

The Evolution of Araliaceae: A Phylogenetic Analysis Based on ITS Sequences of Nuclear Ribosomal DNA

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ABSTRACT. Phylogenetic analyses of ITS sequence data from 70 species and 40 genera of Araliaceae (representing all major lineages within the “core group” of the family) do not support the widely used traditional division of Araliaceae into three tribes. Tribe Aralieae (characterized by imbricate petals) is found nested within a paraphyletic Schefflerieae (whose taxa have valvate petals). There are, however, two large monophyletic groups comprising most araliad genera: the “*Aralia*-*Polyscias*-*Pseudopanax* group” (which includes *Aralia*, *Meryta*, *Munroidendron*, *Panax*, *Pentapanax*, *Polyscias*, *Pseudopanax*, *Reynoldsia*, *Sciadodendron*, *Tetraplasandra*, and their close allies), and the “*Eleutherococcus*-*Dendropanax*-*Schefflera* group” (including *Brassaiaopsis*, *Dendropanax*, *Eleutherococcus*, *Fatsia*, *Hedera*, *Oreopanax*, *Schefflera*, *Sinopanax*, and their close allies). The ITS trees also permit a re-evaluation of several taxonomically important morphological characters (e.g., petal aestivation, leaf architecture, carpel number, and habit), and provide the opportunity to assess traditional generic delimitations in the family. Four of the largest genera appear to be either polyphyletic (*Schefflera*, *Pseudopanax*) or paraphyletic (*Aralia*, *Polyscias*), but further studies will be needed to fully re-define these complex taxa. Outgroup comparisons and the placement of *Astrotricha* and *Osmoxylon* (in basally-branching lineages in Araliaceae) help to confirm a paleotropical origin of the family. The ITS topologies suggest that biogeographic radiations into different tropical/subtropical regions and into the north and south temperate regions occurred early in the history of core Araliaceae. Temperate taxa have arisen several times independently from tropical and subtropical relatives, although a few subtropical taxa may be found nested within temperate clades (e.g., *Pentapanax* within *Aralia*). Migrations between the Old and New Worlds are also suggested for several taxa, including *Aralia*, *Panax*, *Oplopanax*, and the *Sinopanax*—*Oreopanax* generic pair.

Araliaceae (the ginseng family) comprise approximately 55 genera and 1,500 species. The family is most broadly distributed in the tropics and subtropics (especially in southeastern and southern Asia and the Pacific islands), but there are several well-known genera from the temperate zones as well (e.g., *Aralia*, *Hedera*, *Oplopanax*, and *Panax*). The family includes a number of important medicinal plants, such as *Panax* (ginseng) and *Eleutherococcus* (Siberian ginseng), and several well-known ornamentals, including *Hedera* (English ivy), *Schefflera* (the umbrella trees), and *Polyscias*. Araliaceae have

traditionally been allied with Apiaceae on the basis of morphological (Harms 1898; Judd et al. 1994) and anatomical evidence (Metcalf and Chalk 1950), and this treatment has been largely supported by recent molecular studies (Plunkett et al. 1996a, 1997). Most systems of classification place Araliaceae and Apiaceae together in the order Apiales (sensu Cronquist 1981, 1988; or its taxonomic equivalent, Thorne 1992; Takhtajan 1987, 1997), which in turn has been placed in or near subclass Rosidae (e.g., Cronquist 1981, 1988). Recent studies, however, suggest that Apiales should be placed in

a broadly defined Asteridae (Chase et al. 1993; Olmstead et al. 1993; Plunkett et al. 1996a; Soltis et al. 1997) closely allied to Pittosporaceae (Plunkett et al. 1996a, 1997; Xiang and Soltis 1998).

Araliaceae are characterized by relatively conserved floral, but diverse vegetative features (Philipson 1970a; Eyde and Tseng 1971). Members of the family possess five sepals, 5–10 (–12) petals, which are free or form a calyptra (as in *Pentapanax* and *Tupidanthus*), mostly 5–10 stamens (rarely to numerous, e.g., 120 in *Tupidanthus*), and a gynoeceum with 2–10 (mostly 5, rarely up to 200 in *Tupidanthus*, or 1 in *Seemannaralia* R. Viguier) locules, and an inferior ovary (rarely superior as in *Dipanax* Seem.) with a nectary disk. Most araliads produce berries or drupaceous fruits that are bird dispersed (Ridley 1930). The leaves of Araliaceae vary from simple, to variously lobed or divided, to palmately and/or pinnately compound. Although most species are trees, shrubs, or woody climbers, there are also a few herbaceous perennials (e.g., some species of *Aralia* and *Panax*).

The major classification systems of Araliaceae include those by Bentham and Hooker (1867), Seemann (1868), Harms (1898), Hutchinson (1967), and Tseng and Hoo (1982). Bentham (1867) recognized five "series" (= tribes) within Araliaceae based on petal aestivation (imbricate vs. valvate), pedicel type (articulate vs. continuous), breeding system (hermaphrodite, polygamo-dioecious, or dioecious), stamen number, and albumen type (ruminate vs. uniform). Seemann (1868) defined the segregate "order" (= family) Hederaceae as distinct from a more narrowly circumscribed Araliaceae. His Hederaceae was divided into five tribes (Cussonieae, Horsfieldieae, Hedereae, Pseudopanaceae, and Plerandreae), and included all araliads having valvate petals and fruits with two or more carpels. As such, it included the vast majority of araliaceous genera, excluding only genera with imbricate petals (e.g., *Aralia* and *Panax*). Harms' (1898) treatment, which remains the most widely used (e.g., in Poyarkova 1973; Hoo and Tseng 1978; Philipson 1979; Shang 1985a; Mabberly 1997), divides Araliaceae into three tribes (Aralieae, Mackinlayeae, and Schefflereae) based largely on petal aestivation. Most araliad genera, having valvate petals, were placed in tribe Schefflereae (36 genera), leaving relatively few genera in tribes Aralieae (11 genera) and Mackinlayeae (three genera) (see Table 1). Hutchinson (1967) recognized seven tribes (Cussonieae, Anomopanaceae, Plerandreae, Aralieae, Mackinlayeae, Panaceae, and Hedereae), but his system was widely criticized by

later workers as "artificial" due to its heavy reliance on inflorescence characters (see Hoo and Tseng 1978; Frodin 1982; Tseng and Hoo 1982; Wen 1991, 1993; Wen et al. 1998). In fact, inflorescence structure may be variable within a single genus (e.g., *Aralia*, Wen 1991, 1993; *Schefflera*, Frodin 1982) or even within a single section (e.g., *Aralia* sect. *Aralia*, Wen et al. 1998). Tseng and Hoo (1982) proposed a system of five tribes: Aralieae, Panaceae, Plerandreae, Tetraplasandreae, and Mackinlayeae. Their system is largely a refinement of Harms' (1898) treatment with a greater emphasis on leaf architecture. They divided Harms' Aralieae into two tribes: Aralieae s. str., with leaves once to several-times pinnately compound, and Panaceae, with simple or palmately compound leaves. They also divided Harms' Schefflereae into Plerandreae (with simple or palmately compound leaves) and Tetraplasandreae (with pinnately compound leaves).

Although Araliaceae lack a modern systematic treatment, data are available from a wide range of taxonomic sources. Floristic studies have helped to enumerate the species of Araliaceae from many regions [e.g., China (Franchet 1896; Li 1942; Hoo and Tseng 1978; Shang 1985a), East Africa (Tennant 1968), Europe (Webb 1968; Stace 1993), Hawaii (Lowry 1986), Japan (Ohwi 1984), Korea (Lee 1993), Malesia (i.e., Indonesia, Malaysia, and the Philippines, Philipson 1979), New Zealand (Allan 1961), North America (Smith 1944), the former U.S.S.R. (Poyarkova 1973), and Vietnam (Ha 1974; Hô 1993)]. Further, revisionary treatments have been completed for several genera [e.g., *Aralia* (Wen 1991), *Delarbrea* (Lowry 1986), *Eleutherococcus* (Kim 1997), *Macropanax* (Shang 1983), and *Schefflera* (Frodin 1975, 1986, 1989; Shang 1984)], and phylogenetic analyses have also been performed for *Aralia* (Wen 1991; Tseng et al. 1993; Wen et al. 1996; Wen et al. 1998; Wen 1999b), *Eleutherococcus* (Kim 1997), *Hedera* (Vargas 1999), *Panax* (Wen and Zimmer 1996), and *Pseudopanax* (Mitchell and Wagstaff 1997). Cytological work has demonstrated that a basic chromosome number of $x = 12$ is highly conserved throughout the family, with diploid numbers mostly of $2n = 24$ or $2n = 48$ (Matsuura and Suto 1935; Sugiura 1936; Rattenbury 1957; Harn and Whang 1963; Graham 1966; Löve and Ritchie 1966; Sokolovskaya 1966; Wardle 1968; Stone and Loo 1969; Hara 1970; Guha 1971; Javurkova 1981; Yang 1981; Löve and Löve 1982; Beuzenberg and Hair 1983; Starodubtsev 1985; Sun et al. 1988); some taxa from *Hedera*, however, have a diploid number as high as $2n = 192$ (Stace 1993; Vargas

TABLE 1. The classification of Araliaceae according to Harms (1898). Modern synonymies are noted in parentheses ("=" denotes synonyms in general use; "cf." denotes synonyms used only in some treatments). Taxa currently excluded from core Araliaceae (sensu Plunkett et al. 1997) are marked with an asterisk (*).

Tribe Schefflereae	Tribe Aralieae	*Tribe Mackinlayeae
<i>Acanthopanax</i> Miq. (= <i>Eleutherococcus</i> Maxim.)	<i>Aralia</i> L.	* <i>Apiopetalum</i> Baill.
<i>Arthrophyllum</i> Blume	* <i>Aralidium</i> Miq.	* <i>Mackinlaya</i> F. Muell.
<i>Astrotricha</i> DC.	* <i>Delarbrea</i> Vieill.	* <i>Pseudosciadium</i> Baill.
<i>Boerlagiodendron</i> Harms (= <i>Osmoxylon</i>)	<i>Horsefieldia</i> (= <i>Harmsiopanax</i>)	
<i>Brassaiopsis</i> Decne. & Planch.	<i>Motherwellia</i> F. Muell.	
<i>Cheirodendron</i> Nutt. ex Seem.	* <i>Myodocarpus</i> Brongn. & Gris.	
<i>Crepinella</i> Marchal (cf. <i>Schefflera</i>)	<i>Panax</i> L.	
<i>Cussonia</i> Thunb.	<i>Pentapanax</i> Seem.	
<i>Didymopanax</i> Decne. & Planch. (cf. <i>Schefflera</i>)	* <i>Porospermum</i> F. Muell. (= <i>Delarbrea</i>)	
<i>Dizygotheca</i> N. E. Brown (cf. <i>Schefflera</i>)	<i>Sciadodendron</i> Griseb.	
<i>Echmiopanax</i> Decne. & Planch. (= <i>Oplopanax</i>)	* <i>Stilbocarpa</i> (Hook. f) Decne. & Planch.	
<i>Eremopanax</i> Baill. (= <i>Arthrophyllum</i>)		
<i>Fatsia</i> Decne. & Planch.		
<i>Gamblea</i> C. B. Clarke		
<i>Gastonia</i> Comm. ex Lam.		
<i>Hedera</i> L.		
<i>Hederopsis</i> C. B. Clarke (= <i>Macropanax</i>)		
<i>Heteropanax</i> Seem.		
<i>Kalopanax</i> Miq.		
<i>Kissodendron</i> Seem. (= <i>Polyscias</i>)		
<i>Macropanax</i> Miq.		
<i>Meryta</i> Forster & Forster f.		
<i>Nothopanax</i> Seem. (= <i>Polyscias</i>)		
<i>Oreopanax</i> Decne. & Planch.		
<i>Osmoxylon</i> Miq.		
<i>Plerandra</i> A. Gray		
<i>Polyscias</i> Forster & Forster f.		
<i>Pseudopanax</i> K. Koch		
<i>Pterotropia</i> Hillebrand		
<i>Reynoldsia</i> A. Gray		
<i>Schefflera</i> Forster & Forster f.		
<i>Sciadopanax</i> Seem. (= <i>Polyscias</i>)		
<i>Tetrapanax</i> (K. Koch) K. Koch		
<i>Tetraplasandra</i> A. Gray		
<i>Trevesia</i> Vis.		
<i>Tupidanthus</i> Hook. f. & Thoms (cf. <i>Schefflera</i>)		

1999). Pollen morphology (Erdtman 1966; Tseng 1971, 1973, 1974; Tseng and Shoup 1978; Tseng et al. 1983; Shoup and Tseng 1977; Shang and Callen 1988; Park and Lee 1989; Henwood 1991; Wen and Nowicke 1999) and wood anatomical features (Viguier 1906, 1909; Metcalfe and Chalk 1950; Rodriguez 1957; Oskolski 1994, 1995, 1996; Oskolski et al. 1997; Oskolski and Lowry 2000) have been examined from many araliad taxa, and secondary chemistry from a few genera has also been reported (e.g., Ng and Walker 1975; Zhou et al. 1975; Lutomski and Nham 1977; Hansen and Boll 1986). The embryology of a few taxa has been published (e.g.,

Ducamp 1902; Singh 1954) and the breeding systems have been documented for *Aralia* (Barrett and Helenurm 1981; Thomson and Barrett 1981; Barrett and Thomson 1982; Bawa et al. 1982; Flanagan and Moser 1985), *Panax* (Hara 1970; Schlessman 1985, 1987, 1990, 1991) and many New Caledonian taxa of the family (Schlessman et al. 1990a, b).

More recently, DNA sequencing studies based on the chloroplast genes *rbcl* and *matK* (Plunkett et al. 1996a, 1997) have provided important insights into the evolution and diversification of Araliaceae and its relationships with Apiaceae and other closely related families. These studies resolved a monophy-

letic group comprising most araliad genera (a clade referred to as "core Araliaceae"), but this core group appears to exclude *Delarbraea*, *Mackinlaya*, and their presumed close relatives (*Apiopetalum*, *Myodocarpus*, and *Pseudosciadium*). Because Plunkett et al. (1996a, 1997) focused on higher-level relationships throughout the order, the number of araliaceous taxa sampled was small, and the relatively conserved *rbcl* and *matK* sequences provided only limited resolution at the intergeneric level in core Araliaceae. Thus, no comprehensive study of relationships among and within the genera of Araliaceae is presently available. Furthermore, many studies over the past three decades have proposed the re-circumscription of araliad genera, but a unified concept of generic delimitation has not been employed. For example, the definitions of several large genera such as *Aralia* (Wen 1993), *Polyscias* (Philipson 1979; Lowry et al. 1989), *Pseudopanax* (Philipson 1965), and *Schefflera* (Frodin 1975; Lowry et al. 1989) have been broadened, and consequently many smaller genera have been taxonomically submerged. In contrast, other studies have segregated smaller genera out of larger ones, including *Chengiopanax* Shang & J. Y. Huang from *Eleutherococcus* (Shang and Huang 1993), *Evodiopanax* (Harms) Nakai from *Eleutherococcus* (Nakai 1924; Ohashi 1987b), *Metapanax* Frodin ex J. Wen & Frodin from *Nothopanax* Miq. (Wen and Frodin, in press), and *Raukava* Seem. from *Pseudopanax* (Mitchell et al. 1997). It is necessary, therefore, to re-evaluate generic concepts in Araliaceae using a phylogenetic framework.

To examine evolutionary relationships among the genera of core Araliaceae, we have analyzed ITS sequence data from representatives throughout the family. Phylogenetic analysis of the internal transcribed spacers of nuclear ribosomal DNA has been successfully applied to several intra- and intergeneric problems in Araliaceae (e.g., Wen and Zimmer 1996; Mitchell and Wagstaff 1997; Wen et al. 1998), and in the closely related family Apiaceae (e.g., Downie et al. 1998; Katz-Downie et al. 1999), as well as many other plant groups (see Baldwin et al. 1995 for a review). On the basis of ITS data from Araliaceae, we herein re-evaluate the traditional classification systems, test the generic limits of several key araliaceous genera, and examine biogeographic relationships within the family.

MATERIALS AND METHODS

Seventy-three ITS sequences, representing 43 genera, were analyzed for the present study (70 se-

quences representing taxa of Araliaceae and three outgroups, table 2). Of these, 45 sequences were newly-derived and the remaining 28 were previously published (marked with asterisks in Table 2, and obtained from GenBank). This sample includes representatives of most genera of core Araliaceae, as well as two or more species from large genera such as *Aralia*, *Dendropanax* Decne & Planchon, *Eletherococcus*, *Polyscias*, *Pseudopanax*, and *Schefflera*. Because Araliaceae have traditionally been allied to Apiaceae (Harms 1898; Thorne 1973, 1992; Cronquist 1981; Judd et al. 1994; Plunkett et al. 1996a, 1997), and because recent molecular data suggest a close relationship of Apiales to Pittosporaceae (e.g., Plunkett et al. 1996a, 1997; Xiang and Soltis 1998), *Daucus carota* and *Hydrocotyle vulgaris* of Apiaceae and *Pittosporum dallii* of Pittosporaceae were included as outgroup taxa.

Total DNAs were extracted using the CTAB method of Doyle and Doyle (1987). DNA amplifications followed the protocol of Wen and Zimmer (1996), and the sequencing strategy of the entire ITS regions (ITS1 and ITS2) and the 5.8S gene followed Wen et al. (1998) or Plunkett et al. (in press). After manually assembling the DNA sequences, the boundaries between the coding and spacer regions were determined by comparisons with the previously published ITS sequences of carrot (*Daucus carota*; Yokota et al. 1989). All newly-derived sequences have been deposited at GenBank (see Table 2 for accession numbers). Because most mutations were base substitutions, manual alignment was straightforward.

Phylogenetic analyses were performed with PAUP* (version 4.0, Swofford 1999) using maximum parsimony (Swofford et al. 1996), maximum likelihood (Felsenstein 1981), and neighbor-joining (Saitou and Nei 1987) methods in which alignment gaps were treated as missing data or as new characters. The maximum parsimony (MP) analysis was performed using a heuristic search with MULPARS and furthest-addition sequence options. Both Fitch and weighted parsimony analyses were employed. The latter weighted transversions over transitions 1.8 times based on the observed ratio. Decay values (Bremer 1988) were calculated by using a reverse constraint and comparing the length differences to the maximally parsimonious trees (MPTs). The amount of support for monophyletic groups revealed in the maximally parsimonious tree(s) (MPTs) was also examined with 1,000 bootstrap replicates (Felsenstein 1985) with 100 trees saved for each due to the large size of the data set. The

TABLE 2. Names, sources, and GenBank accession numbers of the 45 newly derived and 28 previously published (marked with “*”) ITS sequences from Araliaceae and three outgroup taxa. Herbarium acronym follows Holmgren et al. (1990).

Species	Voucher	Geographical origin	GenBank accession
Outgroup			
* <i>Daucus carota</i> L. (Apiaceae)			XI7534
* <i>Pittosporum dallii</i> Cheesem. (Pittosporaceae)	V. Gamble & N. W. Nelson s.n. (CHR 500673)	New Zealand	U63196
* <i>Hydrocotyle vulgaris</i> L. (Apiaceae)			AF077895
Araliaceae			
* <i>Aralia apiooides</i> Hand.-Mazz.	J. Wen 1149 (CS)	Yunnan, China	U66704
<i>Aralia chinensis</i> L.	J. Wen 1136 (CS)	Hainan, China	AF242256
* <i>Aralia hispida</i> Vent.	T. Philbrick s.n. (CS)	Connecticut, USA	U66925
<i>Aralia humilis</i> DC.	J. Wen 4974 (CS)	Arizona, USA	AF242230
* <i>Aralia racemosa</i> L.	J. Wen 1071 (A)	Kentucky, USA	U41675
* <i>Aralia scopulorum</i> Brandg.	J. Wen 565 (OS)	Baja California, Mexico	U66927
* <i>Aralia spinosa</i> L.	J. Wen & H. Dong 976 (A)	Decatur Co., GA	U66928
* <i>Athyrophyllum angustatum</i> (Baill.) Philipson	W. Lee s.n. (CHR 502518)	Riviere Bleue, New Caledonia	U63182
* <i>Astrotricha latifolia</i> Benth.	R. O. Makinson 592M (CHR 452093)	NSW, Australia	U63189
* <i>Astrotricha ledifolia</i> DC.	B.J. Lepshi 666 (CHR 484172)	NSW, Australia	U63190
<i>Brassia actinophylla</i> Endl.	J. Wen 2477 (CS)	Cult. in Botanical Garden, University of Tokyo	AF242245
<i>Brassiaopsis mitis</i> Clarke	J. Wen 2476 (CS)	Cult. in Botanical Garden, University of Tokyo	AF242234
			AF242235
<i>Cephalalaria cephalobotrys</i>	G.M. Plunkett 1519 (MO)	Queensland, Australia	AF229762
* <i>Cheirodendron trigynum</i> (Gaud.) A Heller	T.G. Lammers & R. Holody 5677 (CHR)	Maui, Hawaii	U63183
<i>Cuphocarpus aculeatus</i> Decne. & Planchon	P.P. Lavery 5013 (MO)	Madagascar	AF229737
<i>Gussonia spicata</i> Thunb.	G.M. Plunkett 1341 (WS)	Africa	AF229765
<i>Dendropanax hainanensis</i> (Merr. & Chun) Chun	S. Shi 002 (SYS)	Cult. in South China Bot. Gard.	AF242236
<i>Dendropanax proteus</i> (Champ.) Benth.	S. Shi 001 (SYS)	Cult. in South China Bot. Gard.	AF242237
<i>Dendropanax trifidus</i> (Thunb.) Makino	J. Wen 2461 (CS)	Cult. in Botanical Garden, University of Tokyo	AF242238
<i>Dizygotheca elegantissima</i> R. Viguier & Guillaumin	J. Wen 2488 (CS)	Cult. in Fort Collins, CO	AF242239
			AF242240
* <i>Eleutherococcus nodiflorus</i> (W. W. Sm.) S. Y. Hu	Plant 1976-6252	Royal Botanic Gardens, Kew	U63184
<i>Eleutherococcus sessiliflorus</i> (Rupr. & Maxim.) S. Y. Hu	J. Wen 3112 (CS)	Jilin, China	AF242252
<i>Eleutherococcus simonii</i> Schneid.	J. Wen 1150 (CS)	Yunnan, China	AF242227
<i>Euaraliopsis palmata</i> (Roxb.) Hutch	J. Wen 3092 (CS)	Sichuan, China	AF242250
			AF242251

TABLE 2. Continued.

Species	Voucher	Geographical origin	GenBank accession
<i>Erodiananax eodifolius</i> (Franch.) Nakai	J. Wen 3050 (CS)	Yunnan, China	AF242228
* <i>Fatsia japonica</i> (Thunb.) Decne & Planch.	A. Mitchell s.n. (CHR 502463)	Cultivated in Halswell, New Zealand	U63193
<i>Gamblea pseudoevodinaefolia</i>	P.P. Lowry 4856 (MO)	Vietnam	AF229766
<i>Gastonia rodriguesensis</i>	Acc#: 662-86.06150 (RBG Kew)	Rodrigues, Mauritius (cultivated at Kew)	AF229723
* <i>Hedera helix</i> L.	P.N. Johnson 670 (CHR)	Cult. in Otago, New Zealand	U63186
<i>Hedera helix</i> L.	J. Wen 2481 (CS)	Cult. in Fort Collins, CO	AF242241
<i>Heteropanax fragrans</i> (Roxb.) Seem.	J. Wen 2213 (CS)	Cult. in South Bot. Garden	AF242242
* <i>Kalopanax pictum</i> (Thunb.) Nakai	E. H. Wilson 1680	Cult. in RBG Kew, Acc# 1913-5202	U63187
<i>Macropanax dispersum</i> (Bl.) Ktze.	P.P. Lowry 4940 (MO)	Vietnam	AF229767
* <i>Meryta pauciflora</i> Hemsf. ex Cheesem.	W. Sykes 4655/CI (CHR)	Cook Islands	U63195
* <i>Meryta sinclairii</i> (Hook. f.) Seem.	A. Mitchell s.n. (CHR 500662)	Cult. Christchurch, New Zealand	U63194
<i>Metapanax davidii</i> (Franch.) Frodin ex J. Wen & Frodin	J. Wen 1409 (CS)	Hubei, China	AF242233
<i>Metapanax delavayi</i> (Franch.) Frodin ex J. Wen & Frodin	J. Wen 1217 (CS)	Yunnan, China	AF242232
<i>Munroidendron racemosum</i> (C.N. Forbes) Sherff	G.M. Plunkett 1342 (WS)	Cult. in MoBG 850020	AF229738
<i>Oplopanax japonicum</i> (Nakai) Nakai	J. Wen 517 (CS)	Cult. Nikko Botanical Garden	AF242248
<i>Oreopanax echinops</i> (Schlecht.) Decne.	F. Chiang 1278 (CS)	Cult. in Mexico City, Mexico	AF242249
<i>Osmoxylon geotinkianum</i> Becc.	G.M. Plunkett 1489 (MO)	Cult. Christchurch, New Zealand	AF242229
<i>Osmoxylon novo-guinaensis</i> (Scheff.) Becc.	Acc#: 810791002	New Guinea	AF229727
* <i>Panax ginseng</i> C.A. Meyer	J. Wen 1250 (CS)	(Nat'l Tropical Botanical Garden) New Guinea	AF229726
* <i>Panax trifolium</i> L.	D. Kramer s.n. (CS)	Heilongjiang, China	U41680
<i>Pentapanax racemosum</i> Seem.	Sino-Amer. Bot. Exp. 125 (US)	Mansfield, OH	AF242253
<i>Pentapanax plumosum</i> (L.) Shang	J. Wen 3017 (CS)	Yunnan, China	AF242254
<i>Polyscias australiana</i> (F. v.M.) Philipson	G.M. Plunkett 1500 (MO)	Yunnan, CHINA	AF242255
* <i>Polyscias fruticosa</i> Harms	Acc#: 1547/86	Queensland, Australia	AF229688
<i>Polyscias guilfoylei</i> (Bull.) L. H. Bailey	J. Wen 68 (CS)	Christchurch Botanical Gardens, New Zealand	U63191
<i>Polyscias lecardii</i> (R. Viguier) Lowry	P.P. Lowry 4754 (MO)	Cult. in Fort Collins, Co	AF242246
<i>Polyscias mollis</i> (Benth.) Harms	G.M. Plunkett 1507 (MO)	New Caledonia	AF229701
<i>Polyscias sessiliflora</i>	P.P. Lowry 4981 (MO)	Queensland, Australia	AF229705
* <i>Pseudopanax arboreus</i> (Murr.) Philipson	A. Mitchell s.n. (CHR 500663)	New Caledonia	AF229717
* <i>Pseudopanax chathamicum</i> Kirk	B. Molloy s.n. (CHR 500669)	Cult. in Lincoln, New Zealand	U63165
* <i>Pseudopanax lessonii</i> (DC.) C. Koch	A. Mitchell s.n. (CHR 502421)	Chatham Islands	U63166
* <i>Pseudopanax linearis</i> (Hook. f.) C. Koch	P. Heenan s.n. (CHR 500668)	Christchurch Botanical Garden native section Arthurs Pass, New Zealand	U63177 U63178

TABLE 2. Continued.

Species	Voucher	Geographical origin	GenBank accession
* <i>Raukaua anomala</i> (Hook.) A.D. Mitchell,	Acc# 18225 (CHR 500664)	Peel Forest Nursery, New Zealand	U63164
D. Frodin & M. Heads			
<i>Reynoldsia sandwicensis</i> A. Gray	G.M. Plunkett 1359 (WS)	Hawaii	AF229739
<i>Schefflera arboricola</i> Hayata	J. Wen 2478 (CS)	Cult. in Botanical Garden, Univ. Tokyo, Japan	AF242243
<i>Schefflera candellabra</i> Baillon	P.P. Lowry 4726 (MO)	New Caledonia	AF229728
<i>Schefflera digitata</i> J. R. & J. G. Forst.	A. Mitchell s.n. (CHR 485642)	Cult. in Lincoln, New Zealand	U63188
<i>Schefflera gabriellae</i> Baillon	P. P. Lowry 4648 (MO)	New Caledonia	AF229731
<i>Schefflera hypoleucoides</i> Harms	P. P. Lowry 4920 (MO)	Vietnam	AF229732
<i>Schefflera minutistellata</i> Merrill ex Li	S. Shi 11 (SYS)	Cult. South China Bot. Garden	AF242244
<i>Sciadoendron excelsum</i> Griseb.	F. Chiang s.n. (CS)	Mexico	AF242231
<i>Sinopanax formosana</i> (Hayata) Li	P.P. Lowry 4967 (MO)	Taiwan	AF229768
* <i>Tetrapanax papyriferus</i> (Hook.) K. Koch	A. Mitchell s.n. (CHR 502422)	Cult. in Halswell, New Zealand	U63192
<i>Tetraplasandra huaitiensis</i> A. Gray	G.M. Plunkett 1378 (WS)	Hawaii	AF229740
<i>Trevesia palmata</i> Vis.	G. Hao 901 (CS)	Cult. in South China Bot. Garden	AF242247
<i>Tupidanthus calypttratus</i> J.D. Hook. & Thomson	G.M. Plunkett 1315 (WS)	Cultivated at MO	AF229769

maximum likelihood (ML) analysis was performed with the input order of sequences randomized and the transition/transversion ratio set at 1.8. A neighbor-joining (NJ) tree was constructed using the Kimura two-parameter distance (Kimura 1980).

RESULTS

Characteristics of ITS Sequences of Araliaceae.

The combined length of the entire ITS region (ITS1, 5.8S, and ITS2) from taxa sampled throughout Araliaceae ranged from 600 to 612 bp. The ITS1 region was 218–224 bp in length, the 5.8S gene was 164–166 bp, and the ITS2 region was 215–224 bp. Thirty-two insertions or deletions (indels) were necessary to align the 72 sequences. Of these, 21 indels were located in the ITS1 region, two in the 5.8S gene, and nine in the ITS2 region. The indels ranged in length from 1 to 8 bp, but most were only 1–2 bp long and represented autapomorphies. The single 8-bp indel was a synapomorphic deletion detected in the ITS2 region of the two species of *Osmaxylon* Miq. Little length variation was observed in the 5.8S region, which was 164 bp long in 68 of the 73 sequences. Alignment of the sequences yielded a data matrix of 720 total characters, of which 248 were potentially parsimony informative. Treating gaps as missing data, the Kimura two-parameter distances ranged from 0.663–20.724% among the genera. The highest divergence was between *Gastonia rodriguensis* and *Pentapanax racemosus*; the lowest value was between *Eleutherococcus simonii* and *Kalopanax pictus*. In general, *Gastonia* was the most divergent of all taxa in Araliaceae, with distances ranging from 10.143 to 20.724%.

Phylogenetic Analyses. The parsimony analysis of the entire ITS region resulted in 14,580 maximally parsimonious trees (MPTs) with a total length of 1,267 steps, a consistency index (CI) of 0.487 (0.416 excluding uninformative characters), and a retention index (RI) of 0.599. The strict consensus of the MPTs is presented in Fig. 1. A parsimony analysis in which the alignment gaps were coded as additional binary characters generated over 10,000 MPTs with a total length of 1337 steps, a CI of 0.487 (0.413 excluding uninformative characters), and a RI of 0.594. Analyses in which gaps were treated either as missing data or as new characters generated very similar topologies, but the latter helped to resolve the positions of both *Fatsia* (sister to the clade of *Dendropanax-Hedera-Brassaiopsis-Oreopanax-Gamblea* and allies) and *Tetrapanax* (sister to the clade of *Heteropanax-Schefflera* and

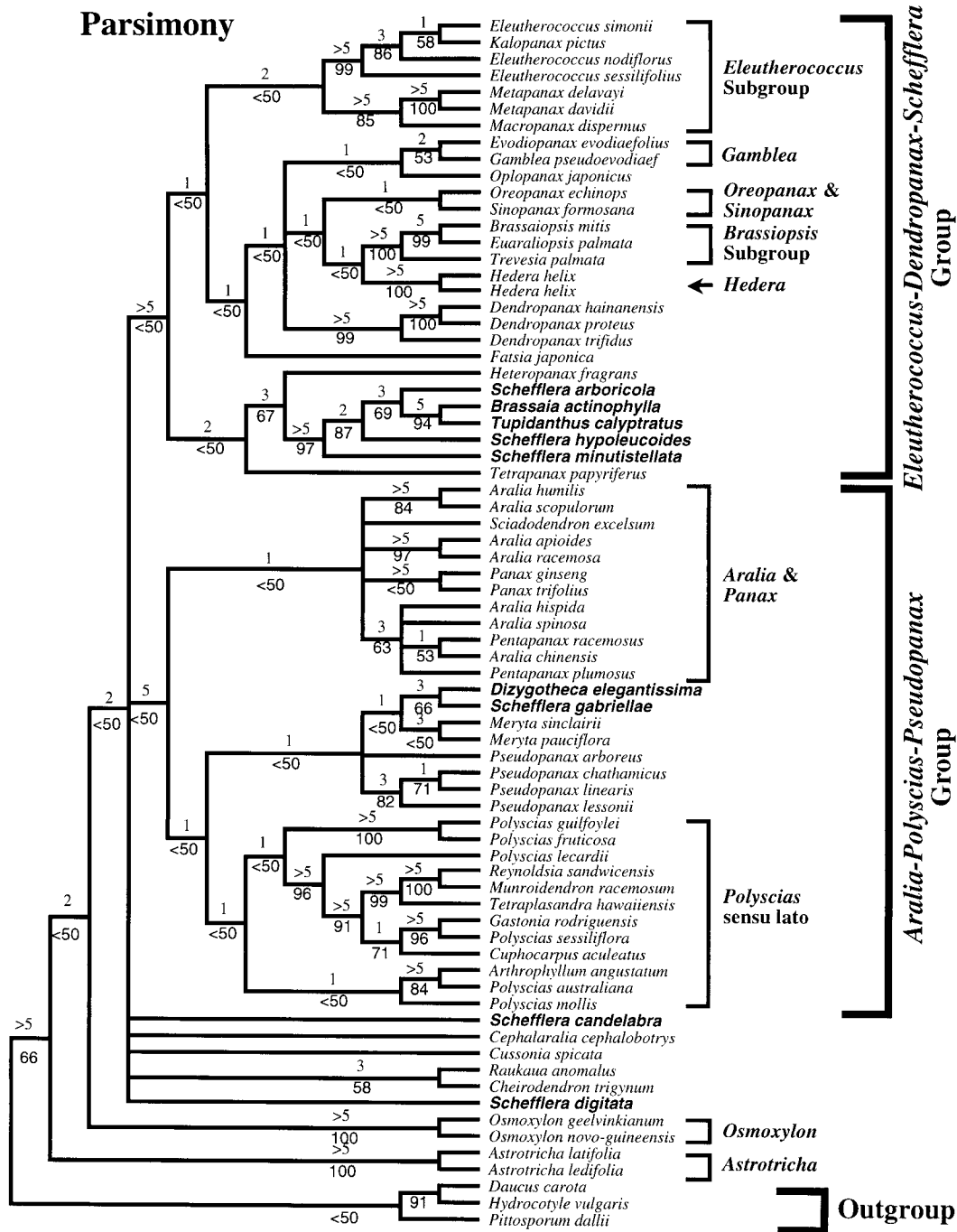


FIG. 1. The strict consensus tree of 14,580 maximally parsimonious trees (MPTs) of the core Araliaceae with the entire ITS sequences. The MPTs have 1267 steps, a CI of 0.487 (0.416 excluding uninformative characters), and a RI of 0.599. Taxa included in the broadly defined *Schefflera* are boldfaced. Numbers above lines are the decay indices and those below are bootstrap values in 1000 replicates, each with 100 trees.

close allies). In addition, the placement of the *Polyscias guilfoylei*—*P. fruticosa* clade differs between the two analyses. This clade is sister to the clade comprising *Polyscias*, *Gastonia*, *Reynoldsia* A. Gray and close allies when gaps were treated as missing data, but in the tree in which gaps were treated as additional characters, the *P. guilfoylei*—*P. fruticosa* clade is sister to a larger clade comprising not only *Polyscias*, *Gastonia*, and *Reynoldsia*, but also *Pseudopanax*, *Meryta* and their close allies. Lastly, a weighted parsimony analysis (weighting transversions over transitions 1.8 times based on actual estimates) for the entire data set generated over 10,000 MPTs with a total length of 1267 steps, a CI of 0.487 and a RI of 0.599. The topology of this analysis is very similar to that in which gaps were treated as new characters, differing only in the relative position of the *P. guilfoylei*—*P. fruticosa* clade.

Trees resulting from the neighbor-joining analysis (Fig. 2) and the maximum likelihood analysis (log likelihood of -7971.08 ; Fig. 3) were largely congruent with the MPTs. There were, however, several notable differences, including the relative positions of *Osmoxylon* and *Astrotricha*, and the positions of *Fatsia japonica*, *Oplopanax japonicus*, *Schefflera candelabra*, *S. digitata*, and *Tetrapanax papyriferus* (cf. Figs. 1–3).

All trees resulting from the analysis of ITS sequences resolve two major clades, labeled the "Aralia-Polyscias-Pseudopanax group," and the "Eleutherococcus-Dendropanax-Schefflera group." The Aralia-Polyscias-Pseudopanax group includes *Aralia*, *Arthropphyllum* Blume, *Cuphocarpus* Decne & Planchon, *Gastonia*, *Meryta*, *Munroidendron* Sherff, *Panax*, *Pentapanax*, *Polyscias*, *Pseudopanax*, *Reynoldsia*, *Sciadodendron*, and *Tetraplasandra*. The Eleutherococcus-Dendropanax-Schefflera group includes *Brassaiopsis* Decne & Planchon, *Dendropanax*, *Eleutherococcus*, *Fatsia*, *Gamblea* C. B. Clarke, *Hedera*, *Heteropanax*, *Kalopanax*, *Macropanax*, *Metapanax*, *Oplopanax*, *Oreopanax*, *Schefflera*, *Sinopanax* H. L. Li, *Trevesia*, and *Tupidanthus*. The Aralia-Polyscias-Pseudopanax group may be further divided into two subclades: a mostly north temperate *Aralia-Panax* clade and the more or less tropical/subtropical *Polyscias-Pseudopanax* clade (although many *Pseudopanax* have a south-temperate to subtropical distribution). Excluded from both major clades, however, were a small number of taxa, including *Schefflera digitata*, *S. candelabra*, *Cussonia spicata*, the *Raukaua anomalus*—*Cheirodendron trigynum* clade, and *Cephalalaria cephalobotrys*. Relative to the major clades, these excluded species form either a polytomy or a basal grade. In all trees,

Astrotricha and *Osmoxylon* form successive sister groups to all other species in core Araliaceae, but the precise placement of these two genera at the base of Araliaceae differs among the MP, NJ, and ML trees (see Figs. 1–3).

DISCUSSION

Phylogenetic Relationships in Araliaceae. The most widely used classification of Araliaceae is that of Harms (1898; see Table 1), who divided Araliaceae into three tribes (Schefflereae, Aralieae, and Mackinlayeae) mostly on the basis of petal morphology and aestivation. Our sample included 27 of the 36 genera from Harms' tribe Schefflereae. Of the nine genera not sampled, eight have been transferred to larger genera [viz., *Boerlagiodendron* to *Osmoxylon* (Philipson 1976; Lowry 1989); *Crepinella* to *Schefflera* (Frodin 1975; Maguire et al. 1984), *Didymopanax* Decne & Planchon to *Schefflera* (Maguire et al. 1984; Frodin 1989); *Eremopanax* Baillon to *Arthropphyllum* (Philipson 1978a); *Hederopsis* to *Macropanax* (Philipson 1979); *Kissodendron*, *Nothopanax*, and *Sciadopanax* to *Polyscias* (Bernardi 1971; Philipson 1978b, 1979; Lowry 1989; see Table 1]. Apart from these, our sample lacked only *Plerandra*. In the trees based on ITS data, Schefflereae appears to be paraphyletic with regard to the four taxa sampled from tribe Aralieae.

Within tribe Aralieae, we sampled four of the 11 genera included by Harms (1898): *Aralia*, *Panax*, *Pentapanax*, and *Sciadodendron*. It is clear, however, that Harms' concept of tribe Aralieae was quite heterogeneous, for all but two (*Motherwellia* and *Harmsiopanax* Warb.) of the seven unsampled genera have now been excluded from core Araliaceae. For example, recent molecular data suggest that the largely New Caledonian genera *Delarbrea* and *Myodocarpus* (along with the New Caledonian endemic *Pseudosciadium*) form a clade within the order Apiales, but outside core Araliaceae (Plunkett et al. 1996a, 1997, and unpublished). *Stilbocarpa* presents a similar situation. This genus of three megaherb species is endemic to the subantarctic islands of New Zealand (Philipson 1965). Hooker (1853) originally referred these species to *Aralia*, and Harms (1898) placed *Stilbocarpa* in tribe Aralieae. A recent study based on ITS sequences, however, suggests that this genus is more closely related to *Schizeilema* (Hook. f.) Domin. and *Azorella* Lam. of Apiaceae (subfamily Hydrocotyloideae) than to any of the araliaceous genera (Mitchell et al. 1999). Lastly, *Aralidium* has been excluded from the order Apiales al-

Neighbor Joining

0.01 changes
 — Araliaceae
 --- Outgroups

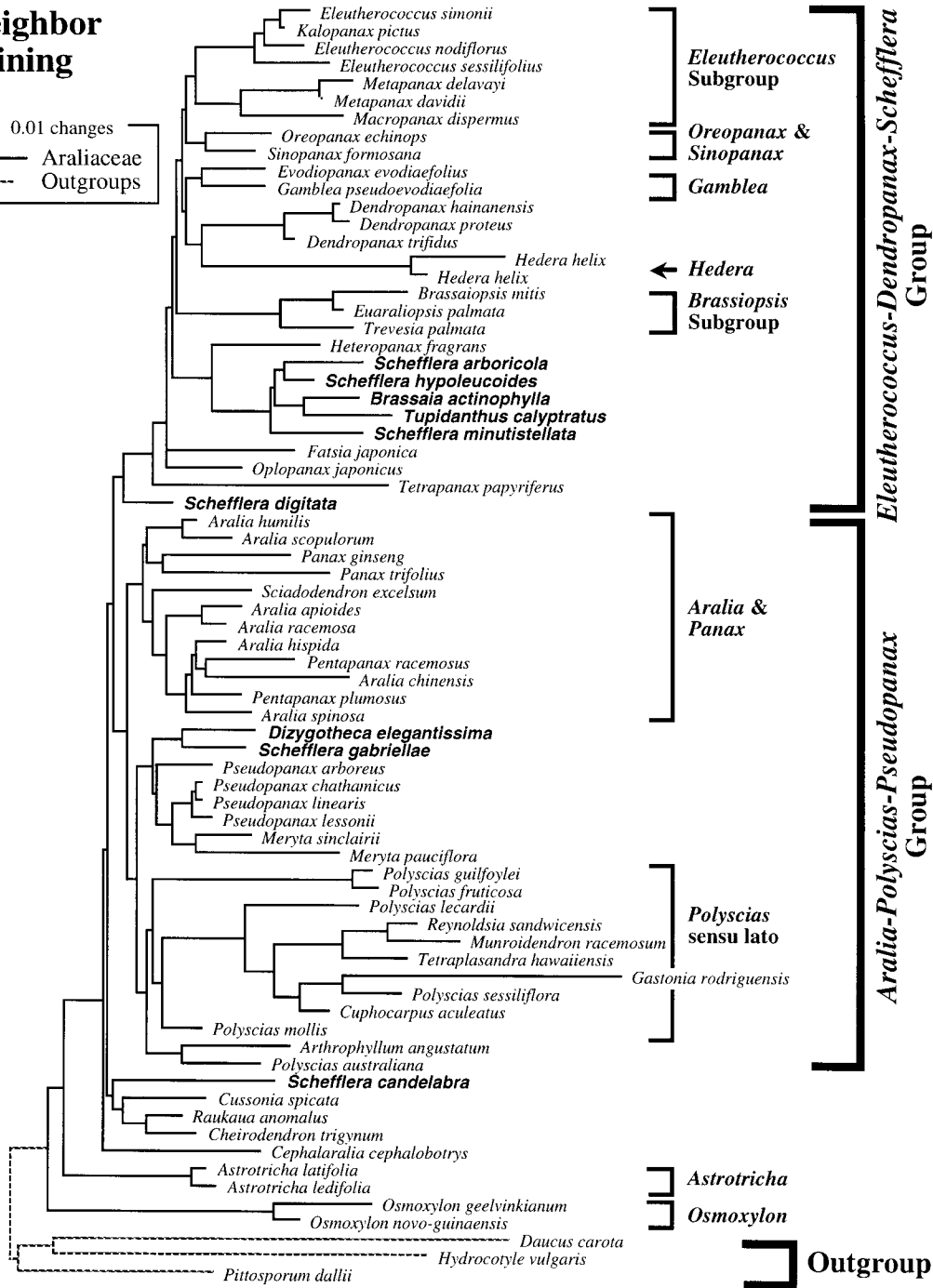


FIG. 2. The neighbor-joining tree of the core Araliaceae based on Kimura two-parameter distances.

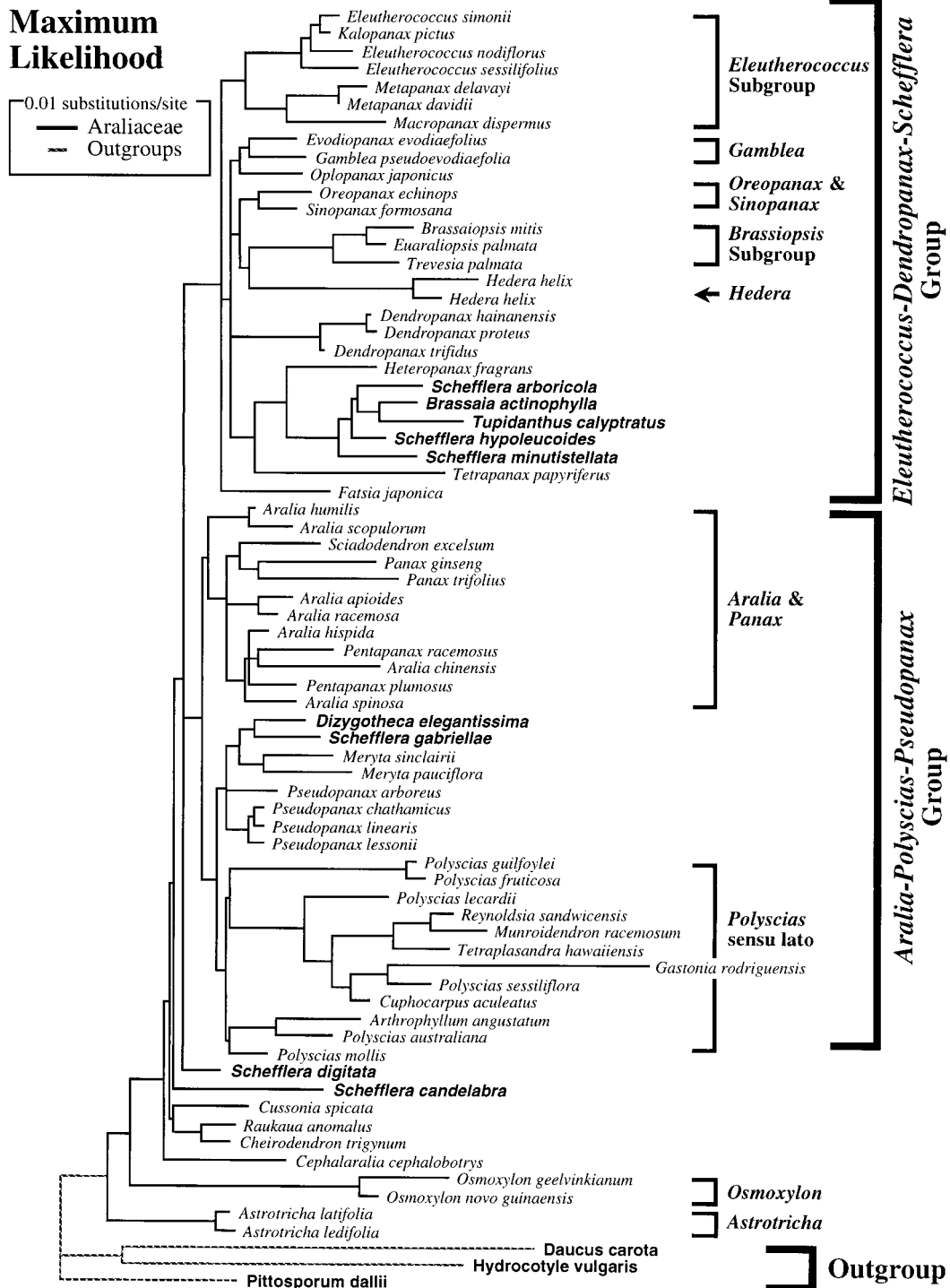


FIG. 3. The maximum likelihood tree of the core Araliaceae constructed from the entire ITS sequences with a log likelihood of -7971.08. The numbers indicate branch length.

together. This monotypic genus from western Malasia is now recognized as its own family, Aralidiaceae (Philipson and Stone 1980), or even its own order, Aralidiales (Takhtajan 1987). Recent studies based on *rbcl* data (Plunkett et al. 1996a; Xiang and Soltis 1998) suggest that *Aralidium* is allied to *Toricellia* DC., *Melanophylla* Baker, and *Griselinia* Forster & Forster f., which are the sister groups to the Apiales-Pittosporaceae clade. Apart from these excluded taxa, all of the genera sampled from tribe Aralieae in the present study form a monophyletic group (Figs. 1–3).

Lastly, tribe Mackinlayeae comprises just three genera: *Apiopetalum* (2 spp. from New Caledonia), *Mackinlaya* (5 spp. from east Malasia and the western Pacific), and *Pseudosciadium* (1 sp. from New Caledonia). All three, however, have been excluded from core Araliaceae on the basis of molecular data (Plunkett et al. 1996a, 1997, and unpublished). Because the focus of the present study is only the core group of Araliaceae, these excluded genera were not sampled herein; their placement within the order Apiales will be addressed in a subsequent study.

Emphasizing the inflorescence architecture and a few other characters including number of stamens, petal aestivation and shape, and endosperm morphology, Hutchinson (1967) recognized seven tribes in Araliaceae. This classification has been criticized by later Araliaceae workers such as Hoo and Tseng (1978), Frodin (1982), Tseng and Hoo (1982), Wen (1993), and Wen and Zimmer (1996) as being artificial, especially on the use of inflorescence structure as a delimiting character at the tribal level. Hutchinson (1967) treated all taxa with racemose or spicate inflorescence in his tribe Cussonieae, which consists of *Agalma* Miq. (= *Schefflera*), *Botryopanax* Miq. (= *Polyscias*), *Cussonia*, *Gelibia* Hutch. (= *Polyscias*), *Munroidendron*, and *Parapentapanax* Hutch. (= *Pentapanax*). The ITS phylogeny clearly suggests that taxa of tribe Cussonieae form a polyphyletic group (Figs. 1–3).

Phylogeny and Taxonomic Status of Araliad Genera. THE POLYPHYLY OF SCHEFFLERA. The largest genus in core Araliaceae is *Schefflera*, and recent taxonomic treatments of the genus (Frodin 1975, 1986, 1989; Maguire et al. 1984; Lowry et al. 1989) have placed several other genera (e.g., *Brassaia* Endl., *Didymopanax*, *Dizygotheca*, *Sciadophyllum* P. Br., and *Tupidanthus*) under its synonymy. Typified by *S. digitata* (from New Zealand; see Frodin 1975), *Schefflera* is presently defined as all araliads with (1) once palmately compound leaves; (2) fused stip-

ules extending into an appendage at the base of the petiole; (3) panicles that have ultimate inflorescences of umbels, capitula, racemules, or spicules; (4) the absence of pedicel articulations; (5) ovaries with 2–5 (or sometimes more) locules; and (6) no prickles or arms on the vegetative organs (Frodin 1975, 1986, 1989). *Schefflera* now includes ~650 species of tropical and warm temperate trees, shrubs, lianas and epiphytes. Harms (1898) originally divided *Schefflera* into two sections: sect. *Cephaloschefflera* Harms (species with sessile flowers) and sect. *Euschefflera* (= sect. *Schefflera*; species with pedicellate flowers), but various other classifications of the genus have also been proposed (e.g., Viguier 1909; Hoo and Tseng 1965, 1978; Shang 1984).

In addition to the six species listed as *Schefflera* in Table 2 (and Figs. 1–3), our sample also included representatives of three additional genera often placed under synonymy with *Schefflera* (viz., *Brassaia*, *Dizygotheca*, and *Tupidanthus*; see Lowry et al. 1989). Even on the basis of this limited sampling, ITS data suggest that *Schefflera* is polyphyletic. The position of the type species, *Schefflera digitata*, is not well resolved in the MPTs, but it forms one of five clades in an unresolved polytomy toward the base of the core Araliaceae clade (Fig. 1). In the NJ tree, *Schefflera candelabra* is placed in a subclade with *Cussonia*, *Raukava*, and *Cheirodendron*, whereas *Schefflera gabriellae* and *Dizygotheca elegantissima* form a small clade with species of *Mertya* and *Pseudopanax*. Lastly, *Schefflera arboricola*, *S. minutistellata*, *S. hypoleucoides*, *Brassaia actinophylla*, and *Tupidanthus calyptratus* form a subclade within the larger *Eleutherococcus-Dendropanax-Schefflera* clade. These results confirm that segregate genera such as *Tupidanthus* and *Brassaia* are closely related to various species presently assigned to *Schefflera*, but this broadly-defined genus appears to comprise no fewer than four different and well-separated evolutionary lineages in core Araliaceae, a result that is congruent with the polymorphic pollen morphology of this genus (Tseng and Shoup 1978). The circumscription of *Schefflera* should be re-evaluated using a phylogenetic framework with both molecular and morphological characters.

THE PLACEMENT OF HETEROPANAX. The genus *Heteropanax* comprises approximately five species from southern Asia and China, and is characterized by bicarpellate ovaries, divided styles, and leaves that are 2–5 times pinnately compound. The phylogenetic position of this genus has, however, been controversial. Seemann (1868) placed it alongside *Brassaiopsis*, *Cussonia*, *Macropanax*, *Sciadopanax* (=

Polyscias), and *Sphaerodendron* Seem. (= *Cussonia*) in his tribe Cussonieae because these taxa all share bicarpellate ovaries, runcate albumen, and an equal number of stamens and petals. Harms (1898) assigned *Heteropanax* to his broadly defined tribe Schefflereae, regarding it as a close relative of *Cussonia* and *Schefflera*. Hutchinson (1967), however, treated it in his tribe Hedereae along with the following genera: *Arthrophyllum*, *Boninofatsia* Nakai (= *Fatsia*), *Brassaiopsis*, *Euaraliopsis* Hutch., *Gamblea*, *Hedera*, *Hederopsis* (= *Macropanax*), *Macropanax*, *Neocussonia* Hutch. (= *Schefflera*), *Oreopanax*, and *Wardenia* King (= *Brassaiopsis*), on the basis of stamen number (equal to petal number), petals characters (unclawed, with valvate aestivation), inflorescence structure (simple or compound umbels or heads, often paniculately or racemosely arranged), and runcate endosperm. Hoo and Tseng (1978) treated *Heteropanax* in their tribe Tetraplasandreae along with many other araliaceous genera with pinnately compound leaves (such as *Polyscias*). More recently, Shang and Callen (1988) proposed a close relationship of *Heteropanax* to *Aralia* and *Panax*. In the ITS trees (Figs. 1–3), *Heteropanax* is sister to one of the *Schefflera* subclades (viz., *S. arborica*, *S. hypoleucoides*, *S. minutistellata*, *Brassaia actinophylla*, and *Tupidanthus calyptratus*) within the *Eleutherococcus-Hedera-Schefflera* group, and is well separated from *Polyscias* and the other genera of Hoo and Tseng's tribe Tetraplasandreae (which are all placed in the *Aralia-Polyscias-Pseudopanax* clade in the ITS trees). The disparity between the morphological characters of *Heteropanax* and those of the *Schefflera* subclade suggests that additional work is needed to address relationships among these taxa.

THE PARAPHYLY OF POLYSCIAS. In Araliaceae, *Polyscias* is second only to *Schefflera* in number of species, with ~130 species mostly from the paleotropics. *Polyscias* was broadly defined by Philipson (1978b, 1979) as comprising those araliads with pinnately compound leaves and articulated pedicels. Treating the Malesian species, Philipson (1978b, 1979) divided the genus into five sections based on morphology of stipules and inflorescences. The present study included ITS sequences from six species of *Polyscias*, but even with this limited sampling, the ITS trees do not support a broad circumscription of this genus. Instead, *Polyscias* appears to form a paraphyletic group within the *Aralia-Polyscias-Pseudopanax* clade. No fewer than six other genera (viz., *Arthrophyllum*, *Cuphocarpus*, *Gastonia*, *Munroidendron*, *Reynoldsia*, and *Tetraplasandra*)

would have to be submerged within *Polyscias* to render it monophyletic.

Within this very broad *Polyscias* clade, *Reynoldsia*, *Munroidendron*, *Tetraplasandra*, *Gastonia*, *Polyscias sessilifolia*, and *Cuphocarpus* form a well supported subclade. Morphological and geographic evidence have been used to suggest a close relationship among *Gastonia*, *Munroidendron*, *Reynoldsia*, and *Tetraplasandra*, a subject discussed in depth by Philipson (1970b), who also noted a close alliance of this complex to *Polyscias*. ITS data confirm a close relationship among all these taxa, and a more detailed treatment of this finding will be addressed in a subsequent publication (G. M. Plunkett and P. P. Lowry, unpublished).

THE POSSIBLE RELATIONSHIP OF SINOPANAX TO OREOPANAX. A sister-group relationship between the monotypic *Sinopanax* and the much larger genus *Oreopanax* (~80 species) is suggested by all three analyses of ITS sequence data (MP, NJ, and ML; see Figs. 1–3). *Sinopanax formosana* is endemic to Taiwan and was originally described by Hayata (1908) as *Oreopanax formosana*. Li (1949) segregated this species to establish a monotypic genus on the basis of its capitate inflorescences. With *Sinopanax formosana* excluded, the remaining ~80 species of *Oreopanax* are found only in Central and South America (although fossil evidence suggests that *Oreopanax* was also once distributed in North America; Dilcher and Dolph 1970). Both genera share palmately-lobed simple leaves, large terminal panicles of small capitate inflorescences, bilocular ovaries, and runcate endosperm. Additional data are needed to explore the disjunct biogeographic relationship between the Asiatic *Sinopanax* and the neotropical *Oreopanax*, and to assess the taxonomic status of these two genera.

THE PROBLEM OF PANAX AND ITS RELATIONSHIP TO ARALIA. The problem of circumscribing the genus *Panax* has resulted in great confusion regarding its phylogenetic position within the family. First described by Linnaeus (1735) in his *Systema Naturae*, *Panax* initially included just two species, *P. quinquefolius* L. and *P. trifolius* (Linnaeus 1753); shortly thereafter, *P. fruticosus* L. was added (Linnaeus 1763). However, Linnaeus' (1754) concept of *Panax* (based mostly on floral morphology) was so broadly defined that it would include most species currently placed in Araliaceae. Consequently, later workers (e.g., de Candolle 1830) referred many additional species to this genus, leading Seemann (1868: 52) to regard *Panax* as "one of the great lumber-rooms of our science." Seemann (1868) thus

narrowed the delimitation of *Panax* to include only the species closely related to *P. quinquefolius* and *P. trifolius*. Harms (1897), discussing the morphology and taxonomic history of *Panax*, followed Seemann's generic concept, and Britton and Brown (1913) designated *Panax quinquefolius* as the type species.

In several systems, such as those by Decaisne and Planchon (1854), Bentham and Hooker (1867), and Clarke (1879), *Panax* (as typified by *P. quinquefolius*) has been submerged within *Aralia*. Confusingly, Bentham and Hooker (1867) placed the ginsengs (e.g., *Panax quinquefolius*) in *Aralia*, but recognized a quite distinct genus "*Panax*" that included species currently fitting the generic concept of *Polyscias* (with a woody habit and valvate aestivation). Bentham and Hooker thus treated *Aralia* (with imbricate petals) and their "*Panax*" in different tribes. Hutchinson (1967) also treated them in different tribes, but to add to the confusion, his "*Panax*" included both the herbaceous ginsengs (true *Panax* as typified by *P. quinquefolius*) and the woody species that are now placed in *Polyscias* (Philipson 1951).

Harms (1897) and Hoo (1961) regarded *Panax* as derivatives of an herbaceous *Aralia*. Hoo (1961) also suggested that *Panax* may have been derived from *Acanthopanax* (= *Eleutherococcus*). Wen (1993), Wen and Zimmer (1996), Wen and Nowicke (1999) have argued on the basis of morphological, molecular, and pollen-ultrastructural data that the closest relative of *Panax* may be *Aralia*, a finding supported by the present ITS analysis (albeit weakly; decay value = 1) (Figs. 1–3). Indeed, the only major difference between the two genera lies in their leaf architecture (palmately compound in *Panax* vs. bi- or tripinnately compound in *Aralia*) and carpel number (2–3 in *Panax* vs. 5–8 in *Aralia*), but Wen (1993) regarded these characters as evolutionarily labile in Araliaceae (e.g., 4–5-locular ovaries are not uncommon in *Panax* as developmental abnormalities; J. Wen, pers. obs.). In contrast, *Panax* and *Aralia* share many features, including imbricate floral aestivation, uniform endosperm, and similar pollen morphology and ultrastructure. Eyde and Tseng's (1971) study of floral vasculature and the combined *rbcl-matK* study of Plunkett et al. (1997) provide further evidence of a close relationship between these two genera.

THE RELATIONSHIP BETWEEN MACROPANAX AND METAPANAX. *Metapanax* is a newly-established genus of two species (*M. davidii* and *M. delavayi*) from China and Vietnam (Frodin 1992; Wen and Frodin, in press). The Chinese species of *Metapanax* were previously included in *Nothopanax* (Hoo and Tseng

1978; Shang 1985a), a genus now submerged within *Polyscias* (Lowry et al. 1989). Philipson (1965) included these Chinese species of "*Nothopanax*" (i.e., *Metapanax*) within *Pseudopanax*, but Hoo and Tseng (1978) suggested a close relationship to *Merrillio-panax* H. L. Li. In our sample, we were able to sample both species of *Metapanax* and several species each of *Pseudopanax* and *Polyscias*, but unfortunately no representatives of *Merrillio-panax* could be included. Given this sampling limitation, the resulting ITS trees suggest that the two species *Metapanax* are most closely related to *Macropanax* (Figs. 1–3), and not to either *Pseudopanax* or *Polyscias*.

This result is well supported by morphological evidence. The two species of *Metapanax* are clearly differentiated from both *Pseudopanax* and *Nothopanax/Polyscias*. *Metapanax* differs from *Pseudopanax* in inflorescence architecture and breeding systems (Mitchell et al. 1997; Wen and Frodin, in press). The species of *Metapanax* are hermaphrodite with terminal umbels arranged racemously, whereas the species of *Pseudopanax* are dioecious and have terminal umbels arranged in umbellate clusters. The two genera are also distinct geographically: *Metapanax* occurs in central and southwestern China and Vietnam, whereas *Pseudopanax* is native to New Zealand, Tasmania, New Caledonia, and Chile. Although the definition of *Polyscias* (including *Nothopanax*) remains poorly-defined at present, *Metapanax* is easily distinguishable from most species of *Polyscias* on the basis of leaf architecture (simple or palmately compound in *Metapanax*, vs. pinnately compound in *Polyscias*, Stone 1965). Lastly, the relationship between *Metapanax* and *Macropanax* suggested by the ITS trees is supported by the shared presence of evergreen leaves, mostly dentate leaflet margin, paniculately arranged umbel inflorescence, hermaphrodite flowers, and a 5-carpellate ovary. The two genera can, however, be distinguished by their different endosperm types (uniform in *Metapanax*, ruminant in *Macropanax*), the division of styles (divided in *Metapanax*, undivided in *Macropanax*), and fruit shape (somewhat flattened in *Metapanax*, globose to subglobose in *Macropanax*) (Shang 1985b).

THE BRASSAIOPSIS—EUARALIOPSIS—TREVESIA SUBCLADE. Species now placed in *Euaraliopsis* were originally included in *Brassaiopsis* Decne & Planchon. Hutchinson (1967), however, established *Euaraliopsis* to accommodate those taxa with simple, lobed leaves; the remaining species of *Brassaiopsis* all have palmately-compound leaves. The two genera do, however, share many characteristics, including un-

jointed pedicels, bilocular ovaries, undivided stigmas, and ruminant endosperm. Hoo and Tseng (1978) accepted the generic status of *Euaraliopsis*, but other workers (e.g., Philipson 1979; Shang 1985c; Hô 1993) treated it under the synonymy of *Brassaiopsis*. Hoo and Tseng (1978) suggested that *Euaraliopsis* may be closely related to *Trevesia* because the leaf lobes of both genera sometimes have pseudopetiolules (see Hoo and Tseng 1978, pl. 1, f. 7), and that *Brassaiopsis* was perhaps related to or a derivative of *Schefflera*. Tseng and Hoo (1982) suggested that *Trevesia*, with its 5-locular ovary, was more "primitive" than *Euaraliopsis*. Philipson (1979) argued that dividing *Brassaiopsis* into two genera: *Brassaiopsis* s. str. and *Euaraliopsis* fragmented a coherent assemblage. Philipson (1979) also suggested a possible close relationship between *Brassaiopsis* s.l. and *Trevesia* based on their similar vegetative characters. *Brassaiopsis* s.l. and *Trevesia* can, however, be distinguished by *Trevesia*'s more massive inflorescences and its ovaries with more locules (5 vs. 2). The ITS trees confirm a close relationship among these three or two genera, suggesting that *Brassaiopsis*, *Euaraliopsis*, and *Trevesia* form a well supported clade (decay index = 5). The generic status and delimitation of *Brassaiopsis*, *Euaraliopsis*, and *Trevesia*, however, need to be carefully examined.

THE PLACEMENT OF HEDERA. The genus *Hedera*, and in particular *H. helix* (English ivy), is well known for its horticultural importance. It comprises 8–12 species from Eurasia, but its taxonomy is highly problematic. The species of *Hedera* are evergreen climbers with heteroblastic foliage in which the juvenile and adult leaves vary within individuals in terms of leaf shape, size, and lobing. They have paniculate umbels, unjointed pedicels, polygamous flowers, valvate aestivation, 5-locular ovaries, and ruminant endosperm. Previous workers (e.g., Harms 1898; Hoo 1961; Shang and Callen 1988) have generally regarded *Hedera* as a closely related to or derived from *Dendropanax*, and this close relationship is supported by the NJ tree of the ITS phylogeny (Fig. 2). The MP and ML trees do suggest that *Hedera* is closely related to *Dendropanax*, but it may be closer to the *Brassaiopsis*—*Euaraliopsis*—*Trevesia* clade (cf. Figs. 1, 3). The phylogenetic position of *Hedera* needs to be explored with additional datasets.

Our sampling included two accessions of *Hedera helix*, both from cultivation. Pairwise comparison of the ITS sequences from these two accessions was 1.0%. Morphologically, *Hedera helix* is a highly variable species, especially with regard to leaf shape

(Stace 1993). The relatively high level of infraspecific variation (in terms of both morphology and the ITS sequences) suggests the need for a careful taxonomic evaluation of the species.

ELEUTHEROCOCCUS AND PUTATIVE RELATIVES. *Eleutherococcus* (often known under its synonym *Acanthopanax*) is a relatively large and diverse genus with 31 species endemic to Asia (Ohashi 1987a; Kim 1997), and delimitation of this genus remains controversial. Morphologically, *Eleutherococcus* includes shrubs with 5-merous flowers, 2–5 carpels, and prickles on the leaves, petioles, or twigs. Harms (1918) also included *Kalopanax* within *Acanthopanax* (i.e., *Eleutherococcus*), but later workers (e.g., Hoo and Tseng 1978; Lee 1993; Ohwi 1984; Shang 1985a; Ohashi 1994) have generally recognized *Kalopanax* as distinct. Mitchell and Wagstaff's (1997) study of morphology and ITS data confirmed Harms' earlier treatment, and this finding is supported by the present (broader) analysis ITS data from throughout Araliaceae. Moreover, sister to this *Eleutherococcus*—*Kalopanax* group is the clade comprising *Macropanax* and *Metapanax*. These four genera are similar in both inflorescence structure and floral morphology, but the two subclades may also be clearly differentiated: *Eleutherococcus* and *Kalopanax* are deciduous and generally have prickles on the stem, whereas *Macropanax* and *Metapanax* are evergreen and unarmed.

Another potential ally of *Eleutherococcus* is the genus *Gamblea* (3 species), which is now thought to include *Evodiopanax* as well (e.g., Mabberley 1997); nomenclatural transfers to *Gamblea*, however, have not yet been formally made. *Gamblea* was first described by Clarke (1879) on the basis of the Himalayan species *G. ciliata* C. B. Clarke. *Evodiopanax*, often treated under synonymy with *Eleutherococcus* (e.g., Harms 1898, 1918; Hoo and Tseng 1978; Ohwi 1984), was originally defined by Nakai (1924) based on material from Japan. Although Kim (1997) recently retained the generic status of *Evodiopanax* (including within it four species from eastern to southeastern Asia), these species share with *Gamblea* many features, including the presence of long and short shoots, polygamo-dioecious flowers, a 4–2-locular ovary, and the lack of prickles. The erection of two distinct genera to accommodate such a homogeneous group of species is likely due to regional treatments lacking a more broadly-based geographical perspective. In the present study, two species from this group were sampled, *Gamblea pseudoevodiaefolia* and *Evodiopanax innocans*. The ITS trees (cf. Figs. 1–3) confirm the close relationship of

Gamblea and *Eviodiopanax*, but suggest that these taxa are not closely allied to *Eleutherococcus* and its relatives.

Character Evolution. The taxonomy of Araliaceae has relied heavily on just a few morphological characters, notably petal aestivation, inflorescence architecture, leaf architecture, and carpel number. The evolution of these characters has been discussed by Philipson (1970a), Eyde and Tseng (1971), Frodin (1982), and Plunkett et al. (1996a, 1997), but these studies have lacked either the phylogenetic framework or the broad sampling available in the present study. Therefore, we review and re-evaluate the evolution of these taxonomically important characters in light of the ITS phylogenies. In doing so, we have applied the principles and concepts of ancestral area analysis (Bremer 1992) to determine plesiomorphic character states using the topology from the parsimony analysis (Fig. 1).

PETAL AESTIVATION. All genera of Araliaceae have valvate aestivation except those traditionally referred to tribe Aralieae (Table 1). The present study included samples from five of these imbricate genera: *Aralia*, *Cephalalaria*, *Panax*, *Pentapanax*, and *Sciadodendron*. The ITS trees suggest that valvate petals were plesiomorphic in core Araliaceae and that imbricate petals evolved independently at least two times: once in *Cephalalaria* and a second time in the clade comprising *Aralia*, *Panax*, *Pentapanax*, and *Sciadodendron*. Several taxa now excluded from core Araliaceae (and not sampled in the present study) also have imbricate aestivation, and thus likely represent additional independent origins of imbrication. For example, the imbricate *Stilbocarpa* (traditionally placed in tribe Aralieae; Harms 1898) is highly divergent from all other araliaceous genera, and the study of ITS sequences by Mitchell et al. (1999) confirms that this genus should be excluded from core Araliaceae. The closely related family Apiaceae is also largely characterized by valvate aestivation, but there are some imbricate members of that family as well. Members of Pittosporaceae, on the other hand, have petals that are either united or imbricate.

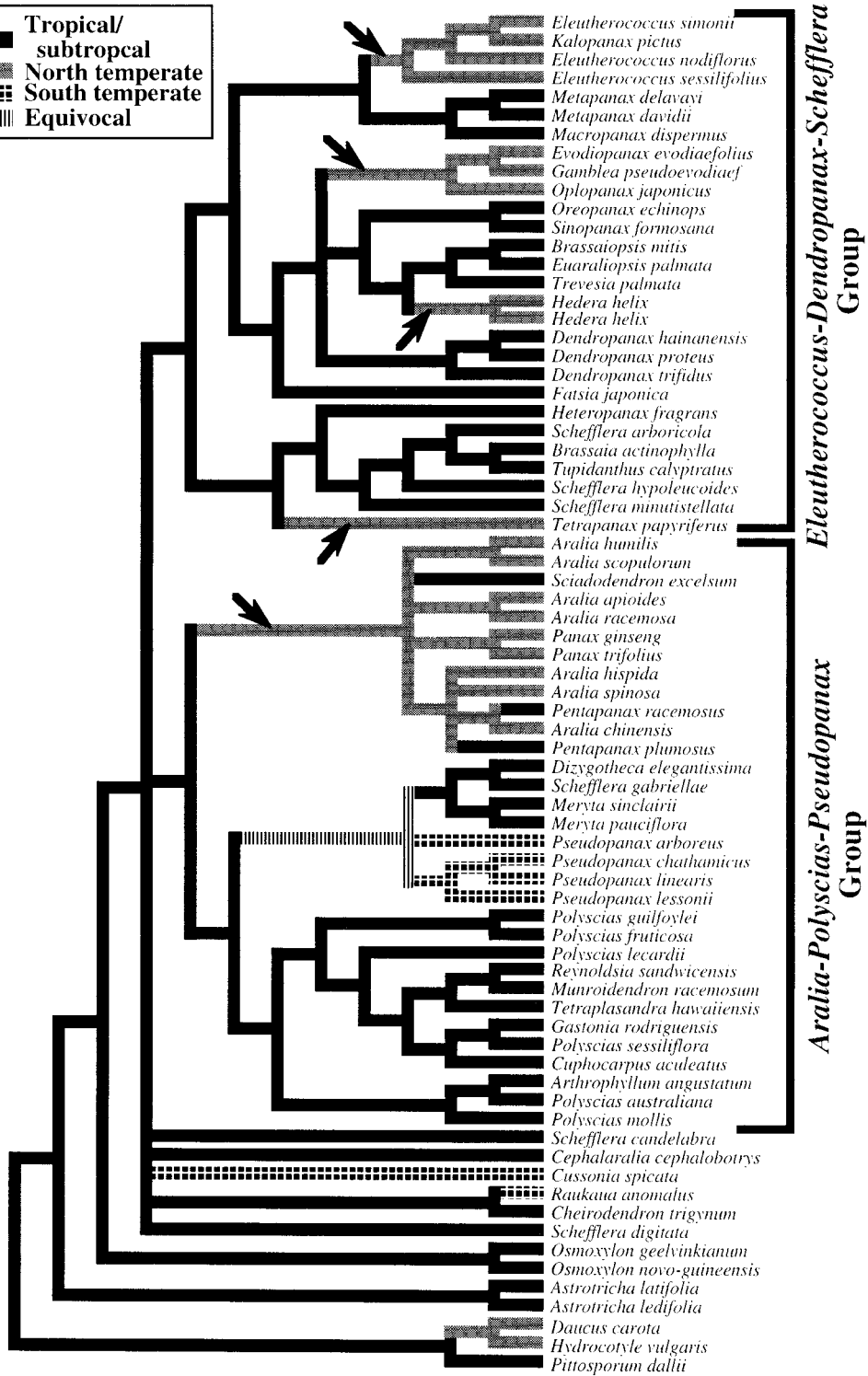
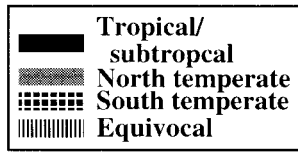
LEAF ARCHITECTURE. Leaf type in Araliaceae is extremely diverse, varying from simple and entire, to simple and variously lobed, to compound (either palmately, ternately, or once-, twice-, or thrice-pinnately compound). Palmately compound leaves are quite common, as exemplified by *Cheirodendron*, *Eleutherococcus*, *Gamblea*, *Macropanax*, *Panax*, *Schefflera*, and most species of *Pseudopanax*. Pinnately compound leaves characterize all or most species of

Aralia, *Arthrophyllum*, *Cephalalaria*, *Gastonia*, *Heteropanax*, *Munroidendron*, *Pentapanax*, *Polyscias*, and *Reynoldsia*. Simple leaves are often regarded as unusual in Araliaceae, but in fact they are found among several genera (e.g., *Astrotricha*, *Dendropanax*, *Fatsia*, *Hedera*, *Hunaniopanax* C. J. Qi & T. R. Cao, *Meryta*, *Oplopanax*, *Oreopanax*, *Sinopanax*, and *Tetrapanax*). Moreover, ancestral character analysis of the ITS trees suggests that simple leaves are ancestral in core Araliaceae, despite the traditional notion that Araliaceae “terminate a long-line of compound-leaved” plants (Cronquist 1981). This result is consistent with the findings of Plunkett et al. (1996a, 1997), who suggested that simple leaves were plesiomorphic throughout the entire order Apiales.

It must be noted, however, that many araliads also have heteroblastic leaves. In these species, the leaf morphology changes in a single individual with developmental stage and/or habitat (e.g., from palmately or pinnately lobed/compound to simple, or vice versa). Well-known examples of heteroblastic leaves are those found in *Hedera*, *Trevesia*, and *Cussonia*. We coded simple leaves as a single character state in the present study, but future studies (with a broader sampling) might address the polarity of this character state within each heteroblastic genus. Further, it cannot be assumed that all simple leaves in Araliaceae are homologous. *Astrotricha* and *Dendropanax*, for example, have simple and undivided leaves with pinnate venation, but the leaves of *Oreopanax*, *Oplopanax*, and *Tetrapanax* are simple and palmately divided, and those of *Trevesia* are simple but variously divided. Lastly, the simple leaves of some species or genera appear to be secondarily derived from compound leaves, such as the unifoliolate leaves in some species of *Polyscias*, or the “simple” leaves of *Meryta* and *Hunaniopanax* (which maintain petiolule articulations along the midrib). “Simple” leaves in *Hunaniopanax* may be evolved from the pinnately compound leaves of its close relatives such as *Pentapanax* (Qi 1988). Thus, additional studies of these genera are needed to more thoroughly assess the polarity and homologies of leaf architecture in core Araliaceae.

CARPEL NUMBER. Most genera in Araliaceae have inferior ovaries with 2–5 carpels (represented by 2–5 locules), each with a single functional ovule (Philipson 1970a). A few genera (e.g., *Gastonia*, *Plerandra*, and *Reynoldsia*), however, have as many as 20 carpels, and the locule number of the anomalous *Tupidanthus calypttratus* can be as great as 200. The polarity of locule number in Araliaceae has received much attention. Most workers (e.g., Harms

Biogeography



1898; Li 1942; Baumann-Bodenheim 1955; Philipson 1970a; Eyde and Tseng 1971) regarded the pluricarpellate ovary as primitive in Araliaceae, a finding that both Philipson (1970a) and Eyde and Tseng (1971) believed was well supported by patterns of floral vasculature. In contrast, some workers have suggested that pentacarpellate (Cronquist 1968, but see also Cronquist 1981) or bicarpellate (Plunkett et al. 1996a, 1997) ovaries were ancestral not only in Araliaceae but throughout Apiales. Determining the precise placement of *Astrotricha* and *Osmoxylon* at the base of core Araliaceae will have an important impact on the interpretation of this character in Araliaceae. The MP trees suggest a basally-branching position for *Astrotricha*, a genus of 15–20 species all having bicarpellate ovaries (see Bean 1991). This topology would be consistent with the theory of Plunkett et al. (1996a, 1997). If, however, *Osmoxylon* occupies this position (as the NJ tree suggests), the interpretation of carpel-number polarity becomes much more difficult. Carpel number in the ~50 species of *Osmoxylon* ranges from 1–25 or more (Philipson 1979), and thus the plesiomorphic condition within this genus would need to be established before carpel-number polarity could be determined for the family. The ambiguity of these results highlights the limitations of a study that uses a small number of exemplar species to represent a much larger group of plants. This limitation notwithstanding, it is clear that pluricarpellate ovaries have evolved from paucicarpellate ovaries at least two times in Araliaceae, once in *Tupidanthus*, and another in *Tetraplasandra* and related genera.

WOODY VS. HERBACEOUS HABIT. Araliaceae comprise mostly woody taxa (trees, shrubs, or woody vines), with only a very few herbs. Although the closely-related family Apiaceae is mostly herbaceous, the basally-branching lineages of core Araliaceae (*Astrotricha* and *Osmoxylon*) and the species of the other close allies of Apiales (e.g., Pittosporaceae) are all woody. This confirms the traditional notion that the woody habit is ancestral in Araliaceae. The herbaceous species of the family are limited to just three genera, *Aralia*, *Panax*, and *Stilbocarpa*. Within *Aralia* (55 spp., Wen 1993), 10 species are herbaceous, including the nine species of

section *Aralia* and the single species of section *Nanae* Harms (*Aralia nudicaulis*). In the present study, we sampled two herbaceous species from section *Aralia* (*A. apioides* and *A. racemosa*); these form a monophyletic group. The placement of section *Aralia* relative to the herbaceous species in *Panax* is unresolved in the MP trees (Fig. 1), but the NJ and ML trees (Figs. 2, 3) indicate that they are not sister groups. This suggests that the herbaceous habit may have evolved independently in *Aralia* and *Panax*. As discussed above, *Stilbocarpa* (not surveyed in the present study) has been excluded from core Araliaceae on the basis of molecular data (Mitchell et al. 1999). Thus, the origin of herbaceousness in this genus can be regarded as independent of that in *Aralia* and *Panax*.

Biogeography. A striking feature of the ITS trees (Figs. 1–3) is the relatively short branch lengths characterizing all the deeper nodes of the trees. Among the possible explanations is that core Araliaceae may have experienced a rapid diversification early in its evolutionary history. In both of the major clades within the family (the *Eleutherococcus*—*Dendropanax*—*Schefflera* group and the *Aralia*—*Polyscias*—*Pseudopanax* group), there are both temperate and tropical subclades (Fig. 4). The present-day distribution of Araliaceae, however, is best developed in the tropics and subtropics (particularly in southeastern/southern Asia and the Pacific islands) and all of the basally-branching lineages in the family (e.g., *Astrotricha*, *Cephalalaria*, and *Osmoxylon*) are endemic to the paleotropics. Coupled with the present-day distributions of Pittosporaceae and the basal lineages of Apiaceae (e.g., the mostly tropical and southern-hemisphere members of subfamily Hydrocotyloideae, and the southern-African, woody species of subfamily Apioideae; see Plunkett et al. 1996b; Downie et al. 1998), Araliaceae appear to have originated in the paleotropics.

Despite their tropical origins, there are many examples of north temperate taxa in the family, including some or all members of *Aralia*, *Eleutherococcus*, *Gamblea*, *Hedera*, *Kalopanax*, *Oplapanax*, *Panax*, and *Tetrapanax*. The ITS topology suggests that the origin of north temperate groups in Araliaceae is quite complex. Broadly speaking, it would appear

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FIG. 4. The strict consensus tree of 10,000 maximally parsimonious trees as in Fig. 1, showing the biogeographic relationships among the tropical/subtropical and temperate taxa. Arrows indicate the evolution of temperate clades from subtropical/tropical ones.

that the *Aralia*—*Polyscias*—*Pseudopanax* group arose in the tropical or subtropical regions, where many members may still be found (e.g., *Arthrophyllum*, *Gastonia*, *Meryta*, *Munroidendron*, *Reynoldsia*, and *Tetraplasandra*). The largely north temperate *Aralia*—*Panax* subgroup, therefore, most likely had a tropical origin. Conversely, in the *Eleutherococcus*—*Dendropanax*—*Schefflera* group it appears that temperate taxa may have arisen independently at least four times in the following clades (Fig. 4): the *Eleutherococcus*—*Kalopanax* clade, the *Evodiopanax*—*Gamblea*—*Oplopanax* clade, the *Hedera* clade, and the *Tetrapanax* clade.

In general, the ITS trees suggest that temperate taxa of Araliaceae are mostly derived from subtropical and tropical members. On a narrower scale, some subtropical/tropical taxa are nested within the temperate ones. For example, the subtropical *Pentapanax* is nested within the largely temperate *Aralia* clade.

A similar pattern may be seen in the southern hemisphere with the mostly south-temperate core group of *Pseudopanax*, which is endemic to New Zealand. The ITS trees (Figs. 1–4) suggest that *Pseudopanax* most likely had a tropical/subtropical origin. Its closest relatives including *Meryta*, *Dyzygotheca*, and *Polyscias*, are all tropical/subtropical. Some species of *Pseudopanax* clearly extend south to the cooler temperate regions of southern New Zealand. Again, the short branch lengths between related tropical/subtropical and temperate lineages suggest that there were rapid diversifications of taxa following the migration of plants into different geographic regions.

Although most of the biogeographic migrations in Araliaceae represent movements across the latitudes, there are several cases where closely-related taxa clearly migrated between the Old and New Worlds. Among these are both palearctic—nearctic migrations (e.g., *Aralia*, *Panax*, *Oplopanax*, most likely through the Bering land bridge; Hopkins 1967; see also Wen and Zimmer 1996; Wen et al. 1996; Wen 1998, 1999a; Wen et al. 1998), and a number of paleotropical—neotropical movements (e.g., *Dendropanax*, *Schefflera*, and the *Oreopanax*—*Sinopanax* generic pair). The tropical examples represent some of the most species-rich genera in Araliaceae, but the monophyly of these large, intercontinental, disjunct genera has not been adequately tested. The abundance of cross-latitude and cross-longitude migrations among and within the genera of Araliaceae makes this family a rich source for future biogeographic studies.

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