (Wen et al., 2001). Morphology does also support the association between *Hedera* and *Dendropanax* since they both have a single style, 3-5 carpels, and entire to 3-5-lobed leaves (Li & Wen, 2013; Valcárcel et al., 2014). The putative sister-group relationship between *Hedera* and *Merrilliopanax* was supported by previous phylogenetic study (Mitchell & Wen, 2004). Morphologically, both genera share simple and lobed leaves, while major differences regarding carpels (5 in *Hedera*, 2 in *Merrilliopanax*) and style (united into a short column in *Hedera*, free or united at base in *Merrilliopanax*).

The sister relationship between the Asian *Sinopanax* and the Neotropical *Oreopanax*. A sister-group relationship between the monotypic *Sinopanax* and the much larger Neotropical genus *Oreopanax* is suggested by Bayesian analysis in the present study and the previous phylogenetic analyses (Wen et al., 2001; Plunkett et al., 2004). *Sinopanax formosana* is endemic to Taiwan and was originally described by Hayata as *Oreopanax formosana*, with which it shares a number of characters, including palmately-lobed simple leaves, large terminal panicles of small capitate inflorescences, and ruminant endosperm. However, Li (1949) argued that the Taiwanese species differs in having a 2-carpellate (vs. 5-carpellate) ovary, a hermaphroditic (vs. polygamo-dioecious or polygamo-monoecious) sexual system, and rather short (vs. long) styles. The Bayesian analysis in the present study further indicates that *Sinopanax* and *Oreopanax* form a clade with the Asian *Fatsia* (Fig. 1). These three genera can be distinguished by their basic inflorescence units (capitulum in *Sinopanax* and *Oreopanax*, umbel in *Fatsia*).

The placement of *Oplopanax*. The genus *Oplopanax* with three species shows an intercontinental disjunct distribution between eastern Asia and western North America (Shang & Lowry, 2007). *Oplopanax* is sister to a large clade that includes the remaining genera of the Asian Palmate group (PB = 96%, PP = 1.0) (Fig. 1), which is consistent with the earlier findings (Mitchell et al., 2012; Valcárcel et al., 2014).

Oplopanax is characterized by a combination of characters including prickly shrubs with palmate lobed leaves, terminal inflorescences, 2-locular ovaries, 2-free or united below and persistent styles, red-yellow fruits at maturity (Frodin & Govaerts, 2003).

Eleutherococcus, *Chengiopanax*, and *Gamblea*. *Chengiopanax* and *Gamblea* have been separated from *Eleutherococcus* (Shang & Huang, 1993; Shang et al., 2000). *Eleutherococcus* has prickles on their stems, *Chengiopanax* and *Gamblea* have none. *Chengiopanax* has undivided styles and large inflorescence, but *Gamblea* has divided styles and small inflorescence. Each of these genera is supported as distinct based on our data, however, the relationships among them need to be explored further with a broader sampling of *Eleutherococcus*.

Osmoxylon. The genus has a wide distribution in the Malesian region, western Melanesia to Vanuatu and is especially well developed in the Philippines and Solomon islands (Frodin & Govaerts, 2003). Morphologically, it is characterized by the ligulate stipules and the marked petiole base with several spiral or transversal crests. The inflorescence is a terminal compound umbel with primary rays terminating into three branches. The genus is a phylogenetically isolated member of Araliaceae (Fig. 1). Only one species occurs in Lan Yu of Taiwan (Shang & Lowry, 2007).

3.3 Biogeographic diversification of Araliaceae in China

Phylogenetic analyses of Araliaceae suggested that the family originated in the Australasian region of the paleotropics and then migrated into different tropical and subtropical regions (Wen et al., 2001; Plunkett et al., 2004). The origin of the Asian Palmate group seems to be Asia based on the ancestral area reconstruction performed by Mitchell et al. (2012). Considering the Chinese members of Araliaceae account for 85% and 100% of the total number of genera in the Asian Palmate Group and the

Aralia–Panax group respectively, we propose that Chinese Araliaceae most likely originated in Asia. The present phylogenetic analyses using multiple markers have not generated a well resolved phylogeny of Chinese Araliaceae. One possible explanation is that Chinese Araliaceae underwent a rapid radiation in its evolutionary history. Our divergence time estimates place the crown of the Asian Palmate group and the *Aralia–Panax* group in the Paleocene (Fig. 2), consistent with the results in Mitchell et al. (2012) and Valcárcel et al. (2014). The orogenies in China (e.g., the formation of the Nanling Mountains during the Cretaceous, the uplift of the Yunnan-Guizhou Plateau and the mountain ranges in southeastern China in the early Cenozoic, and the major uplift of the Tibetan Plateau in the late Tertiary) had led to changes in habitats and climate, accompanied by the changes of land and sea (Hsü, 1983; An et al., 2001), which may have facilitated the radiation of Chinese Araliaceae throughout this region.

The center of diversity of the Chinese Araliaceae is the mountains of southwestern China, which is equal to the Sino–Himalayan region, the southwestern China plateau region, and the Mid–Mekong region proposed by Li (1944). There are 139 species of Araliaceae (belonging to 16 genera) in this region, 59 of which are endemic to China. The high species richness and endemism may have been generated by the rising of the Himalaya resulted from the collision of the Indian and Asian plates in the early Tertiary (An et al., 2001; Spicer et al., 2003). The mountain building processes accompanying the uplift of the Himalaya created regional topographic complexities in the southwestern China (Shi et al., 1998). The topographic diversity and large river systems in the region created a wide range of habitats. The diverse habitats combined with the climatic changes of the late Tertiary and the Quaternary may have facilitated the diversification of Chinese Araliaceae in this region. The similar diversification pattern was reported in the species-rich genus *Rhodiola* (Crassulaceae) by Zhang et al. (2014), who suggested that rapid radiation was promoted by the uplifts of the Himalaya in the Tertiary (see Wen et al., 2014 for additional examples).

Another major area of diversification is the monsoon realm in the South China, where 55 species of Araliaceae (belonging to 14 genera) occur, 31 are endemic to

China. This region is equal to the southern China maritime region and the Gulf of Tonkin region as proposed by Li (1944). Physically this region is characterized by hills and low mountains extending more or less over the whole area because of the formation of the Nanling Mountains during the Cretaceous (Hsü, 1983). This region is also well known for its tropical and subtropical monsoon climate with adequate moisture in summer and warm dry in winter (Zheng, 2013). These favourable conditions maintain greater variety of habitats in South China and thus probably accelerate the speciation, diversification, and preservation for the species of Chinese Araliaceae in this region.

The remaining areas in China include 38 species of araliaceous plants (belonging to 12 genera), 20 of which are endemic to China. The flora of these regions, as a whole, is temperate in nature (Li, 1944). The mountainous topography (e.g., Qinling Mountains, Taihang Mountains, and Changbai Mountains) and humid monsoon climate (except northwestern China and Qinghai–Tibet Plateau) have resulted in a wide variety of habitats within these regions (Zheng, 2013), which may have provided excellent opportunities for the diversification of Chinese Araliaceae there (e.g., the species-rich temperate genus *Eleutherococcus*).

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Table 1 Distribution and classification according to Tseng & Hoo (1982) and molecular phylogenetic studies (Wen et al., 2001; Plunkett et al., 2004) for genera of Chinese Araliaceae

Genus	Number of species (World/China)	Distribution	Tseng & Hoo	Molecular phylogenetic studies
<i>Aralia</i> L. (1753)	69/45	Asia, North America to South America	Tribe Aralieae	The <i>Aralia-Panax</i> group
<i>Brassaiopsis</i> Decne. & Planch. (1854)	ca. 30/24	The Himalayan region to C China, Indochina to W Malesia	Tribe Plerandreae	The Asian Palmate group
<i>Chengiopanax</i> Shang & J. Y. Huang (1993)	2/1	C China and Japan	Tribe Plerandreae	The Asian Palmate group
<i>Dendropanax</i> Decne. & Planch. (1854)	ca. 70/14	The Himalaya, E and SE Asia to W Malesia, C and S America	Tribe Plerandreae	The Asian Palmate group
<i>Eleutherococcus</i> Maxim. (1859)	38/18	E Asia and the Himalaya	Tribe Plerandreae	The Asian Palmate group
<i>Fatsia</i> Decne. & Planch. (1854)	3/1	E Asia (Japan, Taiwan, Ogasawara-shoto)	Tribe Plerandreae	The Asian Palmate group
<i>Gamblea</i> C. B. Clarke (1879)	4/2	E Asia, the Himalayan region to SE Asia	Tribe Plerandreae	The Asian Palmate group
<i>Hedera</i> L. (1753)	15/2	Temperate Eurasia	Tribe Plerandreae	The Asian Palmate group
<i>Heteropanax</i> Seem. (1866)	8/6	The Himalaya to S and SW China, Indochina to SE Asia	Tribe Tetrapiasandreae	The Asian Palmate group
<i>Kalopanax</i> Miq. (1863)	1/1	E Asia	Tribe Plerandreae	The Asian Palmate group
<i>Macropanax</i> Miq. (1856)	17/7	The Himalaya to E and SE Asia, W Malesia	Tribe Plerandreae	The Asian Palmate group
<i>Merrillioanax</i> H. L. Li (1942)	3/3	The Himalayan region to W China	Tribe Plerandreae	The Asian Palmate group
<i>Metapanax</i> J. Wen & Frodin (2001)	2/2	C and W China, N Vietnam	Tribe Plerandreae	The Asian Palmate group
<i>Oplopanax</i> Miq. (1863)	3/1	E Asia, NW North America	Tribe Plerandreae	The Asian Palmate group
<i>Osmoxylon</i> Miq. (1863)	60/1	Taiwan to Borneo, the Phillipines, to New Guinea and nearby Pacific islands	Tribe Plerandreae	The base of core Araliaceae
<i>Panax</i> L. (1753)	18/6	E Asia and E North America	Tribe Panaceae	The <i>Aralia-Panax</i> group
<i>Schefflera</i> J. R. Forst. & G. Forst. (1775) [†]	ca. 450/36	Asia, only the Asian group is referred to here	Tribe Plerandreae	The Asian Palmate group
<i>Sinopanax</i> H. L. Li (1949) [‡]	1/1	Taiwan	Tribe Plerandreae	The Asian Palmate group
<i>Tetrapanax</i> K. Koch (1859) [‡]	1/1	Taiwan (native), mainland China (introduced)	Tribe Plerandreae	The Asian Palmate group
<i>Trevesia</i> Vis. (1840)	10/1	S China, and NE India through SE Asia to W Malesia	Tribe Plerandreae	The Asian Palmate group

†*Schefflera* is the largest genus of Araliaceae, with 600-900 species. Recent studies have shown that *Schefflera* is polyphyletic (Plunkett et al., 2005; Li & Wen, 2014). The 450 or so species in Table 1 refer to only a group of closely related Asian species of *Schefflera*; ‡The genus is endemic to China.

Table 2 Voucher information and GenBank accession numbers for Chinese Araliaceae and related taxa used in this study. Nomenclatural standard for the published species follows Frodin & Govaerts (2003). All collections are deposited at the US National Herbarium of the Smithsonian Institution (Washington DC)

Taxa	Voucher	<i>ndhF</i>	<i>trnL-F</i>	<i>rps16</i>	<i>atpB-rbcL</i>	<i>rpl16</i>	<i>psbA-trnH</i>	ITS
<i>Aralia apioides</i> Hand.-Mazz.	China, Yunnan, <i>Wen et al. 1752</i>							
<i>Aralia bipinnata</i> Blanco	Philippines, Luzon, <i>Wen 8276</i>							
<i>Aralia castanopsicola</i> (Hayata) J. Wen	China, Taiwan, <i>Wen 9428</i>							
<i>Aralia continentalis</i> Kitag.	China, Jilin, <i>Wen 5545</i>							
<i>Aralia echinocaulis</i> Hand.-Mazz.	China, <i>Wen 12035</i>							
<i>Aralia excelsa</i> (Griseb.) J. Wen	Costa Rica, <i>Wen 6779</i>							
<i>Aralia fargesii</i> Franch.	China, <i>Wen 12090</i>							
<i>Aralia glabra</i> Matsum.	Japan, <i>Soejima 1085</i>							
<i>Aralia henryi</i> Harms [§]	China, Yunnan: Marlipo, <i>Wen 10640</i>	KC952426	KC952074	KC952162	KC952602	KC952250	KC952514	KC952338
<i>Aralia leschenaultii</i> (DC.) J. Wen	China, Yunnan: Gongshan, <i>R. Li 499</i>							
<i>Aralia spinifolia</i> Merr.	China, Taiwan, <i>Wen 9449</i>							
<i>Aralia stellata</i> (King) J. Wen [†]	Thailand, Doichiang Dao: Doi Luang Valley, <i>Maxwell 03-505</i>	GU054745	GU055125	GU055030	GU054555	GU054935	GU054840	GU054650
<i>Aralia vietnamensis</i> Ha [†]	China, Yunnan: Lvchun, <i>Shui 81844</i>	GU054761	GU055141	GU055046	GU054571	GU054951	GU054856	GU054666
<i>Arthropphyllum diversifolium</i> Blume [‡]	Malaysia, Pahang: Cameron, <i>Wen 8372</i>	JX106024	JX106183	JX106144	JX106064	JX106224	JX106104	JX106265
<i>Astrotricha latifolia</i> Benth. [‡]	Australia, Queensland: <i>P. I. Forster 7547</i>	JX106026	JX106185	JX106146	JX106066	JX106226	JX106106	JX106267
<i>Brassaiopsis hispida</i> Seem. [‡]	China, Yunnan: Gongshan, <i>Wen 5031</i>	JX106027	JX106186	JX106147	JX106067	JX106227	JX106107	JX106268
<i>Chengiopanax fargesii</i> (Franch.) C. B. Shang & J. Y. Huang [†]	China, Hunan: Xinning, <i>Wen 9316</i>	GU054746	GU055126	GU055031	GU054556	GU054936	GU054841	GU054651
<i>Cussonia paniculata</i> Eckl. & Zeyh. [‡]	South Africa, Eastern Cape: <i>Wen 10072</i>	JX106030	JX106189	JX106149	JX106070	JX106230	JX106110	JX106271
<i>Cussonia thyrsoflora</i> Thunb. [‡]	South Africa, Eastern Cape: <i>Wen 10057</i>	JX106032	JX106191	JX106151	JX106072	JX106232	JX106112	JX106273
<i>Dendropanax arboreus</i> (L.) Decne. & Planch. [†]	Costa Rica, San Jose: Canton, <i>Wen 7045</i>	GU054787	GU055167	GU055072	GU054597	GU054977	GU054882	GU054692

<i>Dendropanax burmanicus</i> Merr.†	China, Yunnan: Gongshan, <i>H. Li 33274</i>	GU054781	GU055161	GU055066	GU054591	GU054971	GU054876	GU054686
<i>Dendropanax caloneurus</i> (Harms) Merr.†	Vietnam, Lao Cai: Sa Pa, <i>Wen 6063</i>	GU054712	GU055092	GU054997	GU054522	GU054902	GU054807	GU054617
<i>Dendropanax caucanus</i> Harms†	Costa Rica, Puntarenas: Canton, <i>Wen 7018</i>	GU054726	GU055106	GU055011	GU054536	GU054916	GU054821	GU054631
<i>Dendropanax chevalieri</i> (R. Vig.) Merr.†	Vietnam, Lao Cai: Sa Pa, <i>Wen 6079</i>	GU054783	GU055163	GU055068	GU054593	GU054973	GU054878	GU054688
<i>Dendropanax dentiger</i> (Harms) Merr.†	China, Hunan: Xinning, <i>Wen 9306</i>	GU054749	GU055129	GU055034	GU054559	GU054939	GU054844	GU054654
<i>Dendropanax globosus</i> M. J. Cannon & Cannon†	Costa Rica, Puntarenas: Monteverde, <i>Wen 6848</i>	GU054714	GU055094	GU054999	GU054524	GU054904	GU054809	GU054619
<i>Dendropanax hainanensis</i> (Merr. & Chun) Chun†	China, Hunan: Mangshan, <i>Y. F. Deng 16240</i>	GU054750	GU055130	GU055035	GU054560	GU054940	GU054845	GU054655
<i>Dendropanax lancifolius</i> Ridl.†	Malaysia, Pahang: Cameron, <i>Wen 8362</i>	GU054774	GU055154	GU055059	GU054584	GU054964	GU054869	GU054679
<i>Dendropanax maingayi</i> King†	Malaysia, Pahang: Cameron, <i>Wen 8364</i>	GU054728	GU055108	GU055013	GU054538	GU054918	GU054823	GU054633
<i>Dendropanax oligodontus</i> Merr. & Chun†	China, Hainan: Lingshui, <i>Wen 6603</i>	GU054784	GU055164	GU055069	GU054594	GU054974	GU054879	GU054689
<i>Dendropanax poilanei</i> Bui†	Vietnam, Lam Dong: Lac Duong, <i>Wen 11049</i>	GU054772	GU055152	GU055057	GU054582	GU054962	GU054867	GU054677
<i>Dendropanax proteus</i> (Champ. ex Benth.) Benth.†	China, Guangdong: Heishiding, <i>Wen 5780</i>	GU054716	GU055096	GU055001	GU054526	GU054906	GU054811	GU054621
<i>Eleutherococcus sieboldianus</i> (Makino) Koidz.†	Japan, Chiba-ken: Narita-shi, <i>Wen 8538</i>	GU054706	GU055086	GU054991	GU054516	GU054896	GU054801	GU054611
<i>Eleutherococcus simonii</i> (Simon-Louis ex Mouill) Hesse [§]	China, Yunnan: Kunming, <i>Wen 10657</i>	KC952427	KC952075	KC952163	KC952603	KC952251	KC952515	KC952339
<i>Fatsia oligocarpella</i> Koidz.†	Japan, <i>H. Kato 30041</i>	GU054755	GU055135	GU055040	GU054565	GU054945	GU054850	GU054660
<i>Gamblea innovans</i> (Siebold & Zucc.) C. B. Shang [‡]	Japan, <i>Soejima 1094</i>	JX106033	JX106192	JX106152	JX106073	JX106233	JX106113	JX106274
<i>Gastonia custispongia</i> Lam.†	Belgium, Belgium Botanical Garden: cult. <i>Wen s.n.</i>	GU054756	GU055136	GU055041	GU054566	GU054946	GU054851	GU054661
<i>Harmsioplanax ingens</i> Philipson [‡]	Indonesia, Papua: Jayawijaja, <i>Wen 10749</i>	JX106034	JX106193	JX106153	JX106074	JX106234	JX106114	JX106275
<i>Hedera sinensis</i> (Tobler) Hand.-Mazz.†	Vietnam, Lao Cai: Sa Pa, <i>Wen 5980</i>	GU054732	GU055112	GU055017	GU054542	GU054922	GU054827	GU054637

<i>Heteropanax fragrans</i> (Roxb. ex DC.) Seem.‡	Thailand, Chiang Mai: Chiang Dao, <i>Wen</i> 7492	JX106035	JX106194	JX106154	JX106075	JX106235	JX106115	JX106276
<i>Kalopanax septemlobus</i> (Thunb.) Koidz.†	China, Hunan: Xinning, <i>Wen</i> 9341	GU054740	GU055120	GU055025	GU054550	GU054930	GU054835	GU054645
<i>Macropanax dispermus</i> (Blume) Kuntze†	Indonesia, West Java: Bandung, <i>Wen</i> 10137	GU054702	GU055082	GU054987	GU054512	GU054892	GU054797	GU054607
<i>Macropanax maingayi</i> (C. B. Clarke) Philipson†	Malaysia, Langat: Langat, <i>Wen</i> 8355	GU054741	GU055121	GU055026	GU054551	GU054931	GU054836	GU054646
<i>Macropanax rosthornii</i> (Harms) C. Y. Wu & G. Hoo†	China, Sichuan: Dujiangyan, <i>Wen</i> 9264	GU054708	GU055088	GU054993	GU054518	GU054898	GU054803	GU054613
<i>Macropanax serratifolius</i> K. M. Feng & Y. R. Li	China, Yunnan: Jingping, <i>Wen</i> 10530							
<i>Macropanax undulatum</i> Seem.	China, Yunnan: Hekou, <i>Wen</i> 10569							
<i>Merrillioanax chinensis</i> H. L. Li§	China, Yunnan: Gongshan, <i>Wen</i> 5065	KC952457	KC952105	KC952193	KC952633	KC952281	KC952545	KC952369
<i>Merrillioanax listeri</i> (King) H. L. Li‡	China, Yunnan: Gongshan, <i>Wen</i> 5038	JX106036	JX106195	JX106155	JX106076	JX106236	JX106116	JX106277
<i>Meryta denhamii</i> Seem.‡	Belgium, Belgium Botanical Garden: cult. <i>Wen</i> s.n.	JX106037	JX106196	JX106156	JX106077	JX106237	JX106117	JX106278
<i>Metapanax davidii</i> (Franch.) J. Wen & Frodin†	China, Sichuan: Dujiangyan, <i>Wen</i> 9266	GU054720	GU055100	GU055005	GU054530	GU054910	GU054815	GU054625
<i>Metapanax delavayi</i> (Franch.) J. Wen & Frodin†	China, Yunnan: Lufeng, <i>Wen</i> 9146	GU054707	GU055087	GU054992	GU054517	GU054897	GU054802	GU054612
<i>Oplopanax elatus</i> (Nakai) Nakai†	China, Jilin: Wusong, <i>Wen</i> 5418	GU054757	GU055137	GU055042	GU054567	GU054947	GU054852	GU054662
<i>Oreopanax polycephalus</i> Harms†	Peru, Dpto. Pasco: Oxapampa, <i>Wen</i> 8595	GU054733	GU055113	GU055018	GU054543	GU054923	GU054828	GU054638
<i>Oreopanax xalapense</i> (Kunth) Decne. & Planch.†	Costa Rica, Heredia: Barva, <i>Wen</i> 6934	GU054734	GU055114	GU055019	GU054544	GU054924	GU054829	GU054639
<i>Osmoxylon novoguineense</i> (Scheff.) Becc.‡	Indonesia, West Papua, <i>Wen</i> 10706	JX106039	JX106199	JX106158	JX106079	JX106240	JX106119	JX106281
<i>Osmoxylon pectinatum</i> (Merr.) Philipson‡	China, Taiwan: Luta, <i>Wen</i> 9411	JX106040	JX106200	JX106159	JX106080	JX106241	JX106120	JX106282
<i>Panax bipinnatifidus</i> Seem.	China, Yunnan: Gongshan, <i>R. Li</i> 714							
<i>Panax trifolius</i> L.†	US, Maryland: Baltimore, <i>Wen</i> 10099	GU054796	GU055176	GU055081	GU054606	GU054986	GU054891	GU054701
<i>Panax wangianus</i> S. C. Sun	<i>Wen</i> 12167							

<i>Pittosporum illiciooides</i> Makino [*]	China, Zhejiang: Anji, <i>Wen 8486</i>	JX106041	JX106201	JX106160	JX106081	JX106242	JX106121	JX106283
<i>Plerandra insolita</i> A. C. Sm. [‡]	US, Hawaii: Oahu, cult. <i>Wen 7076</i>	JX106042	JX106202	JX106161	JX106082	JX106243	JX106122	JX106284
<i>Polyscias australiana</i> (F. Muell.) Philipson [‡]	Indonesia, Papua: Keerom, <i>Wen 10707</i>	JX106043	JX106203	JX106162	JX106083	JX106244	JX106123	JX106285
<i>Polyscias nodosa</i> (Blume) Seem. [‡]	Indonesia, SE Sulawesi: Konawe, <i>Wen 10303</i>	JX106044	JX106204	JX106163	JX106084	JX106245	JX106124	JX106286
<i>Polyscias schultzei</i> Harms [‡]	Indonesia, Papua: Jayawijaja, <i>Wen 10730</i>	JX106045	JX106205	JX106164	JX106085	JX106246	JX106125	JX106287
<i>Pseudopanax arboreus</i> (L. f.) K. Koch [‡]	Belgium, Belgium Botanical Garden: cult. <i>Wen s.n.</i>	JX106047	JX106207	JX106166	JX106087	JX106248	JX106127	JX106289
<i>Pseudopanax laetevirens</i> (Gay) Franch. [§]	Chile, Valdivia: <i>Wen 7728</i>	KC952443	KC952091	KC952179	KC952619	KC952267	KC952531	KC952355
<i>Pseudopanax valdiviensis</i> (Gay) Harms [§]	Chile, Valdivia: <i>Wen 7719</i>	KC952444	KC952092	KC952180	KC952620	KC952268	KC952532	KC952356
<i>Raukaua anomalus</i> (Hook.) A. D. Mitch. [‡]	New Zealand: cult. A. Mitchell <i>s.n.</i>	JX106050	JX106210	JX106169	JX106090	JX106251	JX106130	JX106292
<i>Schefflera actinophylla</i> (Endl.) Harms [§]	US, Hawaii: Oahu, cult. <i>Wen 7056</i>	KC952460	KC952108	KC952196	KC952636	KC952284	KC952548	KC952372
<i>Schefflera angulata</i> (Pav.) Harms [†]	Peru, Oxapampa: <i>Wen 8589</i>	GU054735	GU055115	GU055020	GU054545	GU054925	GU054830	GU054640
<i>Schefflera arboricola</i> (Hayata) Merr. [§]	China, Taiwan: Nantou, <i>Wen 9448</i>	KC952452	KC952100	KC952188	KC952628	KC952276	KC952540	KC952364
<i>Schefflera aromatica</i> (Blume) Harms [§]	Indonesia, West Java: Cibodas, <i>Wen 10668</i>	KC952437	KC952085	KC952173	KC952613	KC952261	KC952525	KC952349
<i>Schefflera bodinieri</i> (H. Lév.) Rehder [§]	China, Yunnan: Jinping, <i>Shui 81850</i>	KC952428	KC952076	KC952164	KC952604	KC952252	KC952516	KC952340
<i>Schefflera delavayi</i> (Franch.) Harms [§]	China, Hunan: Xinning, <i>Wen 9347</i>	KC952414	KC952062	KC952150	KC952590	KC952238	KC952502	KC952326
<i>Schefflera digitata</i> J. R. Forst. & G. Forst. [‡]	New Zealand, Canterbury: Lincoln, S. Oliver <i>s.n.</i>	JX106057	JX106217	JX106176	JX106097	JX106258	JX106137	JX106299
<i>Schefflera heptaphylla</i> (L.) Frodin [§]	China, Taiwan: Taoyuan, <i>Wen 9386</i>	KC952447	KC952095	KC952183	KC952623	KC952271	KC952535	KC952359
<i>Schefflera hypoleucooides</i> Harms [§]	China, Yunnan: Pingbian, <i>Wen 8446</i>	KC952419	KC952067	KC952155	KC952595	KC952243	KC952507	KC952331
<i>Schefflera insularum</i> (Seem.) Harms [§]	Philippines, Luzon: Laguna, <i>Wen 8258</i>	KC952448	KC952096	KC952184	KC952624	KC952272	KC952536	KC952360
<i>Schefflera leucantha</i> R. Vig. [§]	Thailand, Chiang Mai: cult. <i>Wen 7369</i>	KC952455	KC952103	KC952191	KC952631	KC952279	KC952543	KC952367
<i>Schefflera longipedicellata</i> (Lecomte) Bernardi [‡]	Madagascar, Antsiranana: Antsiranana, <i>Wen 9564</i>	JX106059	JX106219	JX106178	JX106099	JX106260	JX106139	JX106301
<i>Schefflera myriantha</i> (Baker) Drake [‡]	Madagascar, Antsiranana: Antsiranana, <i>Wen 9570</i>	JX106060	JX106220	JX106179	JX106100	JX106261	JX106140	JX106302
<i>Schefflera oxyphylla</i> (Miq.) R. Vig. [§]	Malaysia, Selangor: Kuala Langat, <i>Wen 8351</i>	KC952478	KC952126	KC952214	KC952654	KC952302	KC952566	KC952390

<i>Schefflera papuana</i> Ridl. [§]	Indonesia, West Java: Bogor, cult. <i>Wen 10151</i>	KC952411	KC952059	KC952147	KC952587	KC952235	KC952499	KC952323
<i>Schefflera pentandra</i> (Pav.) Harms [†]	Peru, Huampal: <i>Wen 8619</i>	GU054722	GU055102	GU055007	GU054532	GU054912	GU054817	GU054627
<i>Schefflera petelotii</i> Merr. [§]	Vietnam, Ninh Binh: Cuc Phuong, <i>Wen 10918</i>	KC952468	KC952116	KC952204	KC952644	KC952292	KC952556	KC952380
<i>Schefflera pueckleri</i> (K. Koch) Frodin [§]	Vietnam, Lam Dong: Lac Duong, <i>Wen 11061</i>	KC952469	KC952117	KC952205	KC952645	KC952293	KC952557	KC952381
<i>Schefflera rugosa</i> (Blume) Harms [§]	Indonesia, West Java: Bogor, cult. <i>Wen 10158</i>	KC952412	KC952060	KC952148	KC952588	KC952236	KC952500	KC952324
<i>Schefflera scandens</i> (Blume) R. Vig. [§]	Indonesia, West Java: Cibodas, <i>Wen 10114</i>	KC952407	KC952055	KC952143	KC952583	KC952231	KC952495	KC952319
<i>Schefflera sepikiana</i> Harms [§]	Indonesia, Papua: Jayawijaja, <i>Wen 10724</i>	KC952436	KC952084	KC952172	KC952612	KC952260	KC952524	KC952348
<i>Schefflera shweliensis</i> W. W. Smith [‡]	China, Xizang: Tzayu, <i>Wen 9199</i>	JX106062	JX106222	JX106181	JX106102	JX106263	JX106142	JX106304
<i>Schefflera wardii</i> Marquand & Airy Shaw [§]	China, Xizang: Linzhi, <i>Wen 9224</i>	KC952420	KC952068	KC952156	KC952596	KC952244	KC952508	KC952332
<i>Sinopanax formosanus</i> (Hayata) H. L. Li [†]	China, Taiwan: Kaohsiung, <i>Wen 9390</i>	GU054723	GU055103	GU055008	GU054533	GU054913	GU054818	GU054628
<i>Tetrapanax papyrifer</i> (Hook.) K. Koch [†]	Indonesia, West Java: Bogor, cult. <i>Wen 10135</i>	GU054758	GU055138	GU055043	GU054568	GU054948	GU054853	GU054663
<i>Tetraplasandra hawaiiensis</i> A. Gray [‡]	US, Hawaii: Oahu, cult. <i>Wen 7075</i>	JX106063	JX106223	JX106182	JX106103	JX106264	JX106143	JX106305
<i>Trevesia palmata</i> (Roxb. ex Lindl.) Vis. [§]	China, Yunnan: Hekou, <i>Wen 8460</i>	KC952421	KC952069	KC952157	KC952597	KC952245	KC952509	KC952333
<i>Trevesia sundaica</i> Miq.	Indonesia, West Java: Bogor, <i>Wen 10162</i>							

[†]Sequences of taxa from Li & Wen (2013); [‡]Sequences of taxa from Mitchell et al. (2012); [§]Sequences of taxa from Li & Wen (2014); and the remaining sequences were generated for the present study.

Table 3 Characters of the plastid and the nuclear ITS data sets

	Aligned length (bp)	Number of variable sites (%)	Number of informative sites (%)	Model selected by AIC
<i>ndhF</i>	1918	370 (19.3%)	163 (8.5%)	TVM+I+G
<i>trnL-F</i>	1013	213 (21.0%)	85 (8.4%)	TVM+G
<i>rps16</i>	937	210 (22.4%)	76 (8.1%)	GTR+G
<i>atpB-rbcL</i>	841	143 (17.0%)	61 (7.3%)	TVM+G
<i>rpl16</i>	1184	240 (20.3%)	105 (8.9%)	TVM+I+G
<i>psbA-trnH</i>	567	181 (31.9%)	97 (17.1%)	K81uf+I+G
ITS	652	334 (51.2%)	228 (35.0%)	GTR+I+G
Combined plastid and ITS data matrix	7112	1691 (23.8%)	815 (11.5%)	—

Fig. 1. The Bayesian tree of Chinese Araliaceae derived from analysis of the combined plastid and ITS data. Parsimony bootstrap values (PB) for maximum parsimony analysis in 500 replicates $> 50\%$ are shown in the left and Bayesian posterior probabilities (PP) ≥ 0.95 are indicated in the right. Dash shows that the PB value lower than 50% or the PP value lower than 0.95. The branch to Araliaceae is truncated to allow for better display of the topology of the tree.

Fig. 2. Chronogram of Chinese Araliaceae inferred from combined plastid and internal transcribed spacer data using BEAST. Nodes labeled A or B indicate fossil calibration points. Nodes labeled 1–2 are indicated with age estimates and are discussed in the text.