

Phylogenetic affinities of Monimiaceae based on cpDNA gene and spacer sequences

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Abstract

Nucleotide sequence data from the chloroplast *rbcl* gene and the *trnL-trnF* intergenic spacer of 58 species in 38 genera were used to infer the phylogenetic affinities of Monimiaceae to other Laurales, and to assess whether the family in the traditional wide sense is monophyletic. Besides Monimiaceae, the Laurales comprise Calycanthaceae, Gomortegaceae, Hernandiaceae, and Lauraceae. Magnoliaceae and Myricaceae were used as outgroups. Based on recent molecular data, Amborellaceae and Chloranthaceae, which have sometimes been included in the order, do not belong in the Laurales, and indeed *trnL-trnF* sequences of *Amborella* (Amborellaceae) and *Hedyosmum* (Chloranthaceae) were too different to be unambiguously aligned with the remaining sequences. Parsimony analyses of the *trnL-trnF* and *trnL-trnF-rbcl* data groups the genera into five major clades, Calycanthaceae, Atherospermataceae, *Gomortega*, Siparunaceae, and a weakly supported Monimiaceae s.str.-Lauraceae-Hernandiaceae clade. *Rbcl* data alone provide no resolution at the family level. Many aspects of traditional intra-familial classification of Monimiaceae are supported except that the sole perfect-flowered member of the family, the monotypic Sri Lankan *Hortonia*, is not basal (13 of 15–22 genera sampled). Instead, there are two major clades in Monimiaceae. One comprises the functionally dioecious monospecific *Peumus* from Chile plus the morphologically and functionally dioecious small genera *Monimia* from the Mascarenes and *Palmeria* from eastern Australia and New Guinea. The other consists of *Hortonia* and all remaining genera. The atherospermatoids are supported in their traditional circumscription (14 species, 7 genera, of which 10 and 6 were sampled). The neotropical genus *Siparuna*, different from recent classifications that have stressed its isolation, is genetically and morphologically very close to the West African species *Glossocalyx longicuspis*. Both taxa have unisexual flowers of the same general morphology, and both have unitegmic ovules. From the current data it seems that monoecy is basal in *Siparuna*, but more complete sampling of species with a faster evolving genetic marker is needed for a fuller understanding of the evolution of monoecy and dioecy in this genus.

Keywords: Atherospermataceae, Monimiaceae, Siparunaceae, Laurales, molecular phylogenetics, fossil record, biogeography

Introduction

Among the most noteworthy elements of the Laurales with respect to floral morphology and biogeography are the Monimiaceae. The

Monimiaceae in the traditional wide sense (e.g. Perkins & Gilg 1901; Money *et al.* 1950; Philipson 1993) comprise 28–34 genera dis-

tributed in the tropics and subtropics. They have figured prominently in discussions of the history of land masses inhabited by their living and extinct members (Croizat 1952; Mädler 1960; Süss 1960; Rufflé 1965; Knappe & Rufflé 1975; Takhtajan 1973; Thorne 1973; Raven & Axelrod 1974), and they have been the subject of much floral morphological, developmental, and palynological work (e.g. Endress 1979, 1980a, b, 1992; Endress & Lorence 1983; Sampson 1993, 1996, 1997 and references therein; Foreman & Sampson 1987; Sampson & Foreman 1990). However, doubts about their monophyly have hampered understanding of the biogeography and evolution of the group (Pichon 1948; Takhtajan 1969; Schodde 1970; Smith 1972; Raven & Axelrod 1974; Endress 1972; Behnke 1981, 1988). In addition, subfamilial concepts are unclear and have varied greatly (Table 1). These problems are due to the lack of a single predominant feature or morphological synapomorphy that would characterize the family and to conflicting distributions of characters used by different workers to subdivide it. Thus, as pointed out by Smith (1972), the Monimiaceae have remained a catch-all family even after the removal of *Trimenia* and *Piptocalyx* (as Trimeniaceae; Gibbs 1917) and *Amborella* (Amborellaceae; Pichon 1948).

The most recent treatment (Philipson 1993; Table 1) recognizes six subfamilies defined by a combination of characters, including sexual system, perianth structure, anther opening (whether by slits or valves), ovule position (basal or hanging), fruit type (achenes or drupes), wood anatomy (phloem rays narrow or wide), and number of integuments (one or two). Previous treatments (Table 1), most importantly those of Perkins & Gilg (1901) and Money *et al.* (1950), recognized two or four subfamilies, based on different weightings of the same set of characters.

As expected, ideas about evolutionary relationships among the subfamilies conflict. Thus, Money *et al.* (1950) considered *Hortonia*, with a single species in Sri Lanka (*H. ovalifolia* Wight and *H. angustifolia* Trimen in my view are identical with *H. floribunda* Wight ex Arn.), as the most basal group, probably because of its bisexual flowers, a trait absent from all other Monimiaceae s.l.; they thus accorded *Hortonia* subfamily rank. Endress (1980b) and Sampson (1993), on the other hand, have stressed the links between *Horto-*

nia and two of the other subfamilies, namely the Atherospermatoidae and the Monimioideae (the last have varied widely in circumscription: see Table 1 and below). Schodde (1969, 1970), by contrast, saw no link between *Hortonia* and the Atherospermatoidae and indeed argued for the exclusion of the latter from the Monimiaceae. Schodde's analysis of the distribution among Lauralean families of 45 mainly morphological, anatomical, and palynological characters showed that atherospermatoids were closer to Gomortegaceae than to the remaining Monimiaceae. The atherospermatoids in Schodde's analysis consist of seven small genera with a total of 14–16 species.

The Monimioideae, which in earlier classifications comprise the bulk of monimiaceous genera and slightly over half the species, have had a third of their genera variously included or excluded due to differential weighting of particular characters. Thus, *Xymalos* was transferred to Trimeniaceae (Hutchinson 1964); *Hortonia* separated as Hortoniaceae (Smith 1972); and *Peumus* excluded as Peumoideae (Schodde 1970). *Peumus* and *Hedycarya* have also been seen as deserving family status because of their unusual sieve tube plastids. Later they were re-included into the Monimiaceae (Behnke 1981, 1988). Recently, the trend has been to separate *Peumus* and *Monimia* as Monimioideae s.str. from the other monimioid genera, which for nomenclatural reasons results in the establishment of a sixth subfamily, Mollinedioideae, for the remaining genera (Thorne 1974). Philipson subsequently (1987, 1993) transferred *Palmeria* from Mollinoideae to Monimioideae *sensu* Thorne because of its close similarity to *Monimia*.

The *Siparuna-Glossocalyx* group, finally, has been seen as part of the Atherospermatoidae (Perkins & Gilg 1901), as deserving subfamily status (Money *et al.* 1950), as completely unrelated to all other Monimiaceae and being a separate family (Schodde 1970), or as consisting of two genera „as distinct as any of the other groups which have been accorded family rank“ and requiring subdivision (Philipson 1987, 1993). This led to the establishment of Glossocalycoideae for the monotypic West African genus *Glossocalyx* (*G. brevipes* Benth. is here considered a synonym of *G. longicuspis*).

The primary goals of this study were to investigate the molecular support for the mono-

Table 1. A comparison of major recent treatments of Monimiaceae. Genera appear in the authors' original sequences, and subfamilies have been numbered in the sequence in which they were treated by those authors. Six monotypic genera recognized by Perkins & Gilg (1901) and Money *et al.* (1950), but synonymized by Philipson (1993), are omitted

Perkins & Gilg (1901)	Money <i>et al.</i> (1950)	Philipson (1993)
1. Monimioideae Endl. <i>Hortonia</i> Wight	1. Hortonioidae Money <i>et al.</i> <i>Hortonia</i>	1. Hortonioidae <i>Hortonia</i>
<i>Peumus</i> Molina	3. Monimioideae <i>Peumus</i>	6. Monimioideae <i>Peumus</i>
<i>Amborella</i> Baill.	[Amborellaceae Pichon]	[Amborellaceae]
<i>Hedycarya</i> Forst. & Forst. <i>Levieria</i> Becc.	<i>Hedycarya</i> <i>Levieria</i> <i>Decarydendron</i> Danguy <i>Kibaropsis</i> Vieill. ex Jérémie	5. Mollinedioideae Thorne <i>Hedycarya</i> <i>Levieria</i> <i>Decarydendron</i> <i>Kibaropsis</i>
<i>Piptocalyx</i> Oliv. <i>Trimenia</i> Seem.	[Trimeniaceae Gibbs]	[Trimeniaceae]
<i>Xymalos</i> Baill.	[Trimeniaceae] <i>Xymalos</i>	[Trimeniaceae] <i>Xymalos</i>
<i>Macropeplus</i> Perk. (= <i>Mollinedia</i>)	<i>Macropeplus</i>	<i>Macropeplus</i>
<i>Mollinedia</i> R. & P.	<i>Mollinedia</i>	<i>Mollinedia</i>
<i>Macrotorus</i> Perk. (= <i>Mollinedia</i>)	<i>Macrotorus</i>	<i>Macrotorus</i>
<i>Ehippiandra</i> Decne.	<i>Ehippiandra</i>	<i>Ehippiandra</i>
<i>Matthaea</i> Blume	<i>Matthaea</i>	<i>Matthaea</i>
<i>Stegantthera</i> Perk.	<i>Stegantthera</i>	<i>Stegantthera</i>
<i>Tetrasynandra</i> Perk.	<i>Tetrasynandra</i>	<i>Tetrasynandra</i>
<i>Wilkiea</i> F. Muell.	<i>Wilkiea</i>	<i>Wilkiea</i>
<i>Kibara</i> Endl.	<i>Kibara</i>	<i>Kibara</i>
<i>Lauterbachia</i> Perk.	<i>Lauterbachia</i>	<i>Lauterbachia</i>
<i>Palmeria</i> F. Muell.	<i>Palmeria</i>	<i>Austromatthaea</i> L. S. Smith
<i>Monimia</i> Thouars	<i>Monimia</i>	<i>Parakibara</i> Philipson
<i>Tambourissa</i> Sonn.	<i>Tambourissa</i>	<i>Faika</i> Philipson
<i>Hennecartia</i> Poiss.	<i>Hennecartia</i>	<i>Kairoa</i> Philipson
2. Atherospermatoideae Endl.	2. Atherospermatoideae	2. Atherospermatoideae
<i>Nemuaron</i> Baill.	<i>Nemuaron</i>	<i>Nemuaron</i>
<i>Daphnandra</i> Benth.	<i>Daphnandra</i>	<i>Daphnandra</i>
<i>Laurelia</i> Juss.	<i>Laurelia</i>	<i>Laurelia</i>
<i>Atherosperma</i> Labill.	<i>Atherosperma</i>	<i>Atherosperma</i>
<i>Doryphora</i> Endl.	<i>Doryphora</i>	<i>Doryphora</i>
	<i>Dryadodaphne</i> S. Moore	<i>Dryadodaphne</i>
	4. Siparunoideae Money <i>et al.</i>	3. Siparunoideae
<i>Siparuna</i> Aubl.	<i>Siparuna</i>	<i>Siparuna</i>
<i>Glossocalyx</i> Benth.	<i>Glossocalyx</i>	4. Glossocalycoideae Thorne
		<i>Glossocalyx</i>

phyly of Monimiaceae s.l., to assess their phylogenetic relationships within Laurales, and to test some of the earlier hypotheses about generic relationships within Monimiaceae.

Besides Monimiaceae s.l., core-Laurales comprise Calycanthaceae, Gomortegaceae, Hernandiaceae, and Lauraceae (Hallier 1905; Takhtajan 1987; Cronquist 1981; Dahlgren 1989; Thorne 1992). These authors

variously included Amborellaceae, Trimeniaceae, and/or Chloranthaceae in Laurales but at least in the case of Amborellaceae and Chloranthaceae this is not supported by molecular evidence (Qiu *et al.* 1993; Chase & Cox, in press; Savolainen *et al.*, manuscript; K. Ueda, pers. comm.). Trimeniaceae have not yet been sequenced, but morphological data argue against its placement in core-Laurales (e.g. Endress & Igersheim 1997 and references therein). For the present assessment of phylogenetic relationships of Monimiaceae within Laurales, 59 species representing 35 lauralean and three outgroup genera were sampled; two sequences of Amborellaceae and Chloranthaceae that were generated proved too different from the remaining lauralean (and also outgroup) sequences to be aligned unambiguously.

The genetic markers used are the large subunit of ribulose-1,5-bisphosphate carboxylase (*rbcL*) and the non-coding tRNA spacer region *trnL-trnF* of the chloroplast genome. An earlier study (Renner *et al.* 1997), based on morphological data and separate analyses of two smaller molecular data sets from the same genome regions, already indicated that the Monimiaceae in the wide sense are probably not monophyletic, but sampling density and number of informative characters were low. The present study, which is based on much denser sampling and the combination of two fully parallel data sets, still leaves family relationships within Laurales poorly resolved but provides considerable resolution within families. It is intended to guide future work on key morphological characters that need to be reinvestigated in the monimiaceous clades, and in Laurales, to contribute to a comprehensive natural classification of the order. Another goal is to begin the reinterpretation of Monimiaceae biogeography and breeding system evolution made necessary by the molecular data.

Materials and Methods

The accessions from which DNA was extracted are listed in Table 2. In most cases, leaves included in this study came from field-collected plants and had either been preserved in silica gel or prepared as standard herbarium vouchers. A few leaves also came from fresh plants. In all, 57 *trnL-trnF* and 38 *rbcL* sequences from 59 species are in-

cluded, of which 37 and 19, respectively, are newly reported here while the remainder were available from earlier work (Renner *et al.* 1997) or, in the case of 15 *rbcL* sequences, were downloaded from GenBank (Table 2). *RbcL* and *trnL-trnF* sequences are from the same species, usually from the same leaf, except in the case of *Hernandia albiflora* for which an *rbcL* but no *trnL-trnF* sequence was obtained and *Cryptocarya* for which a GenBank *rbcL* sequence from *C. obovata* was combined with a *trnL-trnF* sequence from *C. chinensis* (Table 2). Martin & Dowd submitted two *C. obovata* sequences to GenBank that differ from each other; I used the earlier one (L28950) but replaced all nucleotides that differed between the two sequences by the symbol for unknown nucleotide; unknown nucleotides are considered as uncertainties in PAUP analyses.

Within Laurales, Calycanthaceae, Gomortegaceae, and Siparunaceae had all their genera sampled, and Atherospermataceae, Hernandiaceae, and Monimiaceae s.str. most genera (6 of 7, 4 of 5, and 13 of 15–22, respectively). The lower estimate of the number of monimiaceous genera reflects the synonymization of seven monotypic groups as follows (Renner, unpubl. data): *Macropeplus* Perkins and *Macrotorus* Perkins belong in *Mollinedia* Ruiz & Pavón; *Kibaropsis* Vieillard ex Jérémie in *Hedycarya* J. & G. Forst.: *Faika* Philipson, *Kairoa* Philipson, and *Parakibara* Philipson in *Kibara* Endl.; and *Austromatthaea* L.S. Smith in *Matthaea* Blume. The Lauraceae are the only family represented by only a fraction of their genera (4 of 50) but their monophyly is unquestioned. Both their tribes are represented (following the classification of Rohwer 1993): the small and homogeneous Laureae by *Litsea* and the more heterogeneous Perseeae by three genera, namely *Cryptocarya*, which represents one of Rohwer's two subgroups of Perseeae, and by *Persea* and *Cinnamomum*, which represent the other subgroup.

The Monimiaceae s.str. are represented as follows (classification of Philipson 1993; cf. Table 1): (1) *Hortonia floribunda*, the sole member of the Hortoniaceae; (2) all but one genus and 10 of 14 species of Atherospermataceae; (3) nine species of *Siparuna*, sole member of Siparunaceae (Philipson considered the enigmatic *Bracteanthus* a synonym of *Siparuna*); (4) *Glossocalyx longicuspis*, sole member of Glossocalycoideae; (5) two

Table 2. Sources, voucher specimens, and GenBank accession numbers for the species from which *rbcL* and *trnL-trnF* sequences were obtained for this study. Abbreviations used for herbaria follow the Index Herbariorum (Holmgren *et al.* 1990). The word aliquot after a source indicates that a DNA extract received from that colleague was used to obtain the respective sequence

Taxon	Source	GenBank accession numbers	
		<i>rbcL</i>	<i>trnL-trnF</i>
Atherospermataceae			
<i>Daphnandra micrantha</i> (Tul.) Benth.	Melbourne BG 504037	...	AF040668
<i>Daphnandra</i> „crypta“ nom. ined.	Canberra BG 702451	...	AF040669
<i>Daphnandra repandula</i> (F. Muell.) F. Muell.	Hyland s.n. (Sep. 97)	AF052195	AF040670
<i>Doryphora aromatica</i> (F.M. Bailey) L.S. Smith	Ablett <i>et al.</i> 1997	L77211	...
<i>Doryphora sassafras</i> (Endl.) Endl.	Hyland s.n. (Sep. 97)	...	AF040671
<i>Dryadodaphne novoguineensis</i> (Perk.) A.C. Smith	Sydney BG, bed 130	...	AF040672
<i>Laurelia novae-zelandiae</i> Cunn.	Takeuchi 7095 (MO)	1/2 <i>rbcL</i> seq.	AF040673
<i>Laurelia sempervirens</i> (R. & P.) Tul.	Sampson s.n. (Oct. 97)	AF052196	AF040674
<i>Laureliopsis philippiana</i> (Looser) Schodde	Edinburgh BG 19931681	AF052612	AF012402
<i>Nemuaron vieillardii</i> (Baill.) Baill.	Landrum & Landrum 8160 (MO) McKee 12800 (K)	AF040662 1/2 <i>rbcL</i> seq.	AF040675 AF040676
Calycanthaceae			
<i>Calycanthus occidentalis</i> Hook. & Arn.	Missouri BG 897423	AF022951	AF012396
<i>Chimonanthus praecox</i> (L.) Link	Qiu <i>et al.</i> 1993	L12639	...
	Missouri BG 896912	...	AF040677
<i>Idiospermum australiense</i> (Diels) S.T. Blake	Qiu <i>et al.</i> 1993; aliquot	L12651	AF040678
Gomortegaceae			
<i>Gomortega keule</i> (Molina) I.M. Johnson	Ueda <i>et al.</i> 1997 Rodriguez 3070 (CONC)	D89561 AF012404
Hernandiaceae			
<i>Gyrocarpus americanus</i> Jacq.	Qiu <i>et al.</i> 1993; aliquot	L12647	AF012398
<i>Hernandia albiflora</i> (C.T. White) Kubitzki	Ablett <i>et al.</i> 1997	L77210	...
<i>Hernandia moerenhoutiana</i> Guillem.	Mt. Coot-tha BG Brisbane	AF052614	AF052198
<i>Hernandia ovigera</i> L.	Qiu <i>et al.</i> 1993; aliquot	L12650	AF012397
<i>Illigera luzonensis</i> (Presl) Merr.	Fernando 1602 (LBC)	AF050222	AF052199
<i>Sparattanthelium wonotoboense</i> Kosterm.	Munich BG	AF052197	AF053342
Lauraceae			
<i>Cinnamomum camphora</i> (L.) Nees & Eberm.	Qiu <i>et al.</i> 1993 Ueda s.n.	L12641 Ueda, unpubl.
<i>Cryptocarya obovata</i> R. Br.	P.J. Martin & J. Dowd, unpubl.	L28950	...
<i>Cryptocarya chinensis</i> (Hance) Hemsley	Ueda s.n.	...	Ueda, unpubl.
<i>Litsea japonica</i> (Thun.) Juss.	P.J. Martin & J. Dowd, unpubl. Ueda s.n.	U06843 Ueda, unpubl.
<i>Persea americana</i> Mill.	Golenberg <i>et al.</i> 1990 Missouri BG 897543	X54347 AF012401
Magnoliaceae			
<i>Liriodendron chinense</i> (Hemsley) Sarg.	Qiu <i>et al.</i> 1993 Missouri BG 890888	L12654 AF040679
<i>Magnolia hypoleuca</i> Siebold & Zucc.	Qiu <i>et al.</i> 1993 Missouri BG 732556	L12655 AF012395

Table 2. (Continued)

Taxon	Source	GenBank accession numbers	
		<i>rbcl</i>	<i>trnL-trnF</i>
Magnolia macrophylla Michx.	Golenberg <i>et al.</i> 1990 Missouri BG 790346	X54345 AF040680
Monimiaceae			
Hedycarya angustifolia Cunn.	Melbourne BG 940335	...	AF040681
Hedycarya arborea J. & G. Forst.	Qiu <i>et al.</i> 1993; aliquot	L12648	AF012412
Hennecartia omphalandra Poisson	Peña s.n. (MO)	AF022950	AF040682
Hortonia floribunda Wight ex Arn.	Colombo BG	AF040663	AF040683
Kairoa suberosa Philipson	W. Takeuchi 5999 (MO)	...	AF040684
Kibara coriacea (Bl.) Tul.	M. Chase; aliquot	...	AF012413
Kibara rigidifolia A.C. Smith	NSW 200112 (cult. Sydney BG)	AF050221	AF040685
Mollinedia ovata R. & P.	Stáhl <i>et al.</i> 3735 (QCA)	AF050218	AF040686
Monimia ovalifolia Thouars	Strasberg s.n. (Herb. Réunion)	...	AF054896
Palmeria scandens F. Muell.	Bradford 878 (MO)	AF052613	AF052200
Peumus boldus Molina	Edinburgh BG 19870707	AF040664	AF012403
Tambourissa amplifolia (Tul.) A. DC.	Ntl. Trop. BG 940042	...	AF040687
Tambourissa ficus (Tul.) A. DC.	Ntl. Trop. BG 940043	...	AF012410
Tambourissa peltata R. Br. ex Baker	Ntl. Trop. BG 940040	...	AF040688
Tambourissa tau Lorence	Ntl. Trop. BG 940044	AF050219	AF012411
Tetrasynandra pubescens (Benth.) Perk.	Hyland s.n. (Sep. 97)	...	AF040689
Wilkiea huegeliana A. DC.	DeNardi 23593 (UNSW)	AF040665	AF040690
Wilkiea macrophylla (Cunn.) A. DC.	Sydney BG 873525	...	AF040691
Wilkiea sp. nov.	Canberra BG 9613317	...	AF040692
Xymalos monospora (Harvey) Baill.	Gereau & Kayombo 4745 (MO)	AF050220	AF040693
Myristicaceae			
Knema latericia Elmer	Qiu <i>et al.</i> 1993; aliquot	L12653	AF040694
Siparunaceae			
Glossocalyx longicuspis Benth.	Bos 4659 (MO)	AF040666	AF012405
Siparuna aspera (R. & P.) A. DC.	Madriñán <i>et al.</i> 1502 (COL)	...	AF040695
Siparuna brasiliensis (Spreng.) A. DC.	Pignal 309 (P)	AF013246	AF012408
Siparuna depressa Jangoux	Sothers 2109-74 (INPA)	...	AF012407
Siparuna echinata (H.B.K.) A. DC.	Potthast 243 (QCA)	...	AF040696
Siparuna guianensis Aubl.	Chanderbali 247 (MO)	...	AF040697
Siparuna lepidota (H.B.K.) A. DC.	Stáhl 2254 (QCA)	AF040667	AF012406
Siparuna muricata (R. & P.) A. DC.	Merello <i>et al.</i> 1102 (MO)	...	AF040698
Siparuna sessiliflora (H.B.K.) A. DC.	Madriñán <i>et al.</i> 1504 (COL)	...	AF012409
Siparuna thecaphora (P. & E.) A. DC.	Lohmann s.n. (MO)	...	AF040699

of the three genera of Monimioideae; and (6) ten of 12–19 genera of Mollinedioideae.

Total DNA was isolated from leaf tissues using standard methods for plant material (cf. Renner *et al.* 1997). The *rbcl* gene was then amplified using a 26-nucleotide forward primer (1F, ATGTCACCACAAACAGAAAC-TAAAGC) and a 24-nucleotide reverse primer (1460R, CTTTGTAGTAAAAGATTGGG CCGAG). To amplify the entire gene from herbarium material, two internal primers were used in addition to the two mentioned above,

namely 724R (CATGTACCTGCAGTAGC) and 636F (GCGTTGGAGAGATCGTTTCT); where the 636F primer did not work, a complement of the 724R primer was used instead. Primer sequences were received from M. Chase (Fay *et al.* 1997). Primers for amplifying and sequencing the *trnL-trnF* intergenic spacer are the forward (e) and reverse (f) primers of Taberlet *et al.* (1991). Purified double-stranded DNAs were sent for automated sequencing to the DNA core facility of the University of Missouri – Colombia. Both

strands of DNA were sequenced for both markers, and sequences were aligned by eye. To detect sequencing errors, the *rbcL* sequences were translated into amino acids using the programme SeqPup and then compared with Fig. 4 in Kellogg & Juliano (1997), which lists variable and invariable sites in 499 seed plant *rbcL* sequences. Alternative amino acids found in Laurales all occurred at sites already known to be variable within angiosperms, and no stop codons were found in any of the sequences. A total of 1331 nucleotides, from positions 31 to 1362 of the *rbcL* gene, and 445 nucleotides of the *trnL-trnF* intergenic spacer were employed for reconstruction of phylogenetic relationships in Laurales, using the test version 4.0d63 of PAUP* written by David L. Swofford.

Insertions/ deletions (INDELs) occurred only in the *trnL-trnF* data and were treated in two ways: (1) as missing data or (2) as presence/absence characters in a supplemental matrix. Potentially informative but overlapping INDELs where homology assessment was impossible were excluded from the supplemental matrix. Shortest trees were searched for heuristically with the RANDOM addition sequence, tree bisection-reconnection (TBR) branch swapping, MULPARS, STEEPEST DESCENT, and COLLAPSE options of PAUP, and character changes were interpreted with the ACCTRAN optimization. Characters were unweighted. Bootstrap analyses were carried out with 100 replicates, using the SIMPLE addition and nearest-neighbour-interchange (NNI) branch swapping options.

The networks computed by PAUP were rooted by positioning the root along the branch connecting the Laurales to the outgroups *Magnolia*, *Liriodendron*, and *Knema*. These representatives of Magnoliaceae and Myristicaceae were used as outgroups based on molecular phylogenetic trees for lower angiosperms obtained by Y.-L. Qiu (Qiu 1993, pers. comm. 1997), M. Chase (Chase & Albert, in press; Chase & Cox, in press), and V. Savolainen and colleagues (V. Savolainen, pers. comm., 1998). However, these workers, and also K. Ueda (pers. comm.), stress that the sistergroup relationship of Laurales and Magnoliales is poorly supported in their analyses and that additional outgroups need to be sampled to firmly establish the laurlean root. Nevertheless, the dense sampling within Laurales achieved in this study should ensure stable ingroup topologies.

Results

TrnL-trnF sequences of *Amborella trichopoda* Baill. (Amborellaceae) and *Hedyosmum bonplandianum* Kunth (Chloranthaceae) could not be aligned with the remaining 57 *trnL-trnF* sequences because they differed in more than a third of their nucleotides. The analysis of a combined data set of 39 *rbcL* and *trnL-trnF* sequences (1,776 characters, 307 of them parsimony informative; including three informative INDELs, see below) produced 56 equally parsimonious trees of 979 steps length (L) with a consistency index (CI, uninformative characters excluded) of 0.680 and a retention index (RI) of 0.738. A strict consensus of the 56 trees is shown in Fig. 1. The *rbcL-trnL-trnF* data recover the traditional assignments of genera to families, but branching patterns among families are unresolved except for the weakly supported (63% bootstrap) Monimiaceae-Lauraceae-Hernandiaceae clade.

The *trnL-trnF* data set comprises 58 sequences (species), and sampling is thus one-and-a-half times as dense as in the combined analysis. Lengths of the aligned *trnL-trnF* sequences (excluding gaps) vary from 373 bp in *Hedycarya arborea* to 305 bp in *Gyrocarpus americanus* and *Hernandia ovigera*, which share a single long deletion. Two INDELs were potentially informative at the family level: a 6 bp insertion shared by *Gyrocarpus*, *Hernandia ovigera*, *Cryptocarya*, and *Palmeria* and a 1 bp deletion shared by Hernandiaceae, Lauraceae, and Monimiaceae s.str. In addition, there was one informative bp change within a section of the alignment where some taxa had undergone deletions, namely a change from A to G shared by Monimiaceae s.str., some Lauraceae, and Hernandiaceae. When the two informative INDELs and the single nucleotide change were recoded as binary characters and added to the matrix, this did not affect topologies but resulted in slightly higher bootstrap values. These three characters were also used in the combined analysis (above).

Analyses of the *trnL-trnF* data resulted in memory overflow when more than 14,000 equally parsimonious trees had been stored. The high number of trees is due to congeneric species that differ from each other only by one or two nucleotides, resulting in unresolvable polytomies at the tips of the tree. Figure 2 shows one of 14,000 trees with

branch lengths proportional to numbers of nucleotide changes. Among the longest branches are those leading to Gomortegaceae, Calycanthaceae, and Hernandiaceae. (The hypothesized most basal species of the family, *Hazomalania voyroni* from Madagascar (Kubitzki 1993b), is now being added to the data set and may break-up the long hernandiaceous branch.) Clearly, the *trnL-trnF* intergenic spacer evolves too ra-

pidly to provide resolution at the family level within Laurales.

To allow complete searches and proper statistical evaluation of branch support, an additional analysis was performed on a reduced set of 43 *trnL-trnF* sequences. Figure 3 shows the strict consensus of the 333 equally parsimonious trees (445 characters, 140 of them parsimony informative, L = 445 steps, CI = 0.742, RI = 0.809) that

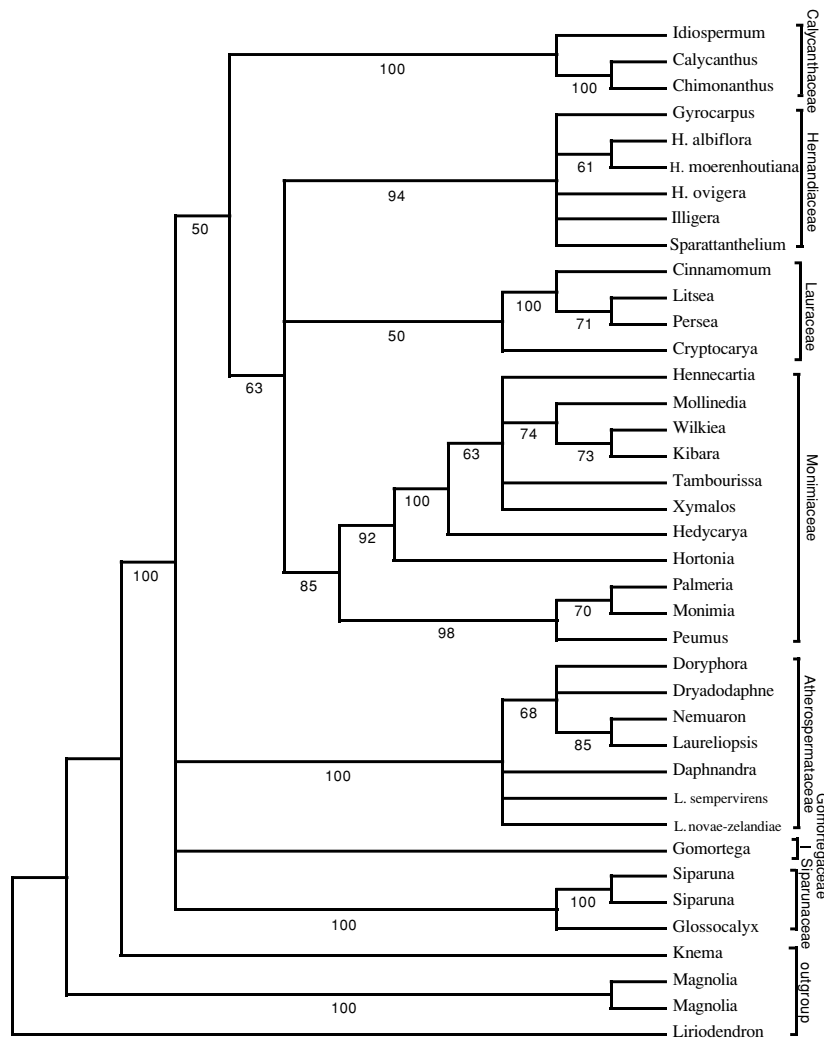


Fig. 1. Strict consensus of 56 equally parsimonious trees for Laurales based on cpDNA *rbcl* and *trnL-trnF* sequences (1776 characters, 307 of them informative, Length = 979 steps, CI = 0.680, RI = 0.738). Numbers below branches represent bootstrap values >50% (100 replicates). H. = *Hernandia* and L. = *Laurelia*; for remaining species names see the *rbcl* column in Table 2.

resulted from this analysis. The relationship between Lauraceae-Hernandiaceae-Monimiaceae s.str. also found in the combined analysis reappears, albeit with even lower bootstrap support (51%). *Siparuna guianensis* and *S. depressa*, the only monoecious species of *Siparuna* sequenced, are basal to the other *Siparuna* species, which are dioecious.

Discussion

Comparison with previous hypotheses on relationships

The results of this study indicate that the Monimiaceae as traditionally circumscribed (Perkins & Gilg 1901; Money *et al.* 1950; Cronquist 1981; Takhtajan 1987; Dahlgren

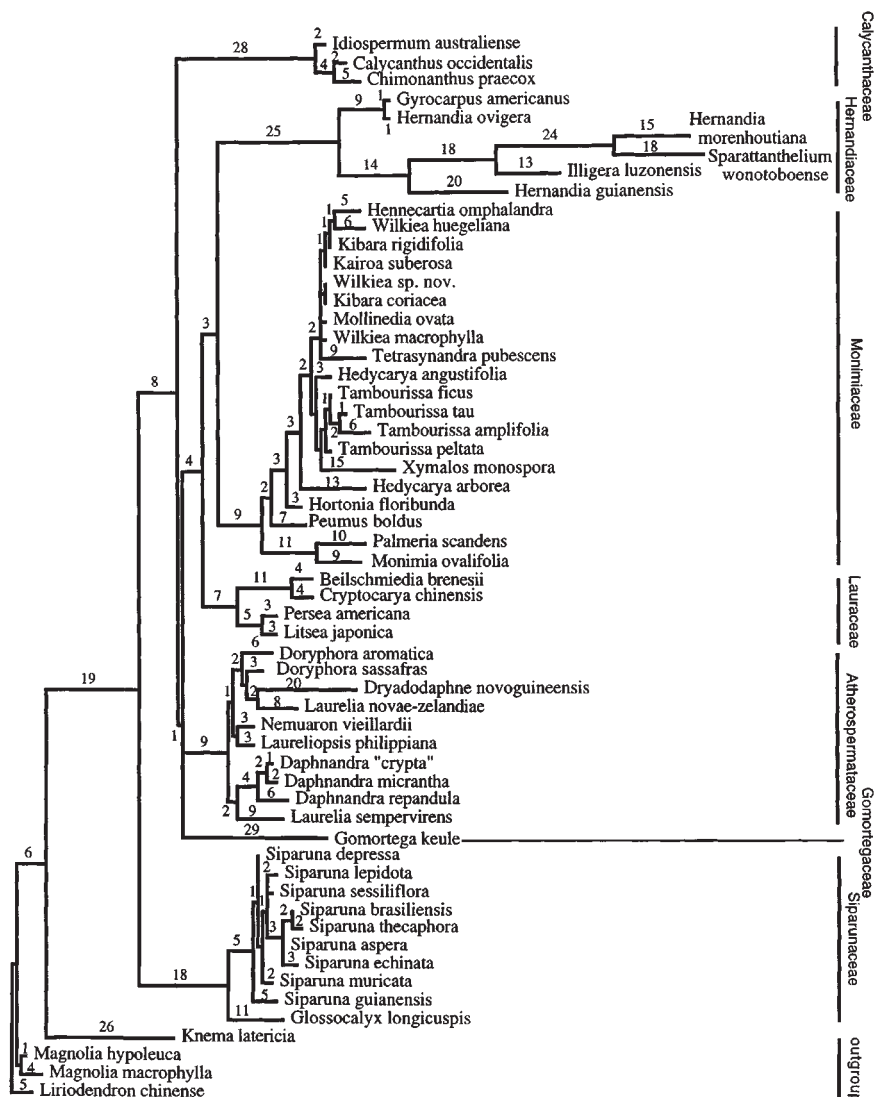


Fig. 2. One of 14,000 equally parsimonious trees held in memory from an analysis of the complete (58 species) *trnL-trnF* data set for Laurales (Length = 463 steps, CI = 0.728, RI = 0.849). Numbers above branches represent numbers of nucleotide substitutions.

1989; Thorne 1974, 1992; Philipson 1993), that is, including Atherospermataceae, Siparunaceae, and Monimiaceae s.str., are polyphyletic. More characters are needed to obtain robust trees for the Laurales, and I am now sequencing additional markers for this purpose. A cladistic analysis of morphological, karyological, and palynological characters (Renner *et al.* 1997) also could not identify the sister group to Monimiaceae s.str., but

united the Atherospermataceae, Gomortegaceae, and Siparunaceae albeit only on the basis of three characters homoplastic within Laurales.

The present molecular data support several aspects of recent morphology-based within-Monimiaceae classifications (Philipson 1987, 1993). Thus, *Peumus*, *Monimia*, and *Palmeria* form a separate clade, sister to all other core-monimioid genera. *Peumus* and

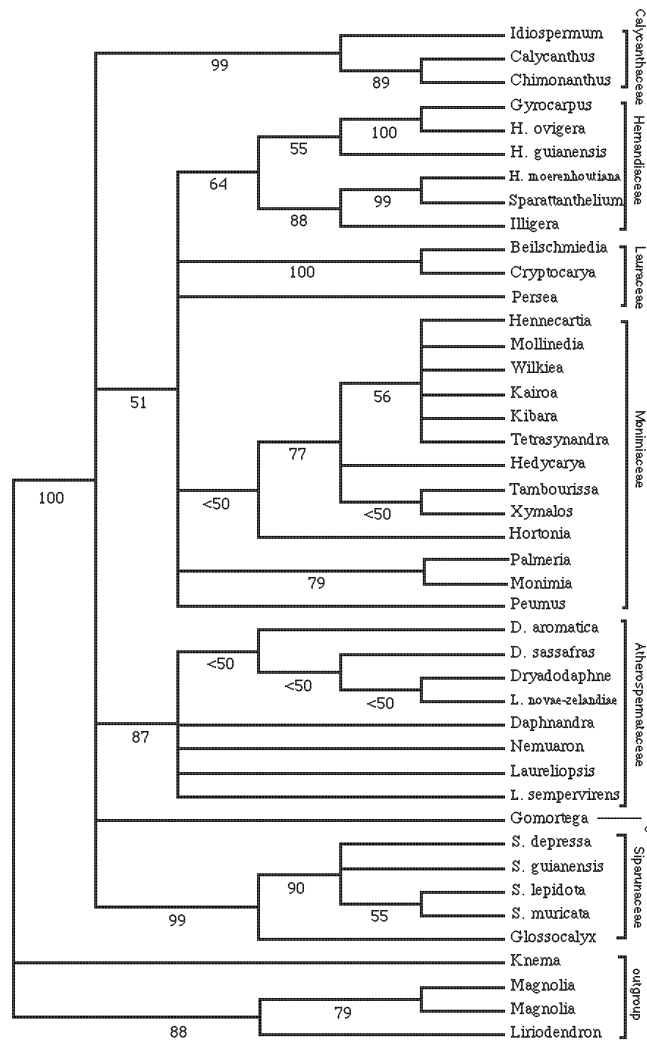


Fig. 3. Strict consensus of 333 equally parsimonious trees obtained from the analysis of a reduced (43 species) *trnL-trnF* data set (445 characters, 140 of them informative, Length = 445 steps, CI = 0.742, RI = 0.809). Numbers below branches represent bootstrap values >50% (100 replicates). D. = *Doryphora*, H. = *Hernandia*, L. = *Laurelia*, and S. = *Siparuna*; see Fig. 2 for remaining species names.

Palmeria had traditionally been seen as isolated from each other (Perkins & Gilg 1901; Garratt 1934; Money *et al.* 1950; Schodde 1970; Behnke 1981, but see Behnke 1988), but Philipson placed them together in a sub-family with *Monimia*, a genus of three species endemic to Mauritius and Réunion and which resembles *Palmeria* in the morphology of the female flowers and fruits. Sampson & Foreman (1990) in a detailed comparison of pollen morphology and ultrastructure furthermore concluded that "*Peumus* pollen is closer to that of *Palmeria* than to any other

member of the Monimiaceae whose pollen has been studied". There is no comparably detailed study of *Monimia* pollen, but a survey of pollen morphology of Malagasy Monimiaceae (Lorence *et al.* 1984) revealed a close resemblance of *Monimia* pollen to that of *Peumus*. *Peumus* consists of a single species of shrubs or treelets endemic in sclerophyllous forests in Chile; it is thus one of very few extratropical Monimiaceae s.str. It also differs from the remainder of the family in having a chromosome number of $n = 39$, rather than $n = 19$ as most other Monimiaceae

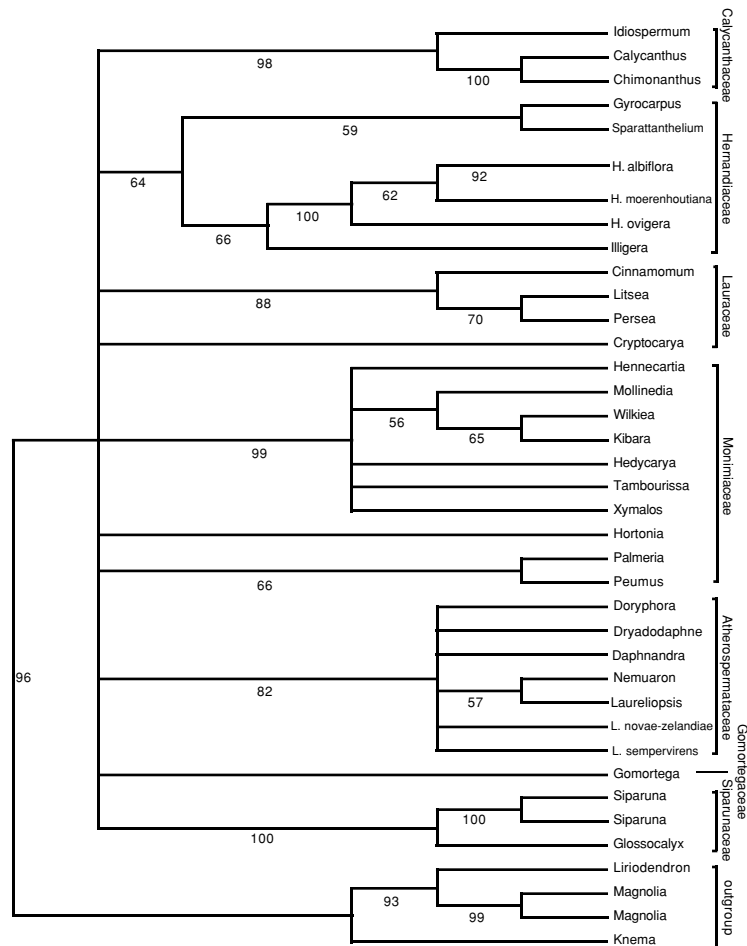


Fig. 4. Strict consensus of 470 equally parsimonious trees obtained from the analysis of the *rbcL* data set (1,331 characters, 173 of them informative, Length = 534 steps, CI = 0.657, RI = 0.750). Numbers below branches represent bootstrap values >50% (100 replicates). H. = *Hernandia* and L. = *Laurelia*; see Table 2 for remaining species names.

(Ehrendorfer *et al.* 1968). *Palmeria*, on the other hand, is a genus of 14 species of lianas that occur mainly in New Guinea, with one species westward to east Sulawesi and three in eastern Australia; it has a chromosome base number of 19. *Peumus* has relatively narrow phloem rays and non-septate fibers (Garratt 1934; Money *et al.* 1950), while *Palmeria* and *Monimia* have the strikingly broad rays and septate fibers typical of most core-Monimiaceae.

Curiously, Bentham (1880b) and Perkins & Gilg (1901; cf. Table 1) placed the New Caledonian *Amborella* next to *Peumus* (Chile). This placement is contradicted by morphology and anatomy (Pichon 1948; Money *et al.* 1950; Endress & Igersheim 1997) as well as by the large estimated average sequence divergence of 30% of an *Amborella trichopodat rnl-trnF* sequence from the remaining 60 sequences (*rbcl* data also place *Amborella* far from Laurales; Qiu *et al.* 1993; Chase & Albert, in press).

Beginning with Money *et al.* (1950), *Hortonia* has been placed in a subfamily by itself (Table 2) and been interpreted as "the least specialized surviving representative of an ancestral monimiaceous stock". This monospecific genus is the sole perfect-flowered Monimiaceae and also has very distinctive pollen (the exine is composed of coarse, hemi-helical bands, extending from one pole to the other). Based on the *rbcl-trnL-trnF* data, *Hortonia* is basal within the larger of the two major clades of Monimiaceae s.str. (Fig. 1).

Morphological circumscriptions of atherospermatoids (Money *et al.* 1950; Schodde 1969, 1970; Philipson 1993) are fully corroborated by the molecular data, but there are too few characters to address the morphology-based hypothesis (Schodde 1969, 1970; Renner *et al.* 1997) that Atherospermataceae are sister to Gomortegaceae. However, in an analysis of representatives of Laurales, Magnoliales, paleoherbs, and gymnosperms for which they sequenced *rbcl*, *atpB* (cpDNA genes) and the nuclear ribosomal 18S gene, Ueda *et al.* (1997) found that *Gomortega* grouped with Atherospermataceae. (Preliminary analyses of an enlarged data set that includes 37 1050 bp-long sequences from the cpDNA *rpl16* intron in addition to the *rbcl-trnL-trnF* sequences analyzed here, show an Atherospermataceae-Gomortegaceae-Siparunaceae trichotomy that is supported at the 72% bootstrap level; Renner, unpubl. data.)

Among the few morphological features suggesting a close relationship between Atherospermataceae and *Gomortega* is the peculiar structure of their sieve tube plastids (Behnke 1981, 1988). Most Monimiaceae s.str., and all Lauraceae, Hernandiaceae, and Siparunaceae, have protein-containing plastids of the same kind as found in most Magnoliaceae and many Myristicaceae (Psc-type plastids in the notation of Behnke 1988). A few monimiaceous genera have starch-containing plastids, and again such plastids are also found in the outgroups (Magnoliaceae and Myristicaceae). By contrast, Calycanthaceae (including *Idiospermum*; Kubitzki 1993a), Atherospermataceae, and *Gomortega* have plastids of the rare Pcsf-type (Behnke 1988). Depending on the eventual position of Calycanthaceae, these plastids either could have evolved twice within Laurales, once in the Calycanthaceae and once in the common ancestor of *Gomortega*/Atherospermataceae, or they could have been inherited from a common ancestor of Calycanthaceae, *Gomortega*, and Atherospermataceae and been lost in Siparunaceae. Traditionally, atherospermatoids have been placed next to siparunoids (Table 2) because the two families share narrow phloem rays (up to about 6 cells wide), a chromosome number of $n = 22$, 2-valvate stamens, and basal ovules. Note that *Gomortega* has a base number of $n = 21$, which could have evolved from $n = 22$. Two-valvate stamens have evolved several times within Laurales, being also found in Hernandiaceae and some species of Lauraceae, but the basal ovules are restricted to Atherospermataceae and Siparunaceae. The gynoceum of *Gomortega* is unique among Laurales in that it consists of a syncarpous, 2- or 3-locular pistil that is completely inferior; ovule position is apical (Leinfellner 1968; Endress & Igersheim 1997).

Within Atherospermataceae, the molecular data support Schodde's (1969, 1970, Schodde in Martínez-Laborde 1983) and Martínez-Laborde's (1988) separation of *Laureliopsis* from *Laurelia*. Prior to Schodde's work, the Chilean-Argentinian *Laureliopsis philippiana* (described in 1934), the only species of *Laureliopsis*, was included in *Laurelia*, a genus comprising one species in Chile and another in New Zealand. In the present analysis, *Laureliopsis* forms a well-supported clade (85% bootstrap in the combined analysis; Fig. 1) with the monotypic New Caledonian *Nemuaron*.

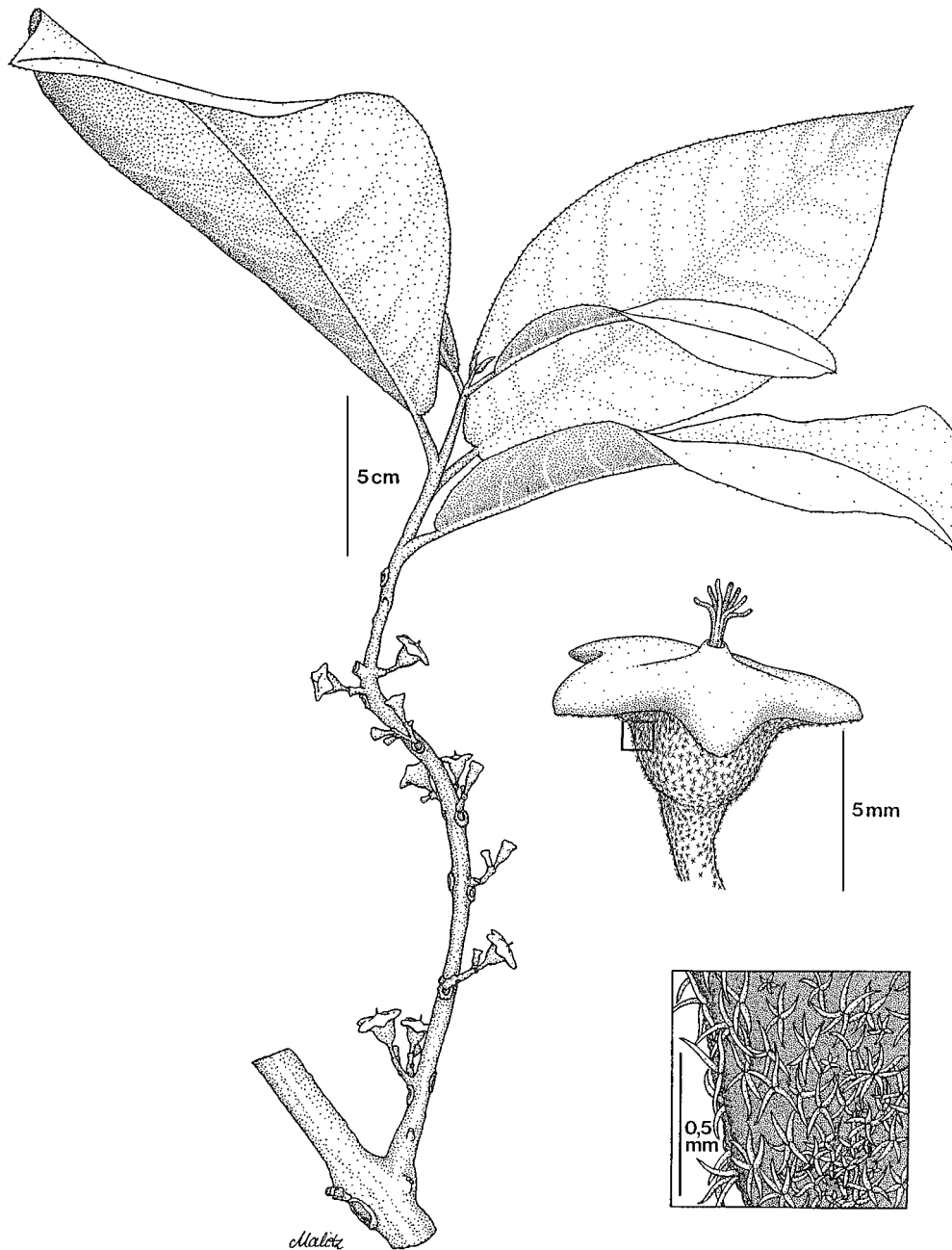


Fig. 5. Habit and female flower of *Siparuna conica* Renner & Hausner. The seven styles of the receptive flower shown to the right emerge through a narrow pore in the center of the floral roof (compare text).

Finally, the molecular data support the older view that *Siparuna* and *Glossocalyx* are closely related (Bentham 1880a; Perkins & Gilg 1901; Money *et al.* 1950; contra Philipson 1987, 1993). This is also in agreement with a morphology-based cladistic analysis that found four synapomorphies uniting these two genera, namely eglandular valvate stamens; disporangiate anthers in which the two thecae open not by two, but by a single or incompletely separated flap; flowers with a floral roof (a membrane that covers the flower center, Fig. 5); and unitegmic ovules (Renner *et al.* 1997).

Implications for the evolution of flowers and breeding systems

Traditional classifications of Monimiaceae have relied heavily on floral morphology, so it is of interest to explore the evolution of floral traits on the molecular trees. Paired nectary glands are present at the base of each of the 9–14, 40–150, or 3–8 fertile stamens of *Peumus*, *Monimia*, and *Hortonia* (see illustrations in Endress & Hufford 1989), respectively, but are lacking in *Palmeria* and all other monimioid genera, implying that such glands were present in the common ancestor of Monimiaceae and lost twice, once with the *Peumus-Palmeria* clade and a second time within the *Hortonia-Hennecartia* clade. *Hortonia* is the only Monimiaceae with fully functional bisexual flowers; it also has large tepals. All remaining genera in the *Hortonia-Hennecartia* clade have unisexual flowers and minute tepals. A parallel change from bisexual flowers and large tepals to unisexual flowers and minute tepals occurred in the *Peumus-Palmeria* clade: tepals in *Peumus* are large, those of *Palmeria* and *Monimia* are reduced. Female *Peumus* flowers retain 6–10 staminodes, indicating that the flowers were once bisexual, *Monimia* and *Palmeria* have strictly unisexual flowers without a trace of vestigial organs.

As illustrated and discussed by Endress (1979, 1980a, 1994: 232), Monimiaceae s.str. have increasingly complete enclosure of the reproductive organs in massive cup-like receptacles that raise the floral periphery around or above the gynoeceum. This trait, too, evolved at least twice within the family, once within the *Peumus-Palmeria* clade (massive female receptacles are found in *Palmeria* and *Monimia*, but not *Peumus*) and once within the

Hortonia-Hennecartia clade (*Hortonia* has only slightly concave female receptacles, the other genera have globose or urceolate female receptacles). An extreme development is reached in *Tambourissa* of Madagascar and the South American *Hennecartia* in which the carpels are completely embedded in very massive receptacles. The single species of *Hennecartia* has the further unusual feature of having only one or two carpels per flower. The only other Monimiaceae with solitary carpels is the East African *Xymalos*, with the sole species *X. monospora*. To obtain more resolution within Monimiaceae s.str., sequences from nuclear regions are currently being added to the cpDNA data (S. Renner, M. Zanis, & D. Soltis, unpubl. data).

Siparuna comprises about 72 species of shrubs, straggling shrubs, and trees and occurs from tropical Mexico throughout Central America and the West Indies and northern South America to Bolivia and Paraguay (Renner & Hausner 1997). Either 56 or 57 of the species are dioecious, while the remaining 14 or 15 are monoecious. The group is most diverse in Andean mid-elevation forests, but some species occur at sealevel or up to 3800 m. Relatively few species of *Siparuna* are found in the Amazon basin, the Guayana region, the Brazilian shield region, and the Atlantic rainforests of Brazil, but is in these regions that the monoecious species outnumber the dioecious ones. The only monoecious species sampled, *S. guianensis* and *S. depressa*, appear basal to two dioecious species in the reduced *trnL-trnF* data set (Fig. 3) and remain basal when all seven dioecious species sequenced so far are included in the analysis (tree not shown). Dioecy thus seems to have evolved within *Siparuna*, but this conclusion remains preliminary until all monoecious species have been sampled. The sister group, *Glossocalyx longicuspis*, is a dioecious straggling shrub that is common along forest margins in Cameroon (D. Thomas, pers. comm. 1996).

Implications for biogeography, and the fossil record of monimioid plants

Monimiaceae s.str.

As circumscribed here, Monimiaceae s.str. are pantropical. In the New World, both their main clades are represented, one by *Mollinedia* (incl. *Macrotorus* and *Macropeplus*) and

Hennecartia, the other by *Peumus*. On the African mainland, their sole extant representative is *Xymalos monospora*, while in Madagascar the same clade is richly represented by *Tambourissa* and its satellites with altogether 58 species (Lorence 1985, this figure includes a few species described after 1985). The Mascarenes are home to members of both major clades, harbouring *Monimia* as well as species of *Tambourissa*, and both clades are also present in New Guinea and tropical eastern Australia.

Fossil woods (*Hedycaryoxylon* spp.) characteristic of Monimiaceae s.str., that is, with strikingly broad rays, have been described from the Lower Oligocene of the eastern Cape province (Mädel 1960) and from the Lower Senonian of Central Germany (Süss 1960). A fossil leaf of *Mollinedia*, from the Eocene, has been found on the Antarctic Seymour Island (Dusén 1908). (Lower Senonian leaves from Central Germany of *Protohedycarya ilicoides* (Heer) Rufflé were first assigned to Monimiaceae s.str. [Rufflé 1965] but then transferred to Atherospermataceae [Knappe & Rufflé 1975]; Maastrichtian leaves of *Protohedycarya pseudoquercifolia* (Kräusel) Rufflé & Knappe (1988) from the Netherlands, which are deeply dissected into eight almost disconnected lobes, in my opinion are not monimiaceous.) The Monimiaceae s.str. thus may have been widespread by the late Cretaceous. Raven & Axelrod (1974) hypothesized that they migrated between South America and Africa (from where they reached Madagascar) and between West Gondwana and Australia across a narrower Indian Ocean, which would require a minimum age of 100 million years.

Siparunaceae, *Gomortegaceae*, and *Atherospermataceae*

Gomortega keule, the sole member of Gomortegaceae, is a rare and highly endangered tall tree (C. Baeza, University of Concepción, Chile, pers. comm. 1997) endemic in Chile, and its pollination and seed dispersal biology are unknown. It has no published fossil record (Friis *et al.* 1997).

The Atherospermataceae, or southern sassafrasses, comprise two species in two genera in Chile and Argentina, and 12 species in five genera in New Guinea, New Caledonia, New Zealand, Tasmania, and

Australia (Schodde 1969, 1970; Martínez-Laborde 1988; Philipson 1993). Ecologically, they are prominent elements of South Chilean laurel forests and temperate evergreen forests of New Zealand and Tasmania where they grow on well-drained or humid sites mainly between 800 and 2400 m elevation. Different from other Laurales, they have dry wind-dispersed achenes.

Lower Oligocene atherospermatoid wood has been described from the eastern Cape Province (Mädel 1960), but Mädel points out the problematic assignment of the 58 pieces of wood, which in her opinion might also belong in the vicinity of *Hortonia* and thus represent Monimiaceae s.str. Undoubtedly atherospermatoid wood (*Atherospermoxylon*), also from the Lower Oligocene, is, however, known from Egypt (Kräusel 1939), and an Eocene leaf has been described from Antarctica (Dusén 1908). Atherospermatoid leaves are also known from the Lower Senonian of Central Germany (Knappe & Rufflé 1975). Thus, in the past, Atherospermataceae seem to have occupied a range similar to Monimiaceae, but they are now extinct in Africa and have only two species in South America. The family appears to comprise two phylogenetically independent Chilean-Australasian disjunctions because its two Chilean members do not form a monophyletic clade (Figs. 1, 4).

The Siparunaceae are restricted to South America and West Africa. The floristic links between tropical Africa and tropical America have long been of interest to plant systematists and biogeographers, largely because of the question of the ages and dispersal histories of the groups involved (Thorne 1973; Raven & Axelrod 1974; Goldblatt 1993). At least 80 ancient to moderately derived angiosperm families are thought to have dispersed directly between Africa and South America before the continents became widely separated, i.e. up to about 62–66 million years ago. Among these must have been Siparunaceae (still extant on both sides of the Atlantic) and Atherospermataceae (with two species in Chile today, but in Africa only known from Lower Oligocene fossil wood).

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