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Phylogenetic relationships in the Hamamelidaceae: evidence from the nucleotide sequences of the plastid gene *mat*K

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Abstract. The Hamamelidaceae is a family that bridges the basal elements of the Rosidae and the "lower" Hamamelidae, thus a better understanding of the phylogeny of the family is important for clarifying evolutionary patterns in the diversification of eudicots. However, subfamilial as well as tribal relationships in the Hamamelidaceae have been controversial. Nucleotide sequences of the chloroplast gene *mat*K were used to study the intergeneric relationships of the family. In the phylogenetic trees, constructed using parsimony analysis, the clade containing *Altingia* and *Liquidambar* (Altingioideae) is sister to a clade that includes all other Hamamelidaceae. *Exbucklandia* and *Rhodoleia* form a clade, suggesting a close relationship between the two genera. *Disanthus* is sister to the monophyletic Hamamelidoideae. The paraphyletic arrangement of *Disanthus*, *Mytilaria* and *Exbucklandia* with respect to the Hamamelidoideae does not support the combination of these genera in one subfamily. In the Hamamelidoideae, the *mat*K phylogeny supports the monophyly of several previously recognized groups with modifications, including the tribes Eustigmateae (incl. *Molinadendron*), Fothergilleae (excl. *Molinadendron* and *Matudaea*), and the subtribe Dicoryphinae. However, the Hamamelideae as traditionally circumscribed is polyphyletic. Apetaly has evolved three times independently in the Hamamelidoideae.

Key words: Hamamelidaceae, Phylogeny, *mat*K gene.

The Hamamelidaceae, a family of 30–31 genera and about 140 species, are distributed in the tropical, subtropical and temperate areas in both the Old and New Worlds (Endress 1993, Zhang and Lu 1995). Uniform characters in the Hamamelidaceae include woody habit, stipulate leaves, 2-carpellate pistils, and multicellular stigmatic papillae (Endress 1989a), but other characters are highly diverse. For example, leaves are persistent or deciduous, simple and pinnately veined or palmately lobed and veined. Most species have bisexual flowers, but some are andromonoecious (both staminate and bisexual flowers found in an individual), and others are monoecious. Flowers are complete and 5-merous in most genera, 4-merous in several genera and variable in others; a few genera have an incomplete perianth or are naked.

As for the systematic position of the Hamamelidaceae, most of the traditional classifications placed the family in the "lower" Hamamelidae, including Cercidiphyllaceae, Tetracentraceae, Trochodendraceae, Daphni-

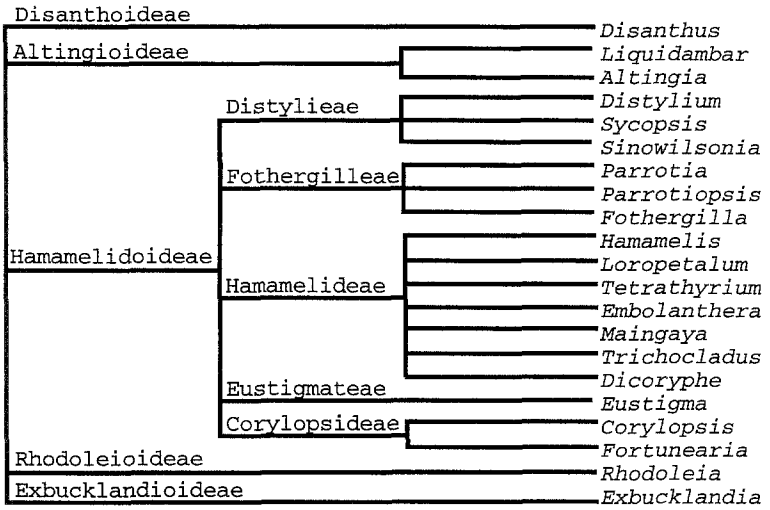
phyllaceae, Platanaceae, Myrothamnaceae and Eupteleaceae (Takhtajan 1980, Cronquist 1988). Endress (1977) envisaged this family as a connecting taxon between the "lower" and the "higher" Hamamelidae (e.g. Betulaceae, Fagaceae, and Juglandaceae). In recent phylogenetic studies the Hamamelidaceae have been placed in a more or less intermediate position between the "lower" hamamelids and some basal elements of rosids (Hufford 1992, Chase et al. 1993, Endress 1993, Morgan and Soltis 1993). Apparently, a more comprehensive study (more taxa and more sources of data) is needed to further assess the systematic position of the Hamamelidaceae.

Morphological analyses of Hamamelidae (Hufford and Crane 1989) and Rosidae (Hufford 1992), including all subfamilies of the Hamamelidaceae, have suggested that the Hamamelidaceae is a monophyletic group. Several broad molecular analyses provided some insights into relationships of the hamamelidaceous members with other eudicots (Chase et al. 1993, Hoot and Crane 1996, Hoot et al. 1997, Soltis et al. 1997, Qiu et al. 1998, Hoot et al. 1999), but none of them has made a convincing argument regarding the monophyly of the Hamamelidaceae due to limited sampling and the conservative nature of the genes utilized. Nevertheless, these molecular studies, especially the triple gene (*apt*B, *rbc*L, 18S) analysis by Hoot et al. (1999), have raised reasonable concern that the Hamamelidaceae may not be monophyletic. Therefore, the monophyly of the Hamamelidaceae needs further testing. The objective of this study, however, is to assess intergeneric relationships of the Hamamelidaceae since the phylogeny within the Hamamelidaceae remains unresolved at both subfamilial and tribal levels.

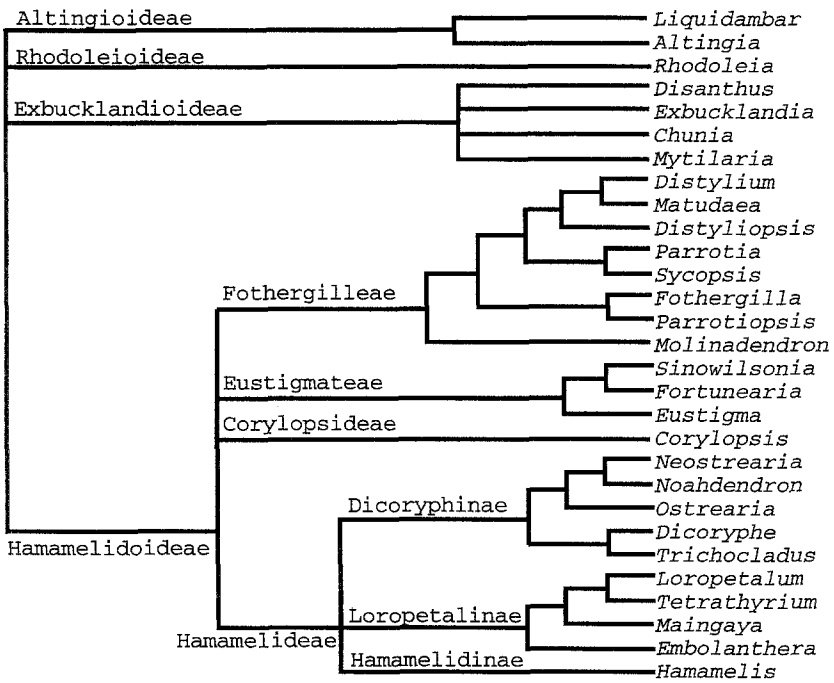
Reinsch (1889) proposed three subfamilies within the Hamamelidaceae [Altingioideae, Bucklandioideae (=Exbucklandioideae) and Hamamelidoideae]. Niedenzu (1891), suggested a two-subfamily system (Bucklandioideae and Hamamelidoideae). The first comprehensive classification was proposed by Harms (1930) (Fig. 1A), who recongnized five subfamilies (Disanthoideae, Hamamelidoideae, Rhodoleioideae, Bucklandioideae, and Liquidambaroideae). Chang (1973, 1979) reviewed the hamamelidaceous flora of China, recognizing the five subfamilies of Harms (1930) but also erecting a new subfamily for *Mytilaria* Lecomte and his own new genus *Chunia*. Endress (1989c) provided a suprageneric scheme for the Hamamelidaceae (Fig. 1B). In this system he combined the three subfamilies, Disanthoideae, Mytilarioideae and Exbucklandioideae, thus recognizing four subfamilies in the Hamamelidaceae (Altingioideae, Rhodoleioideae, Exbucklandioideae, and Hamamelidoideae). Most recently, Takhtajan (1997) retained Disanthoideae, while recognizing Endress's (1989c) combination of the Exbucklandioideae and Mytilarioideae.

Differences of opinion concerning tribal or subtribal delimitations focus on the Hamamelidoideae since the other subfamilies have only one to a few genera. Harms (1930) divided the Hamamelidoideae into five tribes, including Corylopsideae, Distylieae, Fothergilleae, Hamamelidoideae, and Eustigmateae (Fig. 1A). Endress (1989c) revised Harms's (1930) system and recognized four tribes in the Hamamelidoideae by including the Distylieae in the Fothergilleae; he also made some generic rearrangements (Endress 1989b, Fig. 1B).

The *mat*K gene, which encodes a chloroplast maturase and is located in the *trn*K intron, has become increasingly popular for plant molecular systematics for several reasons. First, compared with the *rbc*L gene, the *mat*K gene has a relatively higher substitution rate (Olmstead and Palmer 1994), indicating that it may be more appropriate for systematic studies at lower taxonomic levels, such as tribes and genera. This proposition has been confirmed by several cladistic analyses (Johnson and Soltis 1994, Steele and Vilgalys 1994), including a phylogenetic study of the "higher" Hamamelidae (Manos and Steele 1997). Sequence divergence of the *mat*K gene within a genus is rather small, c. 1%,



A



B

Fig. 1. Two major classification systems of the Hamamelidaceae: **A** Harms (1930), **B** Endress (1989b, c)

providing a limited number of informative sites. However, these sites have proved very useful in resolving interspecific relationships in some genera such as *Liquidambar* (Li et al. 1997a). Second, there is a certain degree of evolutionary constraint imposed by the function of the maturase the *mat*K encodes (Neuhaus and Link 1987, Wolfe et al. 1992). This property facilitates sequence alignment (Soltis et al. 1996, Plunkett et al. 1997). As

pointed out by Hilu and Liang (1997), the *mat*K gene is informative in reconstructing phylogenetic relationships at different taxonomic levels and is a promising source of data to study the molecular systematics of plants. Therefore, in this study we chose to use DNA sequences of the *mat*K gene to investigate phylogenetic relationships within the Hamamelidaceae and to evaluate the existing classification systems of the family.

Materials and methods

Plant materials. Thirty species and 27 (out of 31) genera of the Hamamelidaceae were sampled, representing all of the subfamilies, tribes and subtribes previously proposed by Harms (1930), Chang (1979), and Endress (1989c). Sources, vouchers, and GenBank sequence accession numbers are listed in Table 1.

Molecular techniques. Total genomic DNAs were extracted from fresh or silica gel dried leaves using the standard DNA extraction procedures of Doyle and Doyle (1987). Polymerase chain reaction (PCR^{TM}) amplification, PCR product purification, and sequencing were conducted as described in Li et al. (1997a). An additional sequencing primer, *mat*KF4-2, was designed for *Maingaya* and the sequence is as follows: 5′ TGGTTCAAACCC-TTCGCTACT 3′.

Sequence analysis. Sequence chromatograms were analyzed using the SEQED program (Applied Biosystems, Foster City, CA), and the overlap option was employed to assure correct base-calling. The analyzed sequences were then exported as EDITSEQ files. Base composition, translated amino acid sequences, and codon usage were obtained using the EDITSEQ program. The sequences were aligned using the MEGALIGN program. Both EDITSEQ and MEGALIGN are programs in the DNASTAR software package (version 3.72, Madison, WI).

Phylogenetic analyses. Parsimony analyses were conducted using the test version 4.0d55 of PAUP written by David L. Swofford (Smithsonian Institution). Given the limitations of computer memory and the large sample size, heuristic searches were performed with the following options: TBR (tree bisection reconnection), simple sequence addition, mulpars on, and steepest descent off. Indels in the data matrix were coded as missing data. However, some indels were phylogenetically informative and are discussed below.

Saxifragaceous genera have been shown to be closely allied with the Hamamelidaceae (Hufford 1992, Chase et al. 1993, Endress 1993, Morgan and Soltis 1993). Our preliminary analysis of the *mat*K gene sequences of the Saxifragales, including Saxifragaceae s.l., Paeoniaceae, "lower" hamanelids, and all subfamilies of the Hamamelidaceae, suggested that the Saxifragaceae-Paeoniaceae clade was sister to the Hamamelidaceae clade (possibly including *Cercidiphyllum* and *Daphniphyllum*). Therefore, *Sullivantia sullivantii* (GenBank accession #20130, Saxifragaceae) and *Saxifraga integrifolia* (GenBank accession #20131, Saxifragaceae) were used as outgroups for rooting purposes.

Bootstrap analysis (Felsenstein 1985) of 100 replicates and the constraint decay analysis (Bremer 1988, Morgan 1997) were performed to obtain indices of relative support for individual clades using PAUP.

Skewness of tree length distributions has been proposed to be a level indicator of phylogenetic information contained in a data matrix (Huelsenbeck 1991). The skewness test was implemented using the random tree option of PAUP; 10000 random trees were examined. Another test of phylogenetic information of a data set is the randomization test, which produces the permutation tail probability (PTP) statistics. Data sets with values of PTP < 0.01 are considered to be considerably different from randomized data (Faith and Cranston 1991, Plunkett et al. 1997). The permutation test was performed using the permutation option of PAUP with 100 replicates and heuristic searches.

Aligned sequences were imported into the MacClade computer program, version 3.03 (Maddison and Maddison 1992) to estimate transition (Ts) and transversion (Tv) ratio; to calculate character changes in the first, second and third codon positions using one of the most parsimonious trees; and to compare the competing hypotheses concerning generic relationships of the Hamamelidaceae. The MacClade program was also used to estimate the number of unambiguous changes along branches.

Table 1. Sources and vouchers of the species sequenced for *mat*K gene and used in this analysis

Species	Collector and voucher	Source	GenBank accession number
Altingia excelsa Nor.	Y.-L. Qiu	China	AF013037
Corylopsis sinensis Hemsl.	J.-H. Li 02	Arnold Arboretum, MA.	AF013038
C. spicata Sieb. and Zucc.	J.-H. Li 03	Arnold Arboretum, MA.	AF013039
Dicoryphe stipulacea Jaume St.-Hil.	A. Randrianasolo 543	Tulear, Madagascar	AF013040
Disanthus cercidifolius Max.	A. L. Bogle	Woodlanders, Inc. SC.	U77091
Distyliopsis tutcheri Endress	A. L. Bogle	Woodlanders, Inc. SC.	AF013042
Distylium racemosum Sieb and Zucc.	A. L. Bogle	Woodlanders, Inc. SC.	AF013041
Eustigma oblongifolium Gardn. and Champ.	N.-J. chung	Taiwan	AF013043
Exbucklandia populnea (R. Br.) R. W. Br.	A. L. Bogle	Manuka St. Park, Hawaii	U77092
Fortunearia sinensis R. and W.	J.-H. Li 04	Arnold Arboretum, MA.	AF013044
Fothergilla major Lodd.	J.-H. Li	Univ. of New Hampshire campus	AF013045
Hamamelis virginiana L.	J.-H. Li	Univ. of New Hampshire campus	AF013046
H. vernalis Sarg.	J.-H. Li	Arnold Arboretum, MA.	AF013047
Liquidambar formosana Hance	A. L. Bogle	Univ. of New Hampshire Greenhouse	AF015650
L. orientalis Mill.	T. D. Omar	Univ. of Washington Arboretum	AF015651
Loropetalum sinense (R. Br.) Oliv.	A. L. Bogle	Missouri Bot. Gard.	AF013059
Maingaya malayana Oliv.	L. G. Saw	Forest Research Institute, Kepong, Malaysia	AF025393
Matudaea trinervia Lund.	P. K. Endress	Botanical Garden of Zurich Univ.	AF013048
Molinadendron sinaloense Endress	P. K. Endress	Botanical Garden of Zurich Univ.	AF013049
Mytilaria laosensis Lec.	Z.-C. Luo	Guangxi, China	U77093
Neostrearia fleckeri Smith	P. K. Endress	Botanical Garden of Zurich Univ.	AF013050
Noahdendron nicholasii Endress, Hyland and Tracey	P. K. Endress	Botanical Garden of Zurich Univ.	AF013051
Ostrearia australiana Baill.	P. K. Endress	Botanical Garden of Zurich Univ.	AF013052
Parrotia persica C. A. Mey	A. L. Bogle	Univ. of New Hampshire Greenhouse	AF013053
Parrotiopsis jacquemontiana Rehd.	A. L. Bogle	Harvard Univ. campus	AF013054
Rhodoleia championii Hook. f.	A. L. Bogle	Lyon Arboretum, Honolulu, Hawaii	U77094
Shaniodendron subaequale Deng, Wei and Wang	Y.-L. Qiu	Jiangsu, China	AF013055
Sinowilsonia henryi Hemsl.	J.-H. Li 05	Arnold Arboretum, MA.	AF013056
Sycopsis sinensis Oliv.	A. L. Bogle	Woodlanders, Inc. SC.	AF013057
Trichocladus crinitus Pres.	A. L. Bogle	Longwood Gardens, PA.	AF013058

Table 2. Sequence characteristics of the *mat*K gene

Species	Length	G+ C (%)	Divergence																															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1 *Altingia excelsa*	1512	35	–																															
2 *Corylopsis sinensis*	1515	34	6.1	–																														
3 *Corylopsis spicata*	1515	34	6.1	0.5	–																													
4 *Dicoryphe stipulacea*	1515	34	4.7	2.2	2.2	–																												
5 *Disanthus cercidifolius*	1506	34	6.1	4.4	4.5	3.1	–																											
6 *Distyliopsis tutcheri*	1515	34	5.2	2.7	2.2	1.3	3.8	–																										
7 *Distylium racemosum*	1515	34	5	2.4	1.9	1	3.6	0.3	–																									
8 *Eustigma oblongifolium*	1515	34	5.3	3	3	1.1	3.9	2.1	1.8	–																								
9 *Exbucklandia populnea*	1512	35	5.4	4.8	4.9	3.3	5	3.8	3.6	4.1	–																							
10 *Fortunearia sinensis*	1515	34	5.8	3.2	3.1	1.5	4.3	2.2	1.9	1.5	4.5	–																						
11 *Fothergilla major*	1515	34	5	2.3	2.1	0.9	3.4	1	0.7	1.5	3.6	1.9	–																					
12 *Hamamelis virginiana*	1515	34	4.9	2	2	0.7	3.1	0.9	0.6	1.5	3.4	1.9	0.5	–																				
13 *Hamamelis vernalis*	1515	34	5.3	2.4	2.4	1.1	3.5	1.3	1	1.8	3.8	2.2	0.9	0.4	–																			
14 *Liquidambar formosana*	1512	35	0.5	5.9	6	4.6	5.9	5	4.8	5.2	5.3	5.6	4.8	4.7	5.1	–																		
15 *Liquidambar orientalis*	1512	35	0.9	5.8	5.8	4.4	5.8	4.9	4.6	5	5	5.5	4.7	4.6	5	0.7	–																	
16 *Loropetalum sinense*	1515	34	5.8	2.1	2.2	2	4.1	2.6	2.3	2.8	4.5	3.1	2.2	1.8	2.2	5.6	5.4	–																
17 *Maingaya malayana*	1515	34	5.8	2	2.1	2	4.2	2.1	2.2	2.8	4.5	3.1	2.2	1.8	2.2	5.6	5.5	1.5	–															
18 *Matudaea trinervia*	1515	34	5.9	2.2	2.4	2.2	4.5	2.8	2.5	3	4.9	3.2	2.4	2.1	2.5	5.7	5.6	1.7	1.8	–														
19 *Molinadendron sinaloense*	1521	34	5.2	2.6	2.7	0.7	3.6	1.8	1.5	1.3	3.7	1.7	1.3	1.1	1.5	5	4.8	2.4	2.4	2.6	–													
20 *Mytilaria laosensis*	1515	34	5.7	4.1	4.2	2.4	4.3	3.2	2.8	3.2	3.9	3.5	2.8	2.6	5.4	5.4	5.2	3.6		3.6	3.9	2.9	–											
21 *Neostrearia fleckeri*	1515	34	5.2	2.6	2.6	0.5	3.5	1.7	1.4	1.3	3.7	1.9	1.3	1.1	1.5	5	4.8	2.4	2.4	2.6	1.1	2.8	–											
22 *Noahdendron nicholasii*	1515	34	5	2.4	2.5	0.4	3.4	1.6	1.3	1.3	3.6	1.7	1.1	0.9	1.3	4.8	4.7	2.2	2.2	2.5	1	2.7	0.5	–										
23 *Ostrearia australiana*	1515	34	5.3	2.7	2.8	0.6	3.5	1.8	1.5	1.6	3.8	2	1.4	1.2	1.6	5.1	5	2.5	2.5	2.8	1.3	2.9	0.8	0.7	–									
24 *Parrotia persica*	1515	34	5.5	3.4	3.5	1.8	4.3	2.2	1.9	2.6	4	3	1.9	1.7	2	5.3	5.2	3.2	3	3.5	2.2	3.6	2.2	2	2.3	–								
25 *Parrotiopsis jacquemontiana*	1515	34	4.8	2.1	1.9	0.6	3.2	0.7	0.4	1.4	3.4	1.8	0.3	0.2	0.6	4.6	4.5	1.9	1.9	2.2	1.1	2.5	1	0.9	1.1	1.6	–							
26 *Rhodoleia championii*	1512	34	5.2	4.7	4.8	3	4.6	3.7	3.4	3.8	2.4	4.2	3.4	3.2	3.6	5	4.7	4.2	4.4	4.6	3.4	3.8	3.4	3.3	3.6	4	3.1	–						
27 *Shaniodendron subaequale*	1515	34	5	2.4	2	0.9	3.5	0.6	0.3	1.7	3.5	2.5	0.5	0.5	0.9	4.8	4.6	2.2	2	2.4	3	2.8	1.3	1.1	1.4	1.7	0.3	3.4	–					
28 *Sinowilsonia henryi*	1515	35	5.6	2.8	2.9	1.2	4.1	1.9	1.5	1.7	4.1	1.6	1.7	1.5	1.9	5.4	5.3	2.8	2.8	3	1.1	3.2	1.6	1.5	1.7	2.7	1.4	3.8	1.7	–				
29 *Sycopsis sinensis*	1515	34	5.2	2.5	2	1.1	3.7	0.3	0.1	1.9	3.8	2	0.8	0.7	1.1	5	4.8	2.4	2.3	2.6	1.6	3	1.5	1.4	1.7	2	0.5	3.6	0.4	1.7	–			
30 *Trichocladus crinitus*	1515	34	5.4	3	3	1.1	3.9	2.2	1.9	2	4.2	2.4	1.8	1.6	1.9	5.2	5.1	2.9	2.9	3.2	1.7	3.4	1.3	1.3	1.5	2.7	1.5	4	1.8	2.1	2	–		
31 *Saxifraga intergrifolia*	1518	32	12.4	11.9	12	10.5	11	10.8	10.5	11	11.5	11.6	11	10.4	10.8	12	11.8	11.3	11	11.9	11	12	10.8	10.7	11	11.3	10.4	11	10.4	11.3	11	11.3	–	
32 *Sullivantia sullivantii*	1521	34	8.9	9.1	9.3	7.5	8.3	8.1	7.8	8.1	8.3	8.7	7.8	7.6	8	8.6	8.6	8.6	8.5	9.1	7.9	8.2	8	7.8	7.9	8.4	7.6	8.1	7.8	8.4	8	8.2	8.4	–

Results

Sequence characteristics. The sequence length of the *mat*K gene in the Hamamelidaceae ranged from 1506 bases in *Disanthus* to 1521 bases in *Molinadendron*. In most of the other genera, this gene was 1515 bases long, while in *Altingia* and *Liquidambar* (Altingioideae), *Exbucklandia*, *Rhodoleia*, and *Sinowilsonia*, the *mat*K gene was 1512 bases in length. The number of amino acids ranged from 502 to 507 (for amino acid sequences, see Li 1997). In terms of nucleotide composition, the *mat*K gene was AT rich in the Hamamelidaceae; the GC contents were c. 34% (Table 2). Pairwise sequence divergence basically corresponded to taxonomic levels: 0.5–1% within *Corylopsis*, *Hamamelis*, and *Liquidambar*; 2–3% at generic levels, and 4–6% at the subfamilial level (Table 2). Alignment of the sequences in the Hamamelidaceae required five deletions, two of which were three bases long, while the other three were two, six, and seven bases in length (for the aligned *mat*K sequences, see Li 1997).

The Ts/Tv ratio calculated using the MacClade program was about 1.3 for the *mat*K gene sequences in the Hamamelidaceae, and the relative percentages of character state changes were 32%, 25%, and 43% for the first, second, and third positions of the codon respectively.

Phylogenetic analyses. We have used a 1:1.3 weighting scheme for Ts/Tv substitutions (see above), but did not find any effect on the topology of phylogenetic trees. Therefore, we report only the results of the analyses using unweighted characters and unordered transformations. The parsimony analysis resulted in six equally short trees with a length of 582 steps and a consistency index (CI) of 0.85 (strict consensus tree shown in Fig. 2). *Altingia* and *Liquidambar* formed a well-supported clade [bootstrap percentage (BP) = 100%, decay index (DI) = 8], which was sister to all remaining Hamamelidaceae. *Exbucklandia* and *Rhodoleia* were well-supported as sister genera (BP = 100%, DI = 7). *Mytilaria* and *Disanthus* were paraphyletically arranged with *Disanthus* sister to a well-supported clade equivalent to the Hamamelidoideae. The three Hamamelidoideae clades were: 1) *Corylopsis* and the branch of *Maingaya*, *Loropetalum*, and *Matudaea*, 2) Dicoryphinae Endress and Eustigmateae (sensu Endress 1989c) plus *Molinadendron*, and 3) Fothergilleae (sensu Endress 1989c, excluding the New World *Matudaea* and *Molinadendron*, but including *Hamamelis*). These three clades formed a trichotomy.

Discussion

Phylogenetic usefulness of *mat*K gene. Both g_1 (tree length skewness) statistics and the PTP (permutation tail probability) test have shown that *mat*K data matrices contain a large amount of phylogenetic structure in the *Apiales* ($g_1 = -0.51$, $P < 0.01$, Plunkett et al. 1997) and the Hamamelidaceae ($g = -1.89$, $P < 0.01$, this study), thus quantitatively indicating the usefulness of the *mat*K gene in these phylogenetic studies. At the generic level, informative sites are about 8.6% in the Hamamelidaceae, giving rise to about 130 informative characters. As a result, phylogenetic analyses using the *mat*K data set resolved most of the intergeneric relationships in the Hamamelidaceae. In addition, a higher percentage of phylogenetically informative sites in the *mat*K gene has been reported in other families (Plunkett et al. 1997). Thus, the *mat*K gene is informative in resolving relationships within a family. The sequence divergence of the *mat*K gene between the hamamelidaceous genera and the outgroup genera from the Saxifragaceae is 8–11%, and the sequences are unambiguously alignable. This suggests that the *mat*K DNA sequences are likely to be useful in resolving deep relationships at family or even order levels.

Phylogeny of the Altingioideae. The Altingioideae includes three genera, *Altingia*, *Liquidambar*, and *Semiliquidambar* Chang (Chang 1973, 1979; Bogle 1986; Endress 1989c). *Semiliquidambar* is morphologically

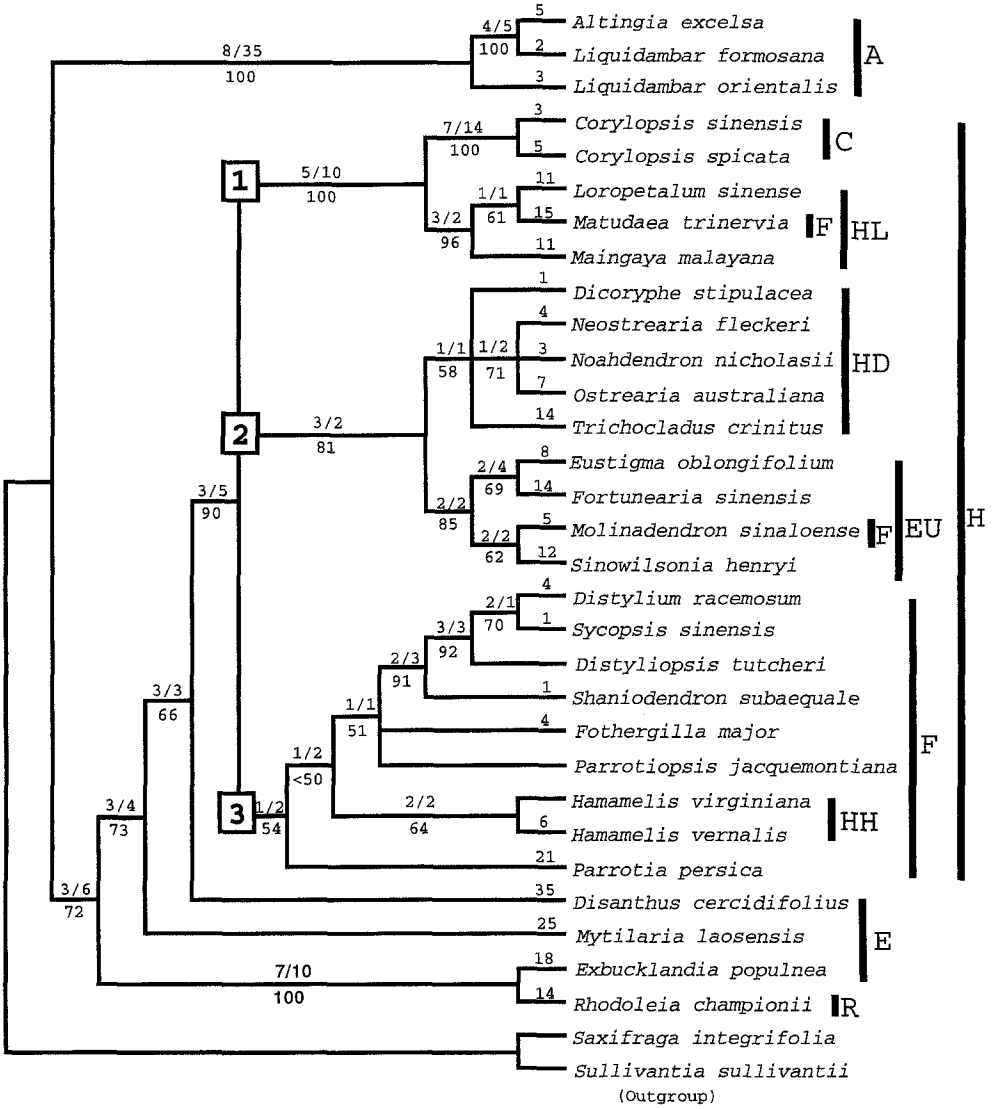


Fig. 2. Strict consensus of the six most parsimonious trees of 582 steps, based on sequences of the *mat*K gene. CI = 0.85, RI = 0.82. Numbers above and below branches are decay indices/the number of unambiguous substitutions and bootstrap percentages respectively; numbers above the terminal branches are unambiguous substitutions; boxed numbers denote the three major clades in the Hamamelidoideae. Groupings on the right side follow Endress (1989c). *A* Altingioideae, E Exbucklandioideae, *H* Hamamelidoideae, *R* Rhodoleioideae, *C* Corylopsideae, *EU* Eustigmateae, *F* Fothergilleae, *HD* Hamamelideae-Dicoryphinae, *HH* Hamamelideae-Hamamelidinae, *HL* Hamamelideae-Loropetalinae

intermediate, and thus has been considered to be a hybrid between the other two genera (Chang 1962; Bogle 1968, 1986). *Altingia* is very similar to the species of *Liquidambar* in many morphological structures (Harms 1930; Tong 1930; Bogle 1968, 1986; Melikian 1973a,b; Rao 1974; Chang 1979; Bogle and Philbrick 1980; Wang 1992). The phylogenetic analysis reported here supports a close relationship between *Altingia* and *Liquidambar* (Fig. 2), with 35 unambiguous nucleotide changes supporting this clade. Species in the

Altingioideae also share a three-base deletion and several synapomorphic amino acid substitutions (Li 1997). Interestingly, the sampled species of *Altingia* (*A. excelsa*) is sister to one of the two *Liquidambar* species, *L. formosana*, suggesting that *Altingia* may be derived from within *Liquidambar*. This result is consistent with *rbc*L analysis (Chase et al. 1993). A more inclusive study of the two genera is needed using sequences of the *mat*K gene or sequences with greater variation to assess this issue.

A long-standing question regarding the Altingioideae has been whether this group should be considered as a separate family (Endress 1989c, Pan et al. 1990, Wang 1992, Takhtajan 1997). In the *mat*K phylogeny the Altingioideae clade was sister to the rest of the Hamamelidaceae, implying that it is reasonable to recognize the group as a family Altingiaceae. Several molecular studies have shown that the Altingioideae may not be sister to the clade of the other Hamamelidaceae (Hoot and Crane 1996, Hoot et al. 1997, Qiu et al. 1998, Hoot et al. 1998), further supporting the distinctiveness of the Altingioideae from other hamamelidaceous members. However, further study is warranted to examine the systematic position of the Altingioideae.

Polyphyly of the Exbucklandioideae. This subfamily, as recently circumscribed by Endress (1989c), consists of four genera, *Disanthus*, *Exbucklandia*, *Mytilaria*, and *Chunia*, the latter was not available for this analysis. Each of the other three genera has been treated as representing a separate subfamily based on morphological characters, which suggests a distant relationship (Harms 1930; Chang 1948, 1979; Pan et al. 1991). The fact that these genera share several morphological characteristics, such as palmately veined leaves; large persistent stipules; and 5–8 ovules in each locule, led Endress (1989c) to propose a subfamily status. Takhtajan (1997), however, moved *Disanthus* out of the Exbucklandioideae and treated the genus as representing the subfamily Disanthoideae.

The *mat*K phylogeny suggests a polyphyletic relationship among these genera (Fig. 2). *Disanthus* and *Mytilaria* belong to separate lineages with 35 and 25 unambiguous character state changes respectively (Fig. 2), while a sister group relationship between *Exbucklandia* and *Rhodoleia* is strongly supported (BP = 100%, DI = 7, Fig. 2). Forcing *Mytilaria*, *Disanthus*, and *Exbucklandia* into a monophyletic clade required 17 more steps than the most parsimonious trees. *Disanthus* is the most closely related genus to the Hamamelidoideae, which is concordant with previous studies (Hufford and Crane 1989, Pan et al. 1991).

Rhodoleioideae. *Rhodoleia* has long been treated as a monotypic subfamily (Harms 1930, Endress 1989c, Takhtajan 1997). However, in the *mat*K-based phylogeny, *Rhodoleia* is allied with *Exbucklandia* in a well-supported clade, suggesting a close relationship of the two genera. Ten unambiguous character changes occur along the branch supporting the relationship. This cladistic pattern agrees with the phylogeny based on *rbc*L data (Qiu et al. 1998). Furthermore, collapsing the clade of *Exbucklandia* and *Rhodoleia* required nine steps more than the minimum character changes. Interestingly, Reinsch (1989) recognized the Bucklandieae, including *Bucklandia* (= *Exbucklandia*) and *Rhodoleia*, based on his comparative study of floral morphology. In the phylogenetic tree the clade of *Rhodoleia* and *Exbucklandia* is in a transitional position between the Altingioideae and the clades of *Mytilaria*, *Disanthus*, and the Hamamelidoideae. This agrees with the implications from floral ontogenetic studies (Bogle 1986, 1989).

Tribal and subtribal relationships in the Hamamelidoideae. There is no doubt that the Hamamelidoideae is a natural group, as shown by previous studies (Bogle and Philbrick 1980; Endress 1989a, b; Hufford and Crane 1989) and by this analysis. In the *mat*K-based phylogeny, the Hamamelidoideae are well supported (BP = 90%, DI = 3, five unambiguous character changes, Fig. 2). However, intergeneric

relationships within the Hamamelidoideae have long been debated (Harms 1930, Schulze-Menz 1964, Chang 1979, Endress 1989c).

Three clades constitute the Hamamelidoideae (Fig. 2). The first clade includes *Corylopsis* and the branch containing *Maingaya*, *Loropetalum*, and *Matudaea*. The relationships of *Corylopsis* and *Maingaya-Loropetalum-Matudaea* are strongly supported (B = 100%, DI = 5, ten unambiguous substitutions, Fig. 2). The fact that *Corylopsis* was phylogenetically far from *Fortunearia* and *Sinowilsonia* supports the separation of *Corylopsis* from the latter two genera, as hypothesized by Endress (1989c) and substantiated by our analysis based on nuclear DNA sequences and morphology (Li et al. 1997b). The well-supported relationship between *Maingaya*, *Loropetalum*, and *Matudaea* is new and unexpected. Interestingly, these genera share several morphological characteristics such as bisexual flowers, long anther connective protrusions, and valvate anther dehiscence. However, *Matudaea* differs strongly from the other two genera in its New World distribution, absence of perianth, and large, variable number of stamens. *Loropetalum* and *Matudaea* form a weakly-supported clade (Fig. 2). In addition, two other morphologically similar taxa (*Embolanthera* and *Tetrathyrium*) were not available for this study. Therefore, the intergeneric relationships of the clade need further study.

The second clade in the Hamamelidoideae associates the subtribe Dicoryphinae with the tribe Eustigmateae (incl. *Molinadendron*). The Dicoryphinae, which includes the five genera exclusively distributed in the Southern Hemisphere (Africa, Madagascar, Australia) forms a monophyletic clade. This result agrees with the unique anther dehiscence pattern that the five genera share (Endress 1989a). Considering their restriction to the Southern Hemisphere and the unique pattern of anther dehiscence, Zhang and Lu (1995) suggested family status for the five genera. However, the *mat*K-based phylogeny does not support this proposition as the Dicoryphinae is closely allied with the Eustigmateae (BP = 81%, DI = 3, Fig. 2). As described above, Endress (1989c) placed both *Fortunearia* and *Sinowilsonia* in the Eustigmateae, which originally included one genus, *Eustigma* (Harms 1930). *Fortunearia* and *Sinowilsonia* were associated based on their similarities in leaf morphology and reduced petals (Schulze-Menz 1964), while the association of *Fortunearia* and *Eustigma* involves several common characteristics, including pedicellate flowers, small petals, sessile anthers, large lenticellate fruits, and phloem in the inflorescence axis containing libriform fibre groups (Endress 1989b). At the nucleotide level, two character changes occur along the branch of the four genera (Fig. 2). *Molinadendron* and *Sinowilsonia* form a clade in the *mat*K-based phylogeny, which agrees with the suggestion that *Molinadendron* is closer to *Fortunearia* and *Sinowilsonia*, or the Fothergilleae group than to *Distylium* (Endress 1967). A close examination of specimens of *Sinowilsonia* and *Molinadendron* revealed that the two genera, along with *Eustigma* and *Fortunearia*, share several characteristics, including linear stipules, naked floral buds, and two prophylls flanking each lateral bud.

The third clade in the Hamamelidoideae corresponds basically to the genera of the tribe Fothergilleae (sensu Endress 1989c), with the exception of excluding *Matudaea* and *Molinadendron* and including *Hamamelis* (Fig. 2). In Harms's system (1930), two tribes were recognized for the apetalous Hamamelidoideae: Distylieae (*Distylium*, *Sinowilsonia*, and *Sycopsis*) and Fothergilleae (*Fothergilla*, *Parrotia*, and *Parrotiopsis*). *Sinowilsonia* has been rightly removed from the Distylieae (Schulze-Menz 1964; Endress 1989b, c). Endress (1989c) combined the two tribes and recognized the Fothergilleae s. l. based on the inherent connection between the two tribes suggested by the discovery of a spontaneous hybrid (*X sycoparrotia*) between *Sycopsis* and *Parrotia* (Endress and Anliker 1968). The *mat*K analysis did not resolve the Distylieae and the Fothergilleae s. str. as monophyletic clades, but clustered them into

one clade, thus supporting the tribal unification proposed by Endress (1989c). This result agrees with our previous study of the group using sequences of internal transcribed spacers of nuclear ribosomal DNA (Li et al. 1997c). Our observations have revealed that flowers are not strictly bisexual, but andromonoecious in the Fothergilleae s. str. This further diminishes the distinctness of the separate tribes of Harms (1930) and supports the union of the genera into one tribe, the Fothergilleae.

As has been pointed out above, *Molinadendron* and *Matudaea* are not placed as members of the Fothergilleae by the *mat*K gene data. The former falls into the clade of the tribe Eustigmateae and the latter into the *Corylopsis-Loropetalum* group. These two genera are apetalous but bisexual, thus supporting their separation from the andromonoecious Fothergilleae. Furthermore, attempting to place *Matudaea* and *Molinadendron* into the Fothergilleae clade entailed 38 more steps than the minimum tree length.

One of the more interesting results from this work is the placement of *Hamamelis*. This analysis placed this genus within the clade of the tribe Fothergilleae (Fig. 2). However, Endress (1989c) treated it as a monogeneric subtribe of the tribe Hamamelideae. *Hamamelis* is characterized by strictly 4-merous flowers and bisporangiate anthers (Endress 1989b, Mione and Bogle 1990). The parsimony analysis with *Hamamelis* removed from the data set did not change the DI, but increased BP from 54 to 69 for the clade of Fothergilleae (tree not shown). This implies a weak relationship between *Hamamelis* and the other genera of the Fothergilleae, and a stronger relationship within the Fothergilleae. The only obvious morphological similarity between *Hamamelis* and the Fothergilleae (*Parrotia*, *Parrotiopsis*, *Shaniodendron*) is the presence of semicraspedodromous venation in both groups. However, the close relationship of *Hamamelis* and the Fothergilleae is supported by other DNA sequence data, including nrDNA ITS (Shi et al. 1998) and *rbc*L gene (Qiu et al. 1998). Also, the recent discovery of a hamamelidaceous fossil flower (*Archamamelis* Endress and Friis) in Upper Cretaceous deposits in Sweden might suggest an ancient relationship among these genera since the fossil flower had bisporangiate anthers, as in extant *Hamamelis*, and a variable number of stamens, as in the Fothergilleae (Endress and Friis 1991).

Loropetalum, *Hamamelis* and the genera of the subtribe Dicoryphinae were previously grouped in the tribe Hamamelideae (Harms 1930, Chang 1979, Endress 1989c). Forcing these taxa into a monophyletic group in the *mat*K-based phylogeny required 21 steps more than the most parsimonious solutions.

Parrotia is morphologically similar to *Shaniodendron* and *Sycopsis* (Bogle 1968, 1970; Endress 1970, 1993; Deng et al. 1992), and a phylogenetic analysis of the Fothergilleae sensu Endress (1989c) using nuclear DNA sequences supports the close relationship of the three genera (Li et al. 1997b). In the *mat*K phylogeny, it appears that *Parrotia* is phylogenetically far distant from the other two genera (Fig. 2), but the clades are weakly supported (BPs < 60%, DIs = 1). Therefore, more evidence is needed to assess their relationships.

Molecular analyses have suggested the possible paraphyly of the Hamamelidaceae (Chase et al. 1993, Hoot et al. 1997, Hoot et al. 1999, Qiu et al. 1998). To assess the possibility in more detail, we are currently gathering complete *mat*K gene sequence data from some basal rosids and "lower" hamamelids. The preliminary results appear to support the monophyly of the Hamamelidaceae, but with a possible inclusion of *Cercidiphyllum* and *Daphniphyllum*.

In summary, at the subfamily level, this study recognizes the monophyly of Altingioideae sensu Endress (1989c), Exbucklandioideae sensu Harms (1930), Mytilarioideae sensu Chang (1973, 1979), Rhodoleioideae sensu Harms (1930), Disanthoideae sensu Harms (1930), and Hamamelidoideae sensu Endress (1989c). Furthermore, it suggests a

close relationship of *Exbucklandia* with *Rhodoleia*, and the paraphyly of Exbucklandioideae sensu Endress (1989c). At the tribal and subtribal levels, the monophyletic groups are the Corylopsideae sensu Endress (1989c), Eustigmateae (sensu Endress 1989c, expanded to include *Molinadendron*), Fothergilleae (sensu Endress 1989c, expanded to include *Hamamelis*), Dicoryphinae, and Loropetalinae Endress (Endress 1989c, expanded to include *Matudaea*). The Hamamelideae sensu Endress (1989c), however, is polyphyletic with its members distributed in three separate lineages. Further study is warranted to assess the monophyly of the Hamamelidaceae.

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