# EVOLUTION OF THE *ARALIA–PANAX* COMPLEX (*ARALIACEAE*) AS INFERRED FROM NUCLEAR RIBOSOMAL ITS SEQUENCES

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The *Aralia–Panax* complex consists of three closely related genera of *Araliaceae* (*Aralia* L., *Panax* L. and *Sciadodendron* Griseb.), widely distributed in temperate, subtropical, and tropical regions of Asia and the Americas. Three major lineages (*Panax*, *Aralia* sect. *Aralia*, and *Aralia* sect. *Dimorphanthus* Miq.) are disjunctly distributed in eastern Asia and North America. Comparative sequencing of the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA was carried out in order to examine the phylogenetic and biogeographic relationships of this complex. Results suggest *Aralia* is paraphyletic, with *Panax* and the Central American monotypic *Sciadodendron* nested within. The monophyly of *Panax* (*P. trifolius* L. maybe excepted), *Aralia* sect. *Aralia* (except *A. henryi* Harms), and *Aralia* sect. *Humiles* Harms is supported. The morphologically isolated *A. hispida* Vent. is embedded within *Aralia* sect. *Dimorphanthus*. The phylogenetic data suggest the need to re-examine the generic delimitation of *Aralia*. None of the presumed intercontinental species pairs between eastern Asia and eastern North America (e.g. *Aralia cordata* Thunb. and *A. racemosa* L., *A. spinosa* L. and *A. stipulata* Franch., and *Panax ginseng* C. A. Mey. and *P. quinquefolius* L.) have been supported as sister species, and the floristic similarity between eastern Asia and eastern North America seems to have been exaggerated by previous workers. Within *Aralia* sect. *Dimorphanthus*, the north temperate series *Dimorphanthus* was paraphyletic, with the subtropical and tropical series *Chinensis* J. Wen and series *Foliolosae* J. Wen nested within. This pattern of differentiation is consistent with the hypothesis of morphological stasis among the closely related disjunct taxa between eastern Asia and eastern North America in series *Dimorphanthus*. Subtropical/tropical *Sciadodendron*, and *Aralia* sect. *Pentapanax* (Seem.) J. Wen are suggested to have derived from temperate elements, although *Araliaceae* have a generally subtropical and tropical distribution.

*Keywords.* *Aralia*, *Araliaceae*, Asian–North American disjunction, biogeography, internal transcribed spacer regions, *Panax*, *Pentapanax*, phylogeny, *Sciadodendron*.

## Introduction

The *Aralia–Panax* complex is composed of three genera (Table 1): *Aralia* (about 55 species), *Panax* (about 11 species), and the monotypic *Sciadodendron* (see Tables 1, 2 for all taxon authorities unless given in the text). A close relationship of the three genera is supported by morphology (Harms, 1897, 1898; Eyde & Tseng, 1971; Wen, 1993), and DNA sequence data (Wen *et al.*, 2001). These three genera are referred to as a complex because they are closely related, but no formal taxonomic

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TABLE 1. Major genera/sections in the *Aralia–Panax* complex

| Taxon | Species no. | Distribution |
|---|---|---|
| *Aralia* L. | c.55 | |
| Sect. *Aralia* | 8 | E Asia, and N America |
| Sect. *Coudenbergia* (Marchal) J. Wen | 3 | S America and Cuba |
| Sect. *Dimorphanthus* Miq. | 26 | Asia and eastern N America |
| Sect. *Humiles* Harms | 3 | SW N America to C America |
| Sect. *Nanae* Harms | 1 | Eastern N America |
| Sect. *Pentapanax* (Seem.) J. Wen | c.15 | Asia |
| *Panax* L. | c.11 | Asia and eastern N America |
| *Sciadodendron* Griseb. | 1 | C America |

designations have yet been made. Taxonomic difficulties with these genera are well known, and over 300 taxonomic names have been published under *Aralia* and *Panax*. At present, major controversies exist concerning the circumscription of species and genera, and relationships among major lineages within the complex. These problems are also common in other large genera in *Araliaceae*, as discussed by Philipson (1970b), Frodin (1975), and Lowry *et al.* (1989). Wen (1993) developed a character-based generic concept of *Aralia*, recognizing the following synapomorphies: pinnately compound leaves, presence of stipules, and 5–8-locular ovaries. This has not been tested by phylogenetic analysis. *Aralia* consists of seven sections (see Table 1) distributed in Asia and the Americas (Harms, 1898; Wen, 1993). Due to the more-or-less constant floral features, these sections were based largely on the following vegetative characters: habit, presence/absence of prickles, leaf architecture, number of locules in the ovary, cuticle types, trichome types, and stomatal distribution. Relationships among the sections remain poorly understood, and the monophyly of the sections has not been tested by phylogenetic analysis.

The *Aralia–Panax* complex plays an important role in understanding the diversification of *Araliaceae* because it includes the majority of the north temperate members of family. *Aralia* is the fourth largest genus in *Araliaceae* (only *Schefflera* J. R. Forst. & G. Forst., *Polyscias* J. R. Forst. & G. Forst. and *Oreopanax* Decne. & Planch. are larger). Harms (1898) considered the *Aralia–Panax* lineage as one of the centres of diversity within *Araliaceae* and suggested that it played a critical role in leading to other lineages in *Araliaceae* and *Apiaceae*. Recent phylogenetic analysis of the core *Araliaceae* suggests that the *Aralia–Panax* complex, along with *Polyscias* and *Pseudopanax* K. Koch and their close relatives, form one of the two major clades of the core *Araliaceae* (Wen *et al.*, 2001).

*Panax* (the ginseng genus) is traditionally important in the Orient, where almost every species of the genus has been used as a tonic, a stimulant or a medicine for fatigue resistance. The genus consists of approximately 11 species with a disjunct distribution in Asia (c.9 spp.) and eastern North America (2 spp.). Linnaeus' (1753,

1754) concept of *Panax* was very broad, as it was primarily based on floral morphology, which is relatively constant and evolutionarily conserved in *Araliaceae* (Philipson, 1970a). Later workers (e.g. de Candolle, 1830) consequently described many araliaceous species within *Panax*. Seemann (1868) narrowed the definition of *Panax* to a group of herbs with palmately compound leaves, whorled leaf arrangement, a single terminal inflorescence, and a bi- or tri-carpellate ovary. This concept was followed by later workers (Harms, 1897, 1898; Hara, 1970; Hoo & Tseng, 1973, 1978; Zhou *et al.*, 1975; Wen & Zimmer, 1996; Choi & Wen, 2000).

Based on the presence of 5-merous flowers and articulated pedicels, Harms (1897) and Eyde & Tseng (1971) suggested that the New Zealand *Stilbocarpa* (Hook.f) Decne. & Planch. may also be closely related to *Aralia* and *Panax*. Vegetatively *Stilbocarpa* shares certain similarities with members of *Apiaceae* subfamily *Hydrocotyloideae* Link. Mitchell *et al.* (1999) have recently shown that *Stilbocarpa* is nested in a clade with southern hemisphere *Apiaceae* genera *Azorella* Lam. and *Schizeilema* (Hook.f.) Domin., very distant from any araliaceous genera.

Within the *Aralia–Panax* complex, three major lineages (*Panax*, *Aralia* sect. *Aralia*, and *Aralia* sect. *Dimorphanthus*) have a disjunct distribution in eastern Asia and North America, a well-known biogeographic pattern occurring in 65 genera of flowering plants and many other groups of organisms (Graham, 1972; Wen, 1999). The *Aralia–Panax* complex has been used to study the evolution of the eastern Asian and eastern North American disjunction (Wen & Zimmer, 1996; Wen *et al.*, 1996, 1998; Choi & Wen, 2000; Wen, 2000). A recent phylogenetic study by Shi *et al.* (1998) reported that *Liquidambar* L., a well-known biogeographic model in the north temperate zone (Hoey & Parks, 1991), is paraphyletic. Two subtropical genera (*Altingia* Noronha and *Semiliquidambar* H. T. Chang) were derived from *Liquidambar*. These results strongly suggest the need to examine eastern Asian and eastern North American disjunctions in a much broader geography than just the north temperate zone. Within the *Aralia–Panax* complex, *Aralia* sect. *Coudenbergia*, sect. *Pentapanax*, and *Sciadodendron* are primarily subtropical and/or tropical. The complex is thus a good candidate to investigate evolutionary diversification and differentiation of closely related temperate and subtropical/tropical species. It provides an ideal system to test the hypothesis of morphological stasis (the lack of drastic morphological changes in a long period of time) in the evolution of eastern Asian and eastern North American disjunctions (Parks & Wendel, 1990; Hoey & Parks, 1991; Wen, 1998, 1999).

Objectives of the present study are to: (i) provide an explicit phylogenetic hypothesis of the *Aralia–Panax* complex and identify major evolutionary lineages; (ii) test the morphological stasis hypothesis for the evolution of eastern Asian–eastern North American disjunctions; and (iii) construct the biogeographic history for this complex (with taxa distributed in temperate Asia, tropical and subtropical Asia, eastern North America, western North America, and South and Central America). Sequences of the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA have been employed for phylogenetic reconstruction.

## MATERIALS AND METHODS

Thirty-five species of the *Aralia–Panax* complex were sampled, representing the major lineages of the complex (Table 2). Three other species of *Araliaceae* (*Dizygotheca elegantissima*, *Metapanax delavayi*, and *Polyscias guilfoylei*) were used as outgroups. Two of the outgroups (*Dizygotheca* N. E. Br. and *Polyscias* J. R. Forst. & G. Forst.) are close relatives of the complex, and *Metapanax* is more distantly related (Wen *et al.*, 2001).

Total DNA was extracted following the CTAB method of Doyle & Doyle (1987) and then purified with CsCl/ethidium bromide gradients. DNA amplifications were performed following Wen & Zimmer (1996). The sequencing strategy followed Wen *et al.* (1998). DNA sequences were assembled, and the boundaries between the coding and spacer regions were determined by comparing with the sequences of carrot (*Daucus carota* L.; Yokota *et al.*, 1989). The sequences were exported to PAUP* (Swofford, 2000). Most mutations were base substitutions, thus allowing manual alignment. All the sequences have been deposited at GenBank (see Table 2 for accession numbers).

Phylogenetic analyses were performed with PAUP* using the maximum parsimony (MP, Swofford *et al.*, 1996), the maximum likelihood (ML, Felsenstein, 1981), and the neighbour-joining (NJ, Saitou & Nei, 1987) methods. Parsimony analysis was performed using a branch-and-bound search with MULPARS and furthest addition sequence options. The amount of support for monophyletic groups revealed in the maximally parsimonious tree(s) (MPTs) was examined with 500 bootstrap replicates (Felsenstein, 1985) with the random addition and the heuristic search options using parsimony. The number of additional steps required to force particular taxa into a monophyletic group was examined using the CONSTRAINTS option in PAUP*. The maximum likelihood (ML) analysis was performed with the input order of sequences randomized and the transition/transversion ratio set at 1.6 based on the observed frequencies in the MPTs of the parsimony analysis. A neighbour-joining tree was constructed using the Kimura two-parameter distance (Kimura, 1980).

## RESULTS

Treating gaps as missing data, the MP analysis generated 1440 maximally parsimonious trees (MPTs) with a length of 379 steps, a consistency index (CI) of 0.683, and a retention index (RI) of 0.741. The strict consensus tree is presented in Fig. 1. Treating gaps as new characters, the parsimony analysis produced 1440 MPTs, with a length of 381 steps, a CI of 0.682, and a RI of 0.746. The strict consensus tree had an identical topology to that of treating gaps as missing data. The ML tree (Fig. 2, with a log likelihood of −3199.93385) differed from the MPTs that two outgroup taxa (*Dizygotheca* and *Polyscias*) were nested within the *Aralia–Panax* complex, and that the relative position of *Panax trifolius*, *Sciadodendron excelsum*, and the *Aralia humilis–A. scopulorum* clade changed (Figs 1, 2). The NJ tree (Fig. 3) was similar to the MPTs; and they differed mostly in the placement of *Sciadodendron*. The ITS phylogeny suggests that *Panax* and *Sciadodendron* were nested within *Aralia*. The monophyly of *Panax* was supported in the MP and NJ analysis. *Aralia* sect. *Pentapanax* (previously known as *Pentapanax* Seem.) formed a clade with *Aralia* sect. *Dimorphanthus*.

TABLE 2. Accessions of the *Aralia–Panax* complex and outgroups sampled for this study

| Species | Voucher | Geographical origin | GenBank accession |
|---|---|---|---|
| *Aralia* sect. *Aralia* | | | |
| *A. cachemirica* Decne. | *Wen* 72 (CS) | Himalayas, cult. at the Arnold Arboretum | U66705 |
| *A. californica* S. Watson | *Ornduff* 8931 (CS) | California, USA, cult. at the Univ. California Bot. Gard. | U66921 |
| *A. cordata* Thunb. | *J. Wen* 2476 (CS) | Tokyo, Japan | U66923 |
| *A. fargesii* Franch. | *J. Wen* 1216 (CS) | Yunnan, China | U41673 |
| *A. henryi* Harms | *J. Wen* 1362 (CS) | Hubei, China | U41672 |
| *A. racemosa* L. | *J. Wen* 895 (A) | North Carolina, USA | U66926 |
| *Aralia* sect. *Dimorphanthus* | | | |
| Series *Chinensis* J. Wen | | | |
| *A. chinensis* L. | *J. Wen* 1136 (CS) | Hainan, China | AF242256 |
| *A. searelliana* Dunn | *J. Wen* 1203 (CS) | Yunnan, China | AF273532 |
| *A. vietnamensis* Ha | *J. Wen* 1210 (CS) | Yunnan, China | AF273541 |
| Series *Dimorphanthus* | | | |
| *A. bipinnata* Blanco | *C. F. Hsieh & W. S. Tang* T1852 (CS) | Taiwan | AF273519 |
| *A. debilis* J. Wen | *J. Wen* 1473 (CS) | Guangdong, China | AF273523 |
| *A. elata* (Miq.) Seem. | *J. Wen* 1145 (CS) | Sichuan, China | AF273526 |
| *A. hispida* Vent. | *T. Philbrick s.n.* (CS) | Connecticut, USA | U66925 |
| *A. spinosa* L. | *J. Wen & H. Dong* 976 (A) | Georgia, USA | U66928 |
| *A. undulata* Hand.-Mazz. | *J. Wen* 1364 (CS) | Hubei, China | AF273540 |
| Series *Foliolosae* J. Wen | | | |
| *A. finlaysoniana* (Wall. ex Don) Seem. | *J. Wen* 1205 (CS) | Yunnan, China | AF273529 |
| *A. spinifolia* Merr. | *J. Wen* 1247 (CS) | Guangdong, China | U41676 |
| *Aralia* sect. *Humiles* | | | |
| *A. humilis* Cav. | *J. Wen* 4974 (F) | Arizona, USA | AF242230 |
| *A. scopulorum* Brandegee | *J. Wen* 565 (OS) | Baja California, Mexico | U66927 |
| *Aralia* sect. *Nanae* | | | |
| *A. nudicaulis* L. | *J. Wen* 849 (A) | North Carolina, USA | U41674 |
| *Aralia* sect. *Pentapanax* | | | |
| *A. gigantea* J. Wen | *Sino-Amer. Bot. Exp.* 125 (US) | Yunnan, China | AF242253,<br>AF242254 |
| *A. plumosa* H. L. Li | *J. Wen* (CS) | Yunnan, China | AF242255 |
| *Dizygotheca elegantissima* R. Vig. & Guillaumin | *J. Wen* (CS) | Cult. in Colorado, USA | AF242239,<br>AF242240 |
| *Metapanax delavayi* (Franch.) J. Wen & Frodin | *J. Wen* (CS) | Yunnan, China | AF242232 |
| *Panax ginseng* C. A. Mey. | *J. Wen* (CS) | Heilongjiang, China | U41680 |
| *P. japonicus* C. A. Mey. | *M. Hasebe s.n.* (CS) | Japan | U41701 |

TABLE 2. (Continued.)

| Species | Voucher | Geographical origin | GenBank accession |
|---|---|---|---|
| *P. major* Ting | *J. Wen* (CS) | Hubei, China | U41683 |
| *P. notoginseng* (Burkill) F. H. Chen | *J. Wen* (CS) | Guangdong, China | U41685 |
| *P. omeiensis* J. Wen | *J. Wen (CS)* | *Sichuan, China* | *U41692* |
| *P. pseudoginseng* Wall. | *Botanic Garden, Univ. of Tokyo* 2218 | Nepal | U41693 |
| *P. quinquefolius* L. | *J. Wen* (CS) | Virginia, USA | U41689 |
| *P. sinensis* J. Wen | *D,-Q. Yang* s.n. | Jiangxi, China | U41703 |
| *P. stipuleanatus* H. T. Tsai & K. M. Feng | *J. Wen* (CS) | Yunnan, China | U41696 |
| *P. trifolius* L. | *W. Hahn* (CS) | Pennsylvania, USA | U41697 |
| *P. wangianus* Sun | *J. Wen* (CS) | Sichuan, China | U41690 |
| *P. zingiberensis* C. Y. Wu & K. M. Feng | *J. Wen* (CS) | Yunnan, China | U41699 |
| *Polyscias guilfoylei* (Bull.) L. H. Bailey | *J. Wen* (CS) | Cult. in Colorado, USA | AF242246 |
| *Sciadodendron excelsum* Griseb. | *F. Chiang s.n.*(CS) | Mexico | AF242231 |

## Discussion

### *Phylogenetic relationships*

*Panax* was supported as monophyletic in the MP and NJ trees, but the ML tree puts *Panax trifolius* in a clade with *Aralia humilis* and *A. scopulorum*. Morphological synapomorphies of *Panax* include palmately compound leaves, whorled leaf arrangement, a single terminal inflorescence, and a bi- or tri-carpellate ovary. *Panax trifolius* is morphologically a highly unusual species, characterized as a small herb with globose main roots, diphasious reproductive system (sex-changing; Schlessman, 1987, 1990, 1991), white petals, 3-locular ovary, and dry fruits. Pollen morphology and exine structure of *P. trifolius* are unique (large grains, highly striate tectum with distinct lirae, and very large columellae) in comparison to those of any other *Panax* and *Aralia* species (Wen & Nowicke, 1999). Palynological, morphological, and molecular data all suggest the phylogenetic isolated nature of *P. trifolius*.

ITS sequence data suggest that *Panax* and *Sciadodendron* are nested within a paraphyletic *Aralia* (Figs 1–3). However, the relationship of *Panax* with different lineages of *Aralia* is not well resolved. The diversification of major lineages in the *Aralia–Panax* complex was perhaps rapid in the early evolutionary history of the group. Additional studies are required to elucidate the relationships among these major lineages, but current evidence suggests the need to re-examine the generic delimitation of *Aralia* and perhaps restrict its concept to maintain the monophyly and nomenclatural stability of *Panax*.

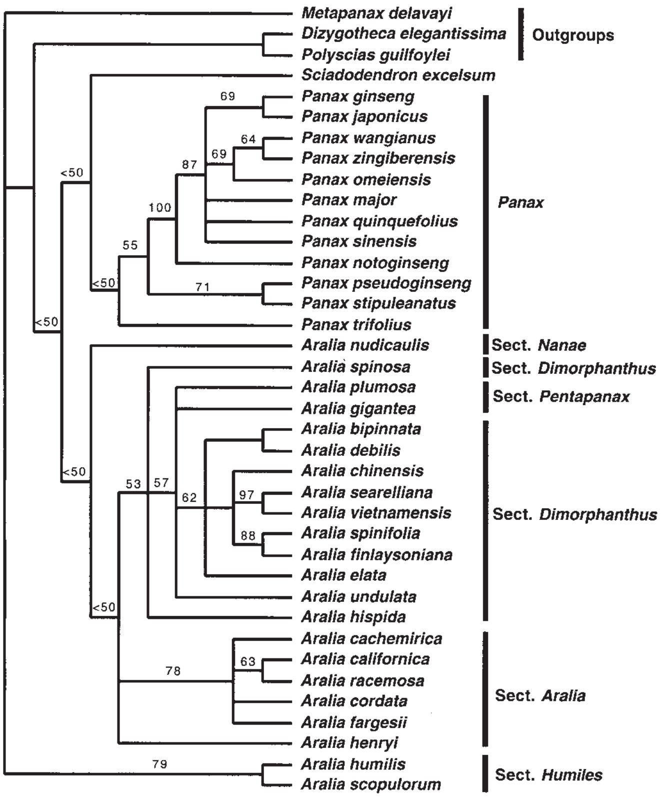

FIG. 1. The strict consensus of the 1440 most parsimonious trees of the *Aralia–Panax* complex with ITS sequences (379 steps, CI = 0.683, and RI = 0.741). Numbers above lines are the bootstrap values in 500 replicates.

*Aralia* sect. *Aralia* comprises approximately eight species of disjunct distribution in Asia and North America: five species in eastern Asia, one in the Himalayas, one in eastern North America, one subspecies in south-western North America, and one species in western North America. *Aralia* sect. *Aralia* was recently redefined (Wen, 1991, 1993; Wen *et al.*, 1998) by uniting two sections previously recognized by Harms (1898): sect. *Aralia* (*A. cachemirica*, *A. californica*, *A. cordata* and *A. racemosa*) and sect. *Anomale* Harms (*A. apioides* Hand.-Mazz., *A. fargesii*, *A. glabra* Matsumura and *A. henryi*) previously distinguishing on presence/absence of a main inflorescence axis. Monophyly of the broadly defined sect. *Aralia sensu* Wen was largely supported by ITS data, except that the position of *A. henryi* was not well resolved. Morphological synapomorphies of *Aralia* sect. *Aralia sensu* Wen, include triternately compound leaves at the base, terminal and axillary inflorescences, and distinct styles. Although *A. henryi* possesses these synapomorphies, it is unique in that it is a small herb with reduced leaves, small inflorescences, rounded bracts, and somewhat dry fruits. It has a restricted distribution in central China, only occurring in western

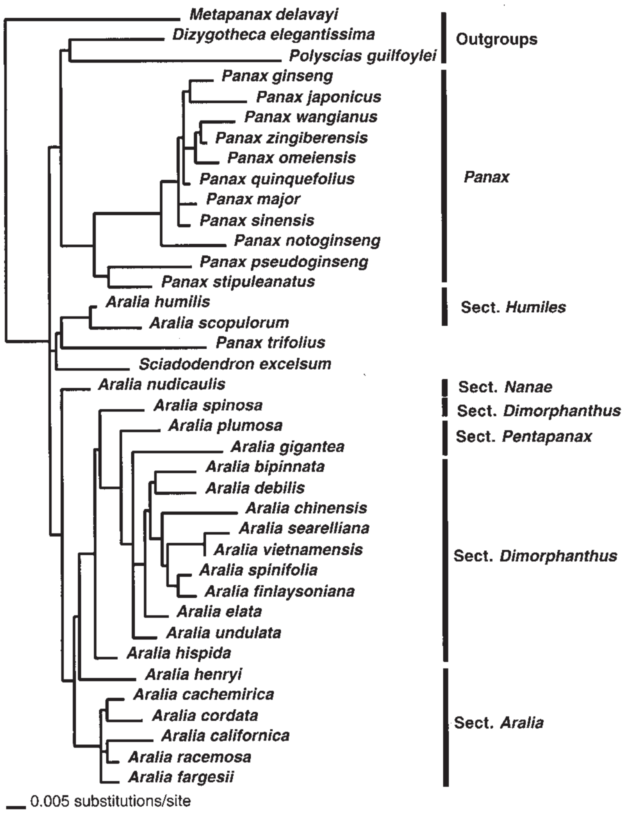

FIG. 2. The maximum likelihood tree of the *Aralia–Panax* complex constructed from the ITS sequences with a log likelihood of −3199.93385.

Hubei and eastern Sichuan provinces. Wen *et al.* (1998) also found that this species fell outside the core *Aralia* clade. The phylogenetic position of *A. henryi* clearly needs further study.

*Aralia hispida* is a small semiwoody (a herb with a woody stem base) species from eastern North America, ranging from Newfoundland to North Carolina, westward to Minnesota, Indiana, and Michigan (Britton & Brown, 1913). Harms (1898) treated it in *Aralia* sect. *Humiles*, with three additional species from south-western North America to Central America: *A. humilis*, *A. regeliana* Marchal, and *A. scopulorum*. Wen (1991, 1993) established the monotypic sect. *Hispidae* because *A. hispida* lacks the synapomorphies of sect. *Humiles* (branched trichome, and presence of stomata on both abaxial and adaxial leaflet surfaces). The ITS phylogeny suggests that *A. hispida* is closely allied to taxa of sect. *Dimorphanthus* (Figs 1–3). Wen (2000) recircumscribed sect. *Dimorphanthus*, in which *A. hispida* has now been included.

*Aralia* sect. *Dimorphanthus* consists of 26 species, two of which are found in eastern North America (*A. hispida* and *A. spinosa*) and the rest in Asia extending from eastern Russia to northern New Guinea (Wen, 2000). *Dimorphanthus* Miq. was

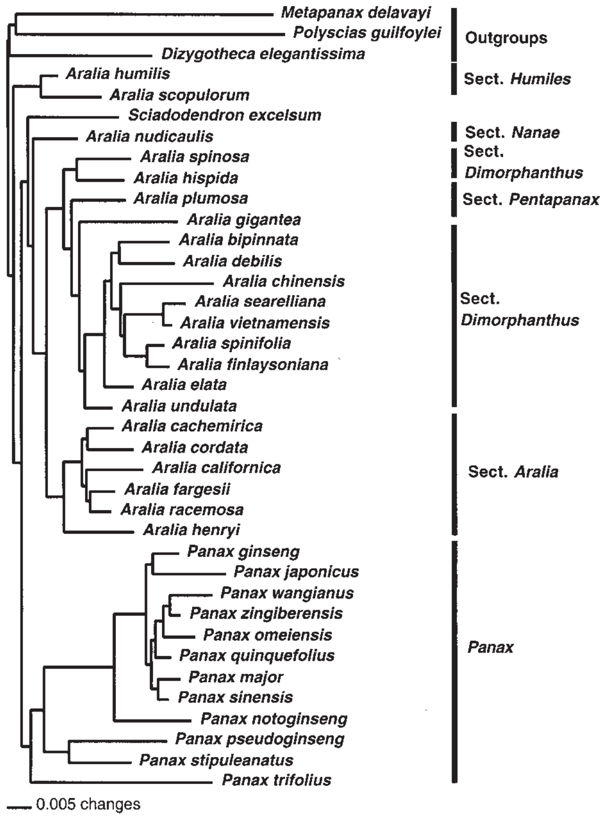

FIG. 3. The neighbour-joining tree of the *Aralia–Panax* complex based on Kimura two-parameter distances.

originally described (Miquel, 1840) as a monotypic genus (including *D. elatus*) from Japan, distinct from the Linnaean *Aralia*. Miquel (1856a) later reduced it to the rank of subgenus within *Aralia*. However, he soon relegated the group to sect. *Dimorphanthus* (Miquel, 1856b) and used this concept consistently in his later works (e.g. Miquel, 1857, 1863). The ITS phylogeny (Figs 1–3) shows the paraphyly of *Aralia* sect. *Dimorphanthus*, within which *Aralia* sect. *Pentapanax* is nested. *Pentapanax* Seemann (1864) ( = *Aralia* sect. *Pentapanax*) consists of approximately 15 species from subtropical, tropical and warm temperate regions of Asia. A close relationship between *Aralia* and *Pentapanax* has long been hypothesized (Harms, 1898; Hoo, 1961; Hoo & Tseng, 1978), with Wen (1993) treating it as a section within *Aralia*. A broad phylogenetic analysis of the core *Araliaceae* confirms that *Pentapanax* is nested within *Aralia* (Wen *et al.*, 2001). The ITS data of the *Aralia–Panax* complex suggest that sect. *Pentapanax* is embedded within sect. *Dimorphanthus* (Figs 1–3). Further study is needed to clarify the relationship of this section.

*Aralia* sect. *Humiles* consists of three species (*A. humilis*, *A. regeliana*, and *A. scopulorum*) from south-western US, Mexico, extending into southern Central America. Its monophyly is supported by the ITS trees (Figs 1–3). Morphological synapomorphies of sect. *Humiles* include branched trichome and the presence of stomates on both the abaxial and adaxial leaflet surfaces. Shang & Li (1988) transferred *Aralia scopulorum* of sect. *Humiles* to the Asiatic *Pentapanax*. The present study, however, shows that *Aralia* sect. *Humiles* and sect. *Pentapanax* do not form a clade, strongly suggesting that the shared characters of lack of prickles, mostly pinnately compound leaves, and presence of bud scales at the base of the inflorescence in these two lineages are evolutionary convergences or symplesiomorphies.

*Sciadodendron* falls within the *Aralia–Panax* complex, but its position is not well resolved (cf. Figs 1–3). The MPTs suggest that it is sister to the *Panax* clade. The ML tree puts it in a clade with the somewhat enigmatic and morphologically isolated *Aralia humilis*, *A. scopulorum*, and *Panax trifolius* from the New World. *Sciadodendron* was placed basal to the core *Aralia* clade in the NJ tree (with only *A. humilis* and *A. scopulorum* excepted). *Sciadodendron* is a monotypic genus distributed in areas of low elevations in western Mexico, Colombia, Honduras, Panama, Guatemala, and Nicaragua. It differs from *Aralia* in its more numerous floral parts, more enlarged anthers, straight (vs. recurved) filaments, and non-arculated pedicels (Gentry, 1993; Wen, 1993). The phylogenetic relationships of these taxa need further study.

*Aralia nudicaulis* is morphologically a very distinctive species and the sole member of *Aralia* sect. *Nanae* (Harms, 1898; Wen, 1991; Tseng *et al.*, 1993). It is a small, unarmed, clonal herb that grows under the forest canopy of eastern North America. It has long horizontal rhizomes and lacks aerial stems, with one leaf and one small inflorescence consisting of three umbels arising from the ground. The pollen has very thin exine, unique in the *Aralia–Panax* complex, and is considered an extreme reduction (Wen & Nowicke, 1999). The ITS trees (Figs 1–3) place *A. nudicaulis* basal to a large clade consisting of *Aralia*, with only *Aralia* sect. *Humiles* excepted.

### *Biogeographic relationships*

Most taxa of *Aralia* occur in the north temperate zone, although members of sect. *Coudenbergia* and sect. *Pentapanax* are primarily subtropical to tropical. The ITS trees (Figs 1–3) suggest the derivation of the subtropical and tropical sect. *Pentapanax* from temperate taxa in this complex, even though *Araliaceae* as a whole are primarily of subtropical and tropical distribution (Wen *et al.*, 2001). Within *Aralia* sect. *Dimorphanthus*, the north temperate series *Dimorphanthus* was paraphyletic, with the subtropical and tropical series *Chinensis* and series *Foliolosae* nested within. Despite that, the older temperate disjunct taxa of series *Dimorphanthus* gave rise to the younger subtropical and tropical taxa (series *Chinensis*, series *Foliolosae*, and sect. *Pentapanax*). Members of the temperate series *Dimorphanthus* are still morphologically coherent and the subtropical and tropical groups are highly distinct from the temperate taxa. This pattern of differentiation is consistent with the hypothesis of morphological stasis (Parks & Wendel, 1990; Wen, 1998, 1999, 2000) among the closely related disjunct taxa between eastern Asia and eastern North America in series *Dimorphanthus*.

The diversification of the *Aralia–Panax* complex across different continents in the north temperate zone is complex. Three lineages of the *Aralia–Panax* complex (*Aralia* sect. *Aralia*, sect. *Dimorphanthus*, and *Panax*) are disjunctly distributed in Asia and North America. The ITS phylogeny (Figs 1–3) supports the independent origin of the disjunct pattern in each of the three lineages.

*Aralia* sect. *Aralia* is disjunctly distributed in eastern Asia, the Himalayas, and eastern and western North America. A species-pair relationship has long been recognized between *A. cordata* from eastern Asia and *A. racemosa* from eastern North America, with the western North American *A. californica* considered to be more distantly related (Li, 1952, 1972). However, Wen *et al.* (1996; 1998) showed that *A. racemosa* did not form a species-pair relationship with the eastern North American *A. cordata*, but in fact was sister to *A. californica*. The two subspecies of *A. racemosa* were seen to form a monophyletic group. Biogeographic analyses show a close area relationship between eastern North America and western North America (Wen *et al.*, 1998). This analysis suggested that the Himalayas were basal and eastern Asia were placed between the Himalayas and North America. The biogeographic analysis and fossil evidence supported the origin of the eastern Asian and eastern North American disjunct pattern in *Aralia* sect. *Aralia* in the mid to late Tertiary via the Bering land bridges (Wen *et al.*, 1998). Comparisons with results of phylogenetic analyses of other genera suggested that floristic connection between eastern North America and western North America may be stronger than previously thought (Xiang *et al.*, 1998; Wen, 1998, 1999), but the floristic similarity between eastern Asia and eastern North America seems to have been exaggerated in the past.

*Aralia* sect. *Dimorphanthus* also shows a disjunct distribution between eastern Asia and eastern North America. Despite previous emphasis on the floristic similarity between the two continents, Wen (1991, 2000) found the relatively basal position of the eastern North American *A. spinosa* and *A. hispida* and the monophyly of the Asiatic taxa. This pattern suggests the antiquity of the intercontinental biogeographic disjunction, specifically, the formation of the intercontinental disjunction prior to the diversification of the Asian clade, which consists of 24 species. Fossil evidence suggests the diversification of the Asiatic taxa by the Miocene (Wen, 2000), prompting Wen to conclude that the minimum divergence time between the Asiatic and eastern North American taxa was probably during the Miocene. Two possible migration routes of plants were proposed between eastern Asia and eastern North America: (i) through the Bering land bridge (Hopkins, 1967), and (ii) across the North Atlantic land bridge (Tiffney, 1985b), the latter being more thermophilic due to its lower latitude and viability for plant migration up to the Oligocene (Tiffney, 1985a,b). The Bering land bridge was available several times during the Tertiary and was present in the Miocene. Assuming a Miocene divergence time between the eastern

Asian and eastern North American taxa in *Aralia* sect. *Dimorphanthus*, the Bering land bridge would be a more plausible hypothesis for the disjunction in this section.

Within *Panax*, approximately nine species are from Asia and about two are from eastern North America (Wen & Zimmer, 1996; Choi & Wen, 2000; Wen, 2001). *Panax ginseng* of eastern Asia and *P. quinquefolius* of eastern North America have been considered to constitute an intercontinental species pair (Li, 1952, 1972). Wen & Zimmer (1996) suggest two independent origins of the eastern Asian–eastern North American disjunction within *Panax*. Two biogeographic disjunctions are detectable within *Panax*. One is the connection of the eastern North American *P. trifolius* with the Himalayan *P. pseudoginseng* and the Chinese *P. stipuleanatus*. The other is the more recent disjunction between the North American *P. quinquefolius* and the eastern Asian *P. ginseng* and *P. japonicus*.

The centre of diversity of *Panax* is the Himalayas, central and western China, with about nine of the 11 species there. The relatively low molecular sequence divergence (ITS regions; Wen & Zimmer, 1996; cpDNA restriction sites, Choi & Wen, 2000) among most Asiatic species suggests that these species have diversified relatively recently. Morphologically they are similar, and occasional intermediates may be present. Most species of *Panax* occur in rich woods in the mountainous regions of central and western China, and the Himalayas. The rise of the Himalayas and the formation of many mountain ranges in central and western China since the late Tertiary and Quaternary (Axelrod *et al.*, 1998) may have created numerous isolated habitats ideal for speciation of *Panax*. Recent evolution of Asiatic species may best explain the taxonomic controversies among *Araliaceae* workers. Only two species occur in eastern North America (*P. quinquefolius* and *P. trifolius*), but they are very distinct and represent different major phylogenetic lines within *Panax*.

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## REFERENCES

AXELROD, D. I., AL-SHEHBAZ, I. & RAVEN, P. H. (1998). History of the modern flora of China. In: ZHANG, A.-L. & WU, S.-G. (eds) *Floristic Characteristics and Diversity of East Asian Plants*, pp. 43–55. Beijing: China Higher Education Press.

BRITTON, N. L. & BROWN, A. (1913). *An Illustrated Flora of the Northern United States, Canada and the British Possessions.* New York: Charles Scribner's Sons.

Candolle, A. P. de (1830). *Araliaceae*. In: Candolle, A. P. de (ed.) *Prodromus Systematis Naturalis Regni Vegetabilis*, Vol. 4, pp. 251–266. Paris: Treuttel & Wurtz.

Choi, H.-K. & Wen, J. (2000). A phylogenetic analysis of *Panax* (*Araliaceae*): integrating evidence of chloroplast DNA and the ITS sequences of nrDNA. *Pl. Syst. Evol.* 224: 109–120.

Doyle, J. J. & Doyle, J. L. (1987). A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.

Eyde, R. H. & Tseng, C. C. (1971). What is the primitive floral structure of *Araliaceae*? *J. Arnold Arbor.* 52: 205–239.

Felsenstein, J. (1981). Evolutionary trees from DNA sequences: a maximum likelihood approach. *J. Molec. Evol.* 17: 368–376.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–91.

Frodin, D. G. (1975). Studies in *Schefflera* (*Araliaceae*): the *Cephaloschefflera* complex. *J. Arnold Arbor.* 56: 427–448.

Gentry, A. (1993). *A Field Guide to the Families and Genera of Woody Plants of Northwest South America (Colombia, Ecuador, Peru) with Supplementary Notes on Herbaceous Taxa.* Chicago, IL: University of Chicago Press.

Graham, A. (ed.). (1972). *Floristics and Paleofloristics of Asia and Eastern North America*. Amsterdam: Elsevier.

Hara, H. (1970). On the Asiatic species of the genus *Panax*. *J. Jap. Bot.* 45: 197–212, plates 10–12.

Harms, H. (1897). *Araliaceae*. In: Engler, A. & Prantl, K. (eds) *Die Natürlichen Pflanzenfamilien*, Vol. 3 (8), pp. 1–62. Leipzig: W. Engelmann.

Harms, H. (1898). Zur Kenntnis der Gattungen *Aralia* und *Panax*. *Bot. Jahrb. Syst.* 23: 1–23.

Hoey, M. T. & Parks, C. R. (1991). Isozyme divergence between eastern Asian, North American and Turkish species of *Liquidambar* (Hamamelidaceae). *Amer. J. Bot.* 78: 938–947.

Hoo, G. (1961). The systematics, relationship and distribution of the *Araliaceae* of China. *Bull. Amoi Univ. (Natural Sciences)* 8: 1–11.

Hoo, G. & Tseng, C.-J. (1973). On the Chinese species of *Panax* Linn. *Acta Phytotax. Sin.* 11: 431–438.

Hoo, G. & Tseng, C.-J. (1978). *Angiospermae, Dicotyledoneae, Araliaceae*. *Flora Reipublicae Popularis Sinicae*, Vol. 54. Beijing: Science Press.

Hopkins, D. M. (ed.) (1967). *The Bering Land Bridge*. Stanford, CA: Stanford University Press.

Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitution through comparative studies of nucleotide sequences. *J. Mol. Evol.* 16: 111–120.

Li, H.-L. (1952). Floristic relationships between Eastern Asia and eastern North America. *Trans. Amer. Phil. Soc.* 42: 371–429.

Li, H.-L. (1972). Eastern Asia–Eastern North America species – pairs in wide ranging genera. In: Graham, A. (ed.) *Floristics and Paleofloristics of Asia and Eastern North America*, pp. 65–78. Amsterdam: Elsevier.

Linnaeus, C. (1735). *Systema Naturae*. Leyden.

Linnaeus, C. (1754). *Genera Plantarum*, 5th edition. Stockholm.

Lowry II, P. P., Miller, J. S. & Frodin, D. G. (1989). New combinations and name changes for some cultivated tropical Old World and Pacific *Araliaceae*. *Baileya* 23: 5–13.

Miquel, F. A. W. (1840). *Commentarii Phytographici*. Leiden.

Miquel, F. A. W. (1856a) [1 May 1856]. Araliacearum indicarum genera et species aliquod novae. *Bonplandia* 4: 137–139.

Miquel, F. A. W. (1856b) [10 Jul 1856]. *Araliaceae*. *Fl. Ned. Ind.* 1: 745–769.

Miquel, F. A. W. (1857). *Araliaceae*. In deVries, W. H. (ed.) *Plantae Indiae Batavae Orientalis*, Vol. 2, pp. 81–92. Lugduni-Batavorum: E. J. Brill.

Miquel, F. A. W. (1863). *Araliaceae* novae, adjecta aliarum specierum praesertim indicarum revisione. *Ann. Mus. bot. Lugd.-Bat.* 1: 1–27.

Mitchell, A. D., Meurk, C. D. & Wagstaff, S. J. (1999). Evolution of *Stilbocarpa*, a megaherb from New Zealand's sub-antarctic islands. *New Zealand J. Bot.* 37: 205–211.

Parks, C. R. & Wendel, J. F. (1990). Molecular divergence between Asian and North American species of *Liriodendron* (Magnoliaceae) with implications of fossil floras. *Amer. J. Bot.* 77: 1243–1256.

Philipson, W. R. (1970a). Constant and variable features of the *Araliaceae*. *Bot. J. Linn. Soc.* 63: 87–100.

Philipson, W. R. (1970b). A redefinition of *Gastonia* and related genera (*Araliaceae*). *Blumea* 18: 497–505.

Saitou, N. & Nei, M. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molec. Biol. Evol.* 4: 406–425.

Schlessman, M. A. (1987). Gender modification in North American ginsengs: dichotomous choice versus adjustment. *BioScience* 37: 469–475.

Schlessman, M. A. (1990). Phenotypic gender in sex changing dwarf ginseng, *Panax trifolium* (*Araliaceae*). *Amer. J. Bot.* 77: 1125–1131.

Schlessman, M. A. (1991). Size, gender, and sex change in dwarf ginseng, *Panax trifolium* (*Araliaceae*). *Oecologia* 87: 588–595.

Seemann, B. (1868). *Revision of the Natural Order of Hederaceae*. London: L. Reeve & Co.

Shang, C.-B. & Li, X.-P. (1988). Studies on *Pentapanax* (*Araliaceae*). In: *Proc. Wuhan Conf. Dendr. Comm. Chinese Forest. Soc. 1988*, pp. 1–15.

Shi, S., Chang, H.-T., Chen, Y., Qu, L. H. & Wen, J. (1998). Phylogeny of the Hamamelidaceae based on the ITS sequences of nuclear ribosomal DNA. *Biochem. Syst. Ecol.* 26: 55–69.

Swofford, D. L. (2000). *PAUP*: phylogenetic analysis using parsimony, version 4.0.* Sunderland, MA: Sinauer Associates, Inc.

Swofford, D. L., Olsen, G. J., Waddell, P. J. & Hillis, D. M. (1996). Phylogenetic inference. In: Hillis, D.M., Moritz, C. & Mable, B. K. (eds) *Molecular Systematics*, 2nd edition, pp. 407–514. Sunderland, MA: Sinauer Associates, Inc.

Tiffney, B. H. (1985a). Perspectives on the origin of the floristic similarity between Eastern Asia and eastern North America. *J. Arnold Arbor.* 66: 73–94.

Tiffney, B. H. (1985b). The Eocene North Atlantic land bridge: Its importance in Tertiary and modern phytogeography of the northern hemisphere. *J. Arnold Arbor.* 66: 243–273.

Tseng, C. C., Wen, J., Hedges, K. L. & Chen, Y. C. (1993). Protein profile as a taxonomic character in *Aralia* (*Araliaceae*). *Cathaya* 5: 69–79.

Wen, J. (1991). Systematics of *Aralia* (*Araliaceae*). PhD dissertation, Ohio State University.

Wen, J. (1993). Generic delimitation of *Aralia* (*Araliaceae*). *Brittonia* 45: 47–55.

Wen, J. (1998). Evolution of the eastern Asian and eastern North American disjunct pattern: insights from phylogenetic studies. *Korean J. Pl. Taxon.* 28: 63–81.

Wen, J. (1999). Evolution of eastern Asian and eastern North American disjunct pattern in flowering plants. *Ann. Rev. Ecol. Syst.* 30: 421–455.

Wen, J. (2000). Internal transcribed spacer phylogeny of the Asian–eastern North American disjunct *Aralia* sect. *Dimorphanthus* (*Araliaceae*) and its biogeographic implications. *Intl. J. Pl. Sci.* 161: 959–966.

Wen, J.(2001). Species diversity, nomenclature, phylogeny, biogeography, and classification of the ginseng genus (*Panax*L., Araliaceae). In: Punja, Z. K. (ed) *Proceedings of the International Ginseng Workshop: utilization of biotechnological, genetic and cultural approaches for North American and Asian ginseng improvement.*Simon Fraser University, Canada (in press).

Wen, J. & Nowicke, J. W. (1999). Pollen ultrastrtucture of *Panax* (the ginseng genus, *Araliaceae*), an eastern Asian and eastern North America disjunct genus. *Amer. J. Bot.* 86: 1624–1636.

Wen, J. & Zimmer, E. A. (1996). Phylogeny and biogeography of *Panax* L. (the ginseng genus, *Araliaceae*): Inferences from ITS sequences of nuclear ribosomal DNA. *Molec. Phylo. Evol.* 6: 166–177.

Wen, J., Jansen, R. K. & Zimmer, E. A. (1996). Phylogenetic relationships and DNA sequence divergence of eastern Asian and eastern North American disjunct plants. In: Nei, M. & Takahata, N. (eds) *Current Topics on Molecular Evolution*, pp. 37–44. Hayama: Pennsylvania State University & the Graduate University for Advanced Studies, Hayama, Japan.

Wen, J., Shi, S., Jansen, R. K. & Zimmer, E. A. (1998). Phylogeny and biogeography of *Aralia* sect. *Aralia* (*Araliaceae*). *Amer. J. Bot.* 85: 866–875.

Wen, J., Plunkett, G. K., Mitchell, A. & Wagstaff, S. (2001) Evolution of *Araliaceae*: a phylogenetic analysis based on the ITS sequences of nrDNA. *Syst. Bot.* 26: 144–167.

Xiang, Q.-Y., Soltis, D. E. & Soltis, P. E. (1998). The eastern Asian and eastern and western North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. *Molec. Phylo. Evol.* 10: 178–190.

Yokota, Y., Kawata, T., Iida, Y., Kato, A. & Tanifuji, S. (1989). Nucleotide sequences of the 5.8S rRNA gene and internal transcribed spacer regions in carrot and broad bean ribosomal DNA. *J. Molec. Evol.* 29: 294–301.

Zhou, J., Huang, W.-G., Wu, M.-Z., Yang, C.-R., Feng, K. M. & Wu, Z. Y. (1975). Triterpenoids from *Panax* Linn. and their relationship with taxonomy and geographical distribution. *Acta Phytotax. Sin.* 13 (2): 29–45, plates 6–7.

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