# PHYLOGENETIC RELATIONSHIPS IN THE HAMAMELIDOIDEAE INFERRED FROM SEQUENCES OF TRN NON-CODING REGIONS OF CHLOROPLAST DNA

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**Abstract**. Two non-coding regions of chloroplast DNA were used to examine phylogenetic relationships in the Hamamelidoideae (Hamamelidaceae). Sequences of *trn*L-*trn*F intergenic spacer and *trn*L intron were informative in resolving relationships among genera and at higher levels. Three major lineages are identified: the *Corylopsis* lineage, the *Trichocladus* lineage, and the *Hamamelis* lineage. Corylopsideae, Hamamelideae, and Dicoryphinae are found to be monophyletic; Loropetalinae and Eustigmateae appear to be paraphyletic, and Hamamelideae and Fothergilleae to be polyphyletic. These results are consistent with previous analyses based on nrDNA ITS sequences and the cpDNA *mat*K gene. Morphological characters, such as apetaly, strap-shaped petal, and wind pollination, which have been used to define suprageneric groups, evolved independently in the three lineages.

**Keywords:** Hamamelidoideae, Hamamelidaceae, phylogeny, chloroplast DNA, *trn*L-*trn*F intergenic spacer, *trn*L intron.

The Hamamelidaceae are a family of 31 genera and more than 140 species distributed in both the Old and New World (Zhang and Lu, 1995). Many species are economically important. *Liquidambar styraciflua* L. (sweetgum), for example, is known for producing the aromatic storax, which has been used in soaps, cosmetics, and so on. Extracts from bark and leaves of *Hamamelis virginiana* L. (witch-hazel) are used in skin cosmetics, shaving lotions, and ointments (Meyer, 1997). Other species are cultivated world-wide as ornamentals, including *Corylopsis* Sieb. & Zucc (winter-hazel) and *Fothergilla* Murray (witch-alder). Systematically, the Hamamelidaceae are said to be "transitional" either between the "lower" Hamamelidae and the "higher" Hamamelidae (Endress, 1967) or between the "lower" Hamamelidae and Rosidae (Hufford, 1992). In any case, it is clear that this group of plants occupies an important position in the evolution of eudicots.

The Hamamelidaceae comprise four (Endress, 1989c), five (Harms, 1930), or six subfamilies (Chang, 1979; Li, 1997), among which the Hamamelidoideae are the largest. This subfamily includes over 75% of the genera (23 out of 31) and about 90% of the species in the Hamamelidaceae. The distribution of the Hamamelidoideae ranges from eastern and southern Africa, Madagascar and the Comoro Islands, to northeastern Australia, and from western, central, and southeastern Asia, to Northern and Central America (Endress, 1989a, b, c; Li, 1997; Zhang and Lu, 1995).

The monophyly of the Hamamelidoideae has been recognized on the basis of morphology (Hufford and Crane, 1989; Li, 1997), and sequences of nrDNA ITS (Shi et al., 1998; Li et al., in press, a) and chloroplast genes (*rbc*L, Qiu et al., 1998; *mat*K, Li et al., in press, b). However, the intergeneric relationships and classification of the Hamamelidoideae have been controversial. The first comprehensive taxonomic treatment of the Hamamelidoideae in this century was proposed by Harms (1930). He recognized five tribes and 17 genera in the subfamily (Table 1). The Corylopsideae, characterized by leaf morphology (basal crowding of secondary veins and terminal veins ending in teeth), included *Corylopsis* Sieb. & Zucc. and *Fortunearia* Rehd. & Wils. The Eustigmateae

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was monotypic, and easily distinguished by purple, enlarged stigmatic surface. The Distylieae included genera that were andromonoecious and mostly had persistent leaves, including *Distylium* Sieb. & Zucc., *Sycopsis* Oliv., and *Sinowilsonia* Hemsl., whereas the Fothergilleae was a tribe of three genera, *Parrotia* C. A. Mey., *Fothergilla* Murray, and *Parrotiopsis* Schneider, and was defined by features such as bisexual flowers and deciduous leaves. The Hamamelideae, characterized by ribbon-shaped petals, was the largest tribe in the Hamamelidoideae and included *Hamamelis* L., *Dicoryphe* Thouars, *Trichocladus* Pers., *Embolanthera* Merr., *Maingaya* Oliv., *Loropetalum* R. Br. ex Rchb., and *Tetrathyrium* Benth. Harms was uncertain about the tribal affiliation of *Ostrearia* Baill.

Additional genera of the Hamamelidoideae have been described since Harms (1930), including *Neostrearia* Smith (Smith, 1958), *Noahdendron* Endress, Hyland & Tracey (Endress et al., 1985), *Matudaea* Lundell (Lundell, 1940), *Shaniodendron* Deng, Wei & Wang (Deng et al., 1992), *Distyliopsis* Endress (Endress, 1970), and *Molinadendron* Endress (Endress, 1969). The latter three genera are segregates from *Hamamelis*, *Sycopsis*, and *Distylium*, respectively.

Endress (1989c) revised the Hamamelidoideae, combining the Distylieae and Fothergilleae based mainly on the discovery of a spontaneous hybrid between *Sycopsis* of the Distylieae and *Parrotia* of the Fothergilleae (Table 1). Within the Hamamelideae, Endress recognized three subtribes: 1) the Dicoryphinae (*Dicoryphe*, *Trichocladus*, *Ostrearia*, *Neostrearia*, *Noahdendron*), found exclusively in the Southern Hemisphere and characterized by a distinct anther dehiscence pattern, 2) the monotypic Hamamelidinae (*Hamamelis*), defined by its strictly 4-merous flowers, and 3) the Loropetalinae (*Loropetalum*, *Embolanthera*, *Tetrathyrium*, and *Maingaya*), characterized by a combination of pentamerous flowers and a two-valvate anther dehiscence pattern. Other features of Endress's classification system are the placement of *Fortunearia* and *Sinowilsonia* in the Eustigmateae, based on their reduced petals and lenticellate fruits, and treatment of Corylopsideae as monogeneric (*Corylopsis*), mainly based on the distinct orbicular petals.

In the past several years the phylogenetic relationships of the Hamamelidaceae have been examined using nucleotide sequence variation in the nrDNA ITS and in the plastid gene *mat*K (Li, 1997; Li et al., 1997; Li et al., 1998a, 1998b; Shi et al., 1998). These data have supported some proposed phylogenetic relationships within the family, but not others, and have suggested some novel phylogenetic and biogeographic connections, particularly within the subfamily Hamamelidoideae. Li (1997) recognized six tribes in Hamamelidoideae, two of which, Corylopsideae and Hamamelideae, are monogeneric (Table 1). The circumscription of the Eustigmateae was expanded to include *Molinadendron* and the Loropetalinae to include *Matudaea*, removing both *Molinadendron* and *Matudaea* from the Fothergilleae. The Hamamelideae, whose members fall into three separate lineages, were seen to be polyphyletic (Li et al., in press, a, b; Shi et al., 1998).

Since the primers were published for three non-coding regions in the single-copy region of chloroplast DNA (Taberlet et al., 1991), several phylogenetic studies have examined DNA sequences of these regions and concluded that they are informative at lower taxonomic levels (among and within genera, and even within species), e.g., Fujii et al. (1997), Gielly and Taberlet (1996), and Kita et al. (1995). We had hoped to use this region to resolve interspecific relationships in several genera in the Hamamelidoideae, e.g. *Hamamelis*. However, sequences differed too little within genera to provide significant resolution (Li et al., 1998c). Instead, as we report here, we found that sequences from two non-coding regions of cpDNA were useful in resolving broader relationships within Hamamelidoideae.

## Materials and Methods

Twenty three species were sampled for this study, representing 22 (out of 23) genera, and all tribes and subtribes of the Hamamelidoideae in previous classification systems (Harms, 1930; Endress, 1989c; Li, 1997). *Disanthus* Maxim., *Exbucklandia* B. W. Br., and *Rhodoleia* Champ. were chosen as outgroups since previous studies have suggested that these are closely related to Hamamelidoideae (Li, 1997; Shi et al., 1998). Sources of material and GenBank accession numbers of the sequences are given in Table 2.

DNA extraction was carried out as described in Li et al. (1997). The polymerase chain reaction (PCR) was performed using the primer pairs c and f of Taberlet et al. (1991) in a Perkin

Elmer thermocycler. Each 50µl reaction included 50–100ng genomic DNA, 5µl of 10 X PCR buffer (GibcolBRL, Grand Island, NY), 3µl of 25 µM MgCl2, 1µl of 10µM primers, and 1–1.5 units of Taq polymerase (Gibcol BRL), and an appropriate amount of distilled water. The PCR thermocycler program consisted of 35 cycles of denaturation at 94°C (2 min), annealing at 55°C (1 min), and extension at 72°C (2 min), followed by a 7 min extension at 72°C. The PCR products, identified by comparison with the low mass DNA size marker (Gibcol BRL), were purified in a 0.8% agarose gel, and were then extracted using a Qiagen gel extraction kit (Qiagen Inc., Santa Clarita, CA ). Purified PCR product was used directly as a template for sequencing reactions using a cycle sequencing kit (Amersham Co., Arlington Heights, IL) and primers c, d, e, and f of Taberlet et al. (1991). The sequences were obtained using an ABI 377 Automated Sequencer and analyzed using Sequencher 3.0 (Gene Codes Corp., Inc., Ann Arbor, MI). All sequences were readily aligned manually. Intron/exon junctions were determined by comparison with corresponding DNA sequences of *Nicotiana tabacum* (GenBank Z00044).

Parsimony analyses were conducted with gaps as missing data and as a fifth character state using the computer program PAUP 3.1.1 (Swofford, 1993). Heuristic searches were conducted using simple sequence addition, TBR branch swapping, and Mulpars on. Characters states were unordered and characters and state changes were equally weighted. Relative support for individual clades was examined using the bootstrap (100 replicates, Felsenstein, 1985) and decay analysis (up to five steps, Bremer, 1988; Donoghue et al., 1992).

## Results

### *Sequence Characteristics*

We have successfully amplified a region of about 1000 base pairs using the primers c and f of Taberlet et al. (1991), including part of the *trn*L 5' exon, *trn*L intron, *trn*L 3' exon, the intergenic spacer of *trn*L and *trn*F, and part of the t*rn*F 5' exon.

The alignment of these sequences, including the *trn*L intron, *trn*L-*trn*F intergenic spacer, *trn*L 3' exon, and partial *trn*F gene, yielded a data matrix of 1025 characters, of which 61 were potentially informative. The data matrix is available from the first author upon request and from TreeBASE (accession # M546; http://phylogeny.harvard.edu/treebase).

The length of the *trn*L intron varied from 512 bases in *Tetrathyrium* to 524 in *Shaniodendron* in the Hamamelidoideae, and from 360–364 bases in the outgroups *Exbucklandia*, *Disanthus*, and *Rhodoleia* (Table 3). The alignment of the intron required 19 indels (1–16 bases in length) and produced a data matrix of 550 characters, of which 30 sites were potentially informative. Sequence divergence among the ingroup genera was 0–3.1%, with an average of 1.6%, and the divergence between the in- and outgroups averaged 3.9% (Table 3). The *trn*L 3' exon ranged from 45 to 51 bases in length. The alignment required four indels, one four bases and the rest of a single base, and produced 51 characters; two of the 11 variable characters were potentially informative. The intergenic t*rn*L-*trn*F spacer varied from 371 to 381 base pairs and the alignment resulted in 388 sites, of which 89 were variable and 29 were potentially informative. The *trn*L-*trn*F spacer diverged from 0-4.9% in the Hamamelidoideae with an average of 2.5%, and from 3.96-7.6% between the in- and outgroup taxa, with an average of 5.9%.

### *Phylogenetic Relationships*

Separate parsimony analyses of individual data sets of *trn*L intron, *trn*L-*trn*F intergenic spacer, *trn*L 3' exon, and *trn*F 5' exon sequences produced phylogenies that were congruent with one another, but with different degrees of resolution. The two exons had little resolution; trees based on the *trnL* intron and the *trnL-trnF* intergenic spacer are shown in Fig. 1. These trees have much in common, and show no strong conflicts; therefore, combination of data seems warranted. Parsimony analysis of the combined data set of 1025 characters, treating gaps as missing, resulted in 26 equally short trees of 205 steps and a consistency index of 0.88. Figure 2 shows the strict consensus tree, which we refer to as the GM tree. Three major clades are apparent in the GM tree: the *Corylopsis* clade (C), the *Hamamelis* clade (H), and the *Trichocladus* clade (T). The C and H clades are strongly supported (bootstrap >98%, decay >3), whereas suport for the T clade is weak (bootstrap = 73%, decay = 1). In the C clade, *Corylopsis* is sister to the clade composed of *Matudaea*, *Maingaya*, *Loropetalum*, and *Tetrathyrium*; and the latter two form a clade. The H clade contains three groups whose rela-

tions are unresolved: *Hamamelis*, *Fothergilla*, and the rest of the genera in the Fothergilleae *sensu* Endress (1989b, c). *Parrotiopsis* is sister to the branch containing *Parrotia* and a polytomy of *Distylium*R, *Shaniodendron*, and a *Distylium*M-*Distyliopsis-Sycopsis* clade. The T clade contains three main lines: *Dicoryphe*, other members of the Dicoryphinae *sensu* Endress (1989c), and the Eustigmateae *sensu* Endress (1989c) plus *Molinadendron*.

A parsimony analysis treating gaps as a fifth character state generated eight shortest trees of 394 steps and a consistency index of 0.79. Fig. 3 is the strict consensus tree, which we will call the G5 tree. The G5 tree is largely congruent with the GM tree, differing only in the following ways: (1) the C clade is sister to the branch containing the H and T clades; (2) within the C clade there is a trichotomy involving *Corylopsis*, *Maingaya-Matudaea*, and *Loropetalum-Tetrathyrium*; and (3) the T clade contains two well resolved branches, one of which includes *Eustigma-Fortunearia* and *Sinowilsonia-Molinadendron*, and the other consisting of the Southern Hemisphere genera, with *Dicoryphe* sister to the rest (Fig. 3).

## Discussion

### *Sequence variation*

The three non-coding regions of the chloroplast genome were suggested to be potentially informative in resolving phylogenetic relationships at different levels (Taberlet et al., 1991). Several studies using these sequences have shown that the intergenic spacer between *trn*L-*trn*F and the *trn*L intron are informative in resolving relationships among species, or even within species (Fujii et al., 1997; Gielly and Taberlet, 1996; Kita et al., 1995). In contrast, Kamiya et al. (1998) concluded that these regions were not informative at the interspecific level in the Dipterocarpaceae . Our study agrees with Kamiya et al., and further suggests that these sequences are not divergent enough to resolve relationships among closely related genera such as *Ostrearia*, *Noahdendron*, and *Neostrearia* (Fig. 1). It has been observed that herbaceous plants tend to have higher variation than woody plants, possibly due to shorter generation times in the former (Gaut et al., 1992). Given that previous studies (Fujii et al., 1997; Gielly and Taberlet, 1996; Kita et al., 1995) were mainly focused on herbaceous plants, this study (together with Kamiya et al., 1998) tends to support that generalization. Between the non-coding segments, the sequence variation was slightly higher in the *trn*L-F intergenic spacer than in the *trn*L intron, with percentages of informative sites being 7.5% and 5.4% respectively. We found only one potentially informative site in the 5' end of *trn*F and two in the *trn*L 3' exon.

### *Phylogeny and Classification*

Three major clades are seen in both the GM and G5 trees (Fig. 2, 3): (1) the *Corylopsis* clade (C), (2) the *Hamamelis* clade (H), and (3) the *Trichocladus* clade (T). These three clades correspond perfectly with those recovered in phylogenetic analyses based on sequences of nrDNA ITS and the cpDNA *mat*K gene (Li et al., in press, a, b). However, in the GM tree (Fig. 2), the T clade is basal and C and H are united, whereas in the G5 tree (Fig. 3), C is basal and H and T form a clade. The sister relationship of the C and H clades is only weakly supported in the GM tree (bootstrap = 67%; decay = 1), while the H-T clade is strongly supported in the G5 tree (bootstrap = 98%; decay = 6). Nine out of the 11 apomorphies supporting the H-T clade are indels. The G5 topology is congruent with trees based on ITS sequences (Li et al., 1998b; Li et al., in press, a; Shi et al., 1998) and cpDNA *mat*K (Li, 1997), on this basis we prefer the G5 tree, with the C clade basal in the Hamamelidoideae.

### *Corylopsideae*

The circumscription of Corylopsideae has been controversial. It contains *Corylopsis* and *Fortunearia* (Harms, 1930), or *Corylopsis*, *Fortunearia*, and *Sinowilsonia* (Shulze-Menz, 1964), or just the genus *Corylopsis* (Endress, 1989c). Our analysis suggests that *Corylopsis* is not closely related to *Fortunearia* or *Sinowilsonia*, supporting Endress's delimitation. Floral ontogeny and embryological studies have also shown that *Corylopsis* is distinct from *Fortunearia* and *Sinowilsonia* (Li and Bogle, 1998). Further, both ITS and *mat*K sequences support this conclusion (Li, 1997; Li et al., 1998b; Shi et al., 1998).

*Hamamelideae*

In Harms's system (1930), Hamamelideae, characterized by strap-shaped petals, is the most diverse tribe, including *Hamamelis*, *Trichocladus*, *Maingaya*, *Embolanthera*, *Tetrathyrium*, *Loropetalum*, *Dicoryphe*, and the three Australian genera. Endress (1989c) did not change the circumscription of the tribe, but he subdivided it into three subtribes: the monogeneric Hamamelidinae, the Dicoryphinae, and the Loropetalinae. However, in our trees (HL, HD, and HH in Figs. 2, 3), these three groups do not form a single clade, but three separate groups, indicating that the Hamamelideae are polyphyletic. *Hamamelis* is shown to be the sister of Fothergilleae. The Loropetalinae, characterized by the horn-like projections of anther connective, are related to *Corylopsis* and *Matudaea*. *Loropetalum* is a genus of one to several species distributed in southeastern Asia and has the smallest leaves in the subfamily. It is very similar to *Tetrathyrium*, a monotypic genus endemic to Hong Kong (Chang, 1979), and it has been suggested that the two genera should be merged (Endress, 1993; De-yuan Hong, pers. com.). Our results are consistent with this position.

The close relationship of the Southern Hemisphere genera, which share a characteristic valvate anther dehiscence pattern, was pointed out by Endress (1989a, b), who treated these genera as subtribe Dicoryphinae. In the GM tree (Fig. 2), the Australian genera were in one clade, while their relationships with the southeastern African *Trichocladus*, and the Madagascan *Dicoryphe* were not well resolved. In the G5 tree (Fig. 3) these five genera form a well-supported clade.

*Eustigmateae*

The Eustigmateae was considered monogeneric by Harms (1930). Shulze-Menz (1964) transferred *Sinowilsonia* from the Distylieae to the Eustigmateae, and Endress (1989c) transferred *Fortunearia* from the Corylopsideae based on several morphological characteristics, including lenticels on fruits and enclosing sepals. In our trees (Figs. 2, 3), *Eustigma*, *Fortunearia*, and *Sinowilsonia* form a well-supported clade along with *Molinadendron*, a Central American genus segregated from *Distylium* and included by Endress (1989c) among the apetalous Fothergilleae. Our results confirm the close relationship of *Molinadendron* to *Sinowilsonia* suggested by Bogle (1970) and Endress (1970).

*Fothergilleae*

The Distylieae of Harms (1930) included *Distylium*, *Sycopsis*, and *Sinowilsonia*, while his Fothergilleae contained *Parrotia*, *Parrotiopsis*, and *Fothergilla*. Endress (1989c) transferred *Sinowilsonia* to the Eustigmateae and combined the remaining five genera, plus *Matudaea*, *Molinadendron*, and *Distyliopsis*, into his Fothergilleae. The recently described *Shaniodendron* (Deng et al., 1992) is also placed in the Fothergilleae, bringing the number of genera in the tribe to nine. Phylogenetic analyses based on morphology and DNA sequences of ITS and *mat*K recognized the monophyly of the Fothergilleae *sensu* Endress, but minus *Matudaea* and *Molinadendron* (Li, 1997). The same basic conclusion is supported here. However, in our trees (Figs. 2, 3), *Fothergilla* does not consistently form a clade with the branch containing the rest of the Fothergilleae *sensu* Li; multiple sources of data are needed to fully resolve these relationships. Nevertheless, these results show that the Distylieae and Fothergilleae of Harms (1930) and the Fothergilleae of Endress (1989c) are not monophyletic as *Matudaea* and *Molinadendron* are related elsewhere.

*Matudaea* is a central American genus and is distinguished by several morphological characters, such as bisexual, hypogynous flowers, elongated anther protrusion, and stellate-lepidote anthers. Lundell (1940) believed that *Matudaea* was closely related to *Distylium* as both of these genera lack petals, and their ovaries are superior. In our trees (Figs. 2, 3) *Matudaea* and *Distylium* are separated, and *Matudaea* is placed instead with the members of Loropetalinae *sensu* Endress (1989a; HL in Figs. 2, 3). This relationship is supported by several morphological characters, e. g., bisexual flowers and distinct anther protrusion.

*Shaniodendron* is a segregate of *Hamamelis* and has been placed in the Fothergilleae (Deng et al., 1992). Parsimony analysis of ITS sequences, with gaps treated as a fifth character state, supported a connection between *Shaniodendron* and *Parrotia* (Li et al., 1997).

On this basis it was proposed that *Shaniodendron* be combined with *Parrotia* (Hao et al., 1998). However, in our trees (Figs. 2, 3), *Shaniodendron* and *Parrotia* are not directly linked. *Distyliopsis* is a segregate from *Sycopsis*, which Endress (1970) believed to be more closely related to *Distylium*. This proposal was supported in ITS analyses (Li et al., 1997). However, our study suggests that *Distyliopsis* is more closely related to *Sycopsis*. In this study, and in previous phylogenetic analyses (Li et al., 1997; Li, 1997), only two species of *Distylium* and one species of *Sycopsis* have been sampled; broader sampling and more data are needed to resolve these relationships.

The apetalous flowers of both *Fothergilla* and *Parrotiopsis* are insect-pollinated, while those of other apetalous genera are wind-pollinated. *Fothergilla* attracts pollinators using the showy, whitish stamen filaments, whereas *Parrotiopsis* employs large, showy bracts (Bogle, 1968, 1970; Endress, 1989b). Phylogenetically, these do not appear to form a clade as indicated by Endress (1989b).

*Evolution of morphological characters*

It is worth pointing out the apparent parallel evolution of several taxonomically important characters. In our trees, the apetalous genera that have been placed in one group (Endress, 1989c), the Fothergilleae, do not form a clade. Instead they are distributed in three clades, which implies that apetaly may have evolved three times independently in the Hamamelidoideae. The shift to apetaly is directly connected with a shift to wind pollination in *Matudaea* and in *Molinadendron*; wind pollination apparently evolved in the main Fothergilleae clade after loss of petals.

Genera with strap-shaped petals have been grouped together in the Hamamelideae (Harms, 1930; Endress, 1989c). In our trees, these genera fall in three different clades: *Loropetalum*, *Maingaya*, and *Tetrathyrium* in the C clade, *Hamamelis* in the H clade, and *Dicoryphe*, *Trichocladus*, *Neostrearia*, *Ostrearia*, and *Noahdendron* in the T clade. Again, this implies homoplasy in a character that has previously been used to delimit taxa within Hamamelidoideae.

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TABLE 1. Classification systems of the Hamamelidoideae.

| GENUS | HARMS (1930) | ENDRESS (1989C) TRIBE | SUBTRIBE | LI (1997) TRIBE |
|---|---|---|---|---|
| *Corylopsis* Sieb. & Zucc. | Corylopsideae | Corylopsideae | | Corylopsideae |
| *Eustigma* Gardn.& Champ. | Eustigmateae | Eustigmateae | | Eustigmateae |
| *Fortunearia* Rehd. & Wils. | Corylopsideae | Eustigmateae | | Eustigmateae |
| *Sinowilsonia* Hemsl. | Distylieae | Eustigmateae | | Eustigmateae |
| *Hamamelis* L. | Hamamelideae | Hamamelideae | Hamamelidinae | Hamamelideae |
| *Embolanthera* Merr. | Hamamelideae | Hamamelideae | Loropetalinae | Loropetaleae |
| *Maingaya* Oliv. | Hamamelideae | Hamamelideae | Loropetalinae | Loropetaleae |
| *Tetrathyrium* Benth. | Hamamelideae | Hamamelideae | Loropetalinae | Loropetaleae |
| *Loropetalum* R. Br. ex Rchb. | Hamamelideae | Hamamelideae | Loropetalinae | Loropetaleae |
| *Dicoryphe* Thouars | Hamamelideae | Hamamelideae | Dicoryphinae | Dicorypheae |
| *Trichocladus* Pers. | Hamamelideae | Hamamelideae | Dicoryphinae | Dicorypheae |
| *Ostrearia* Baill. | uncertain | Hamamelideae | Dicoryphinae | Dicorypheae |
| *Noahdendron* Endress, Hyland & Tracey | | Hamamelideae | Dicoryphinae | Dicorypheae |
| *Neostrearia* L. S. Smith | | Hamamelideae | Dicoryphinae | Dicorypheae |
| *Molinadendron* Endress | | Fothergilleae | | Eustigmateae |
| *Parrotiopsis* Schneider | Fothergilleae | Fothergilleae | | Fothergilleae |
| *Fothergilla* Murray | Fothergilleae | Fothergilleae | | Fothergilleae |
| *Sycopsis* Oliv. | Distylieae | Fothergilleae | | Fothergilleae |
| *Shaniodendron* Deng, Wei, & Wang | | | | Fothergilleae |
| *Parrotia* C. A. Mey. | Fothergilleae | Fothergilleae | | Fothergilleae |
| *Distyliopsis* Endress | | Fothergilleae | | Fothergilleae |
| *Matudaea* Lundell | | Fothergilleae | | Loropetaleae |
| *Distylium* Sieb. & Zucc. | Distylieae | Fothergilleae | | Fothergilleae |

TABLE 2. Species sequenced for *trn* non-coding regions for this analysis.

| SPECIES | COLLECTOR | SOURCE | GENBANK ACCESSION NO. |
|---|---|---|---|
| *Corylopsis pauciflora* Sieb.& Zucc. | *J.-H. Li 01* | Arnold Arboretum, MA. | AF14765 |
| *Dicoryphe stipulacea* Janume St. Hil. | *A. Randrianasolo 543* | Tulear, Madagascar | AF14766 |
| *Disanthus cercidifolius* Max. | A. L. Bogle | Woodlanders, Inc. SC. | AF14767 |
| *Distyliopsis tutcheri* Endress | A. L. Bogle | Woodlanders, Inc. SC. | AF14770 |
| *Distylium myricoides* Hemsl. (DIM) | A. L. Bogle | Woodlanders, Inc. SC. | AF14768 |
| *Distylium racemosum* Sieb.& Zucc. (DIR) | A. L. Bogle | Woodlanders, Inc. SC. | AF14769 |
| *Eustigma oblongifolium* Gardn.& Champ. | N.-J. Chung | Taiwan | AF14771 |
| *Exbucklandia populnea* (R.Br.) R.W. Br. | A. L. Bogle | Manuka State Roadside Park, Hawaii | AF14772 |
| *Fortunearia sinensis* R.& W. | *J.-H. Li 04* | Arnold Arboretum, MA. | AF14773 |
| *Fothergilla major* Lodd. | J.-H. Li | Univ. of New Hampshire campus | AF14774 |
| *Hamamelis virginiana* L. | J.-H. Li | Univ. of New Hampshire campus | AF14775 |
| *Loropetalum chinense* (R.Br.) Oliv. | A. L. Bogle | Missouri Bot. Gard. | AF14776 |
| *Maingaya malayana* Oliv. | L. G. Saw | Kepong, Malaysia | AF14777 |
| *Matudaea trinervia* Lundell | P. K. Endress | Botanical Garden, Zurich, Switzerland | AF14778 |
| *Molinadendron guatemalense* Endress | P. K. Endress | Botanical Garden of Zurich, Switzerland | AF14779 |
| *Neostrearia fleckeri* Smith | P. K. Endress | Botanical Garden of Zurich, Switzerland | AF14780 |
| *Noahdendron nicholasii* Endress, Hyland & Tracey | P. K. Endress | Botanical Garden of Zurich, Switzerland | AF14781 |
| *Ostrearia australiana* Baill. | P. K. Endress | Botanical Garden of Zurich, Switzerland | AF14782 |
| *Parrotia persica* C.A.Mey. | A. L. Bogle | Univ. of New Hampshire greenhouse. | AF14783 |
| *Parrotiopsis jacquemontiana* Rehd. | A. L. Bogle | Harvard Univ. campus | AF14784 |
| *Rhodoleia championii* Hook. f. | A. L. Bogle | Lyon Arboretum, Hawaii | AF14785 |
| *Shaniodendron subaequale* Deng, Wei & Wang | Y.-L. Qiu | Jiangsu, China | AF14786 |
| *Sinowilsonia henryi* Hemsl. | *J.-H. Li 05* | Arnold Arboretum, MA | AF14787 |
| *Sycopsis sinensis* Oliv. | A. L. Bogle | Woodlanders, Inc. SC. | AF14788 |
| *Tetrathyrium subcordatum* Benth. | R. Saunders | Hong Kong | AF14789 |
| *Trichocladus crinitus* Pers. | A. L. Bogle | Longwood Gardens, PA. | AF14790 |

TABLE 3. Sequence divergence of trnL intron (below diagonal) and trnL-F spacer (above diagonal)

| SPECIES | LENGTH | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | SPACER | INTRON | *trnL* | | | | | | | | | | | | |
| 1. *Corylopsis* | 374 | 516 | 50 | - | 2.71 | 1.87 | 2.13 | 1.60 | 2.95 | 1.61 | 2.69 | 3.22 | 3.50 | 2.94 | 1.87 |
| 2. *Matudaea* | 371 | 514 | 51 | 1.17 | - | 2.97 | 2.68 | 2.70 | 4.32 | 2.99 | 4.08 | 4.61 | 4.90 | 4.03 | 2.97 |
| 3. *Loropetalum* | 374 | 514 | 49 | 1.75 | 1.36 | - | 2.13 | 1.06 | 3.22 | 1.88 | 2.97 | 3.49 | 3.78 | 3.47 | 2.42 |
| 4. *Maingaya* | 377 | 514 | 51 | 1.36 | 1.36 | 1.94 | - | 2.13 | 3.49 | 2.15 | 3.24 | 3.76 | 3.78 | 3.46 | 2.67 |
| 5. *Tetrathyrium* | 375 | 512 | 50 | 1.56 | 1.17 | 0.97 | 1.36 | - | 3.49 | 2.16 | 3.24 | 3.76 | 4.05 | 3.46 | 2.41 |
| 6. *Trichocladus* | 376 | 520 | 45 | 2.31 | 2.32 | 2.71 | 2.71 | 2.52 | - | 1.33 | 2.39 | 2.93 | 3.19 | 3.21 | 2.14 |
| 7. *Dicoryphe* | 375 | 520 | 50 | 2.31 | 1.93 | 2.32 | 2.32 | 2.13 | 0.77 | - | 1.07 | 1.59 | 1.87 | 1.88 | 0.81 |
| 8. *Neostrearia* | 375 | 519 | 49 | 2.51 | 2.51 | 2.90 | 2.90 | 2.71 | 0.96 | 0.96 | - | 2.13 | 2.40 | 2.96 | 1.89 |
| 9. *Noahdendron* | 375 | 519 | 50 | 2.13 | 2.34 | 2.73 | 2.34 | 2.54 | 0.96 | 0.77 | 0.77 | - | 2.93 | 3.49 | 2.42 |
| 10. *Ostrearia* | 376 | 521 | 49 | 2.69 | 2.70 | 3.09 | 3.09 | 2.90 | 0.96 | 0.96 | 0.77 | 0.77 | - | 3.76 | 2.70 |
| 11. *Eustigma* | 376 | 520 | 50 | 2.71 | 2.32 | 2.72 | 2.72 | 2.53 | 1.16 | 0.77 | 1.35 | 1.16 | 1.35 | - | 1.33 |
| 12. *Fortunearia* | 375 | 521 | 50 | 2.51 | 2.51 | 2.91 | 2.52 | 2.72 | 1.73 | 1.34 | 1.92 | 1.35 | 1.92 | 0.58 | - |
| 13. *Sinowilsonia* | 368 | 508 | 50 | 2.36 | 2.36 | 2.36 | 2.37 | 2.17 | 1.57 | 1.17 | 1.76 | 1.18 | 1.76 | 0.59 | 0.40 |
| 14. *Molinadendron* | 376 | 515 | 51 | 2.35 | 2.35 | 2.75 | 2.35 | 2.55 | 1.36 | 0.97 | 1.56 | 0.97 | 1.55 | 0.20 | 0.19 |
| 15. *Hamamelis* | 383 | 513 | 50 | 2.55 | 2.56 | 2.56 | 2.56 | 2.37 | 1.35 | 0.77 | 1.55 | 0.98 | 1.55 | 1.35 | 1.54 |
| 16. *DistyliumM* | 375 | 523 | 50 | 2.70 | 2.71 | 2.71 | 2.71 | 2.52 | 1.54 | 1.15 | 1.73 | 1.16 | 1.73 | 1.54 | 1.73 |
| 17. *DistyliumR* | 375 | 523 | 50 | 2.89 | 2.90 | 2.90 | 2.90 | 2.71 | 1.73 | 1.34 | 1.93 | 1.35 | 1.92 | 1.73 | 1.92 |
| 18. *Distyliopsis* | 374 | 522 | 50 | 2.70 | 2.71 | 2.71 | 2.71 | 2.52 | 1.54 | 1.15 | 1.73 | 1.16 | 1.73 | 1.54 | 1.73 |
| 19. *Fothergilla* | 381 | 520 | 50 | 2.32 | 2.32 | 2.32 | 2.33 | 2.13 | 1.15 | 0.77 | 1.35 | 0.77 | 1.34 | 1.15 | 1.34 |
| 20. *Parrotia* | 375 | 520 | 50 | 2.70 | 2.71 | 2.71 | 2.32 | 2.52 | 1.54 | 1.15 | 1.73 | 1.16 | 1.73 | 1.54 | 1.73 |
| 21. *Parrotiopsis* | 381 | 520 | 50 | 2.32 | 2.32 | 2.32 | 2.33 | 2.13 | 1.15 | 0.77 | 1.35 | 0.77 | 1.34 | 1.15 | 1.34 |
| 22. *Shaniodendron* | 375 | 504 | 50 | 2.14 | 2.17 | 2.59 | 2.37 | 2.36 | 1.52 | 1.30 | 1.73 | 1.30 | 1.74 | 1.74 | 1.95 |
| 23. *Sycopsis* | 374 | 522 | 50 | 2.70 | 2.71 | 2.71 | 2.71 | 2.52 | 1.54 | 1.15 | 1.73 | 1.16 | 1.73 | 1.54 | 1.73 |
| 24. *Disanthus* | 364 | 513 | 50 | 5.41 | 5.61 | 6.02 | 5.62 | 5.83 | 4.42 | 4.20 | 4.42 | 4.22 | 4.60 | 4.41 | 4.41 |
| 25. *Exbucklandia* | 369 | 505 | 48 | 4.15 | 4.16 | 4.56 | 4.17 | 4.37 | 3.36 | 2.95 | 3.55 | 2.97 | 3.55 | 3.16 | 3.16 |
| 26. *Rhodoleia* | 364 | 519 | 51 | 4.12 | 4.12 | 4.53 | 4.12 | 4.35 | 3.53 | 3.13 | 3.73 | 3.15 | 3.73 | 3.35 | 3.34 |

TABLE 3. (CONT.) Sequence divergence of trnL intron (below diagonal) and trnL-F spacer (above diagonal)

| SPECIES | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *1. Corylopsis* | 2.46 | 2.14 | 2.14 | 2.72 | 2.44 | 3.01 | 2.42 | 2.44 | 2.41 | 2.44 | 3.01 | 4.47 | 5.91 | 5.59 |
| *2. Matudaea* | 3.58 | 3.22 | 3.76 | 4.37 | 4.09 | 4.66 | 4.05 | 4.09 | 4.04 | 4.10 | 4.66 | 6.46 | 7.07 | 7.60 |
| *3. Loropetalum* | 2.73 | 2.41 | 2.66 | 2.99 | 2.70 | 3.27 | 2.94 | 2.70 | 2.93 | 2.71 | 3.27 | 5.58 | 6.44 | 6.67 |
| *4. Maingaya* | 3.28 | 2.94 | 3.18 | 3.26 | 2.98 | 3.53 | 3.45 | 2.98 | 3.46 | 2.98 | 3.53 | 5.85 | 6.99 | 6.98 |
| *5. Tetrathyrium* | 3.00 | 2.67 | 2.40 | 2.99 | 2.71 | 3.28 | 2.69 | 2.71 | 2.67 | 2.72 | 3.28 | 5.30 | 6.16 | 6.40 |
| *6. Trichocladus* | 2.45 | 2.13 | 2.93 | 3.25 | 2.97 | 3.52 | 3.19 | 2.97 | 3.20 | 2.71 | 3.52 | 5.04 | 6.75 | 6.16 |
| *7. Dicoryphe* | 1.09 | 0.80 | 1.60 | 1.90 | 1.62 | 2.17 | 1.87 | 1.62 | 1.88 | 1.62 | 2.17 | 3.96 | 5.38 | 4.78 |
| *8. Neostrearia* | 2.19 | 1.88 | 2.67 | 2.97 | 2.70 | 3.25 | 2.94 | 2.70 | 2.95 | 2.70 | 3.25 | 4.48 | 6.49 | 5.88 |
| *9. Noahdendron* | 2.45 | 2.41 | 3.22 | 3.52 | 3.25 | 3.79 | 3.47 | 3.25 | 3.48 | 3.26 | 3.79 | 4.80 | 7.06 | 6.47 |
| *10. Ostrearia* | 3.01 | 2.68 | 3.47 | 3.78 | 3.51 | 4.06 | 3.47 | 3.51 | 3.74 | 3.51 | 4.06 | 5.32 | 7.32 | 6.70 |
| *11. Eustigma* | 1.90 | 1.60 | 2.94 | 2.99 | 2.72 | 3.27 | 3.19 | 2.72 | 3.20 | 2.72 | 3.27 | 5.33 | 6.76 | 6.48 |
| *12. Fortunearia* | 0.82 | 0.53 | 1.88 | 2.17 | 1.90 | 2.45 | 2.13 | 1.90 | 2.14 | 1.90 | 2.45 | 4.23 | 5.65 | 5.37 |
| *13. Sinowilsonia* | - | 0.81 | 2.46 | 2.76 | 2.48 | 2.78 | 2.72 | 2.48 | 2.73 | 2.49 | 2.78 | 4.89 | 6.30 | 6.03 |
| *14. Molinadendron* | 0.39 | - | 2.12 | 2.43 | 2.16 | 2.70 | 2.38 | 2.16 | 2.39 | 2.16 | 2.70 | 4.45 | 5.88 | 5.59 |
| *15. Hamamelis* | 0.99 | 1.17 | - | 1.07 | 0.80 | 1.34 | 0.78 | 0.80 | 0.79 | 0.80 | 1.34 | 4.69 | 6.13 | 6.13 |
| *16. DistyliumM* | 1.17 | 1.36 | 0.58 | - | 0.27 | 0.27 | 1.33 | 0.27 | 0.81 | 0.27 | 0.27 | 5.31 | 6.71 | 6.69 |
| *17. DistyliumR* | 1.37 | 1.55 | 0.78 | 0.19 | - | 0.53 | 1.06 | 0.00 | 0.54 | 0.00 | 0.53 | 5.03 | 6.43 | 6.41 |
| *18. Distyliopsis* | 1.17 | 1.36 | 0.58 | 0.00 | 0.19 | - | 1.60 | 0.53 | 1.08 | 0.53 | 0.00 | 5.60 | 7.01 | 6.98 |
| *19. Fothergilla* | 0.78 | 0.97 | 0.20 | 0.38 | 0.58 | 0.38 | - | 1.06 | 1.05 | 1.06 | 1.60 | 4.97 | 6.43 | 6.40 |
| *20. Parrotia* | 1.17 | 1.36 | 0.58 | 0.39 | 0.58 | 0.39 | 0.38 | - | 0.54 | 0.00 | 0.53 | 5.03 | 6.43 | 6.41 |
| *21. Parrotiopsis* | 0.78 | 0.97 | 0.20 | 0.38 | 0.58 | 0.38 | 0.00 | 0.38 | - | 0.54 | 1.08 | 4.44 | 6.45 | 6.42 |
| *22. Shaniodendron* | 1.33 | 1.54 | 0.65 | 0.00 | 0.22 | 0.00 | 0.43 | 0.43 | 0.43 | - | 0.53 | 5.02 | 6.43 | 6.42 |
| *23. Sycopsis* | 1.17 | 1.36 | 0.58 | 0.00 | 0.19 | 0.00 | 0.38 | 0.39 | 0.38 | 0.00 | - | 5.60 | 7.01 | 6.98 |
| *24. Disanthus* | 4.47 | 4.26 | 4.28 | 4.42 | 4.62 | 4.43 | 4.21 | 4.61 | 4.21 | 4.26 | 4.43 | - | 7.28 | 5.93 |
| *25. Exbucklandia* | 3.20 | 2.99 | 3.19 | 3.17 | 3.36 | 3.17 | 2.96 | 3.35 | 2.96 | 3.12 | 3.17 | 3.83 | - | 3.61 |
| *26. Rhodoleia* | 3.39 | 3.18 | 3.38 | 3.35 | 3.54 | 3.35 | 3.15 | 3.54 | 3.15 | 3.54 | 3.35 | 3.61 | 1.59 | - |

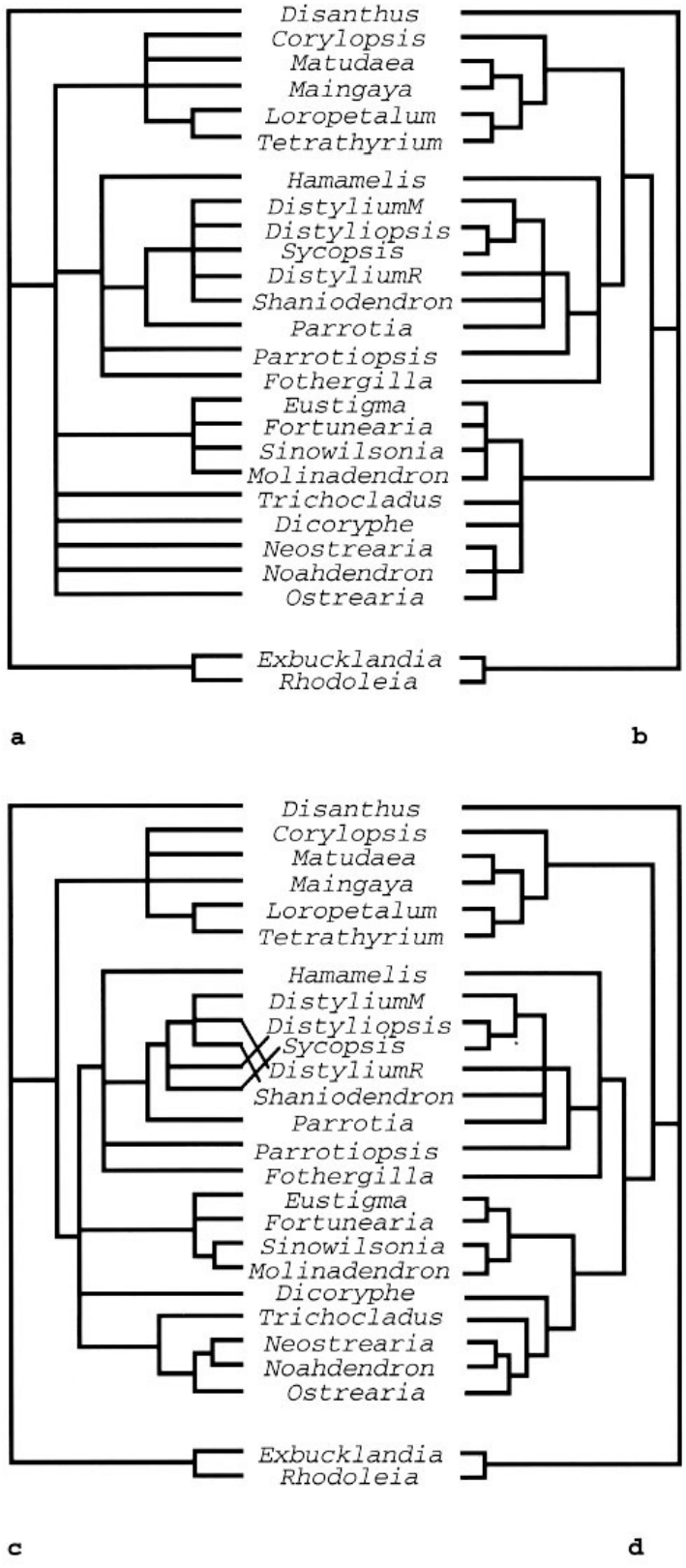


FIGURE 1. Trees of the Hamamelidoideae based on parsimony analysis of separate data sets of the non-coding regions of cpDNA using gaps as missing data (a, b) or as a fifth character state (c, d). a. Strict consensus of 820 trees of 83 steps based on *trn*L intron data, CI = 0.89, RC = 0.81; b. Strict consensus of two trees of 102 steps based on the *trn*L-*trn*F spacer data, CI = 0.92, RC = 0.84; c. Strict consensus of 64 trees of 178 steps based on *trn*L intron data, CI = 0.83, RC = 0.70; d. Strict consensus of two trees of 177 steps based on the *trn*L-*trn*F spacer data, CI = 0.81, RC = 0.71.

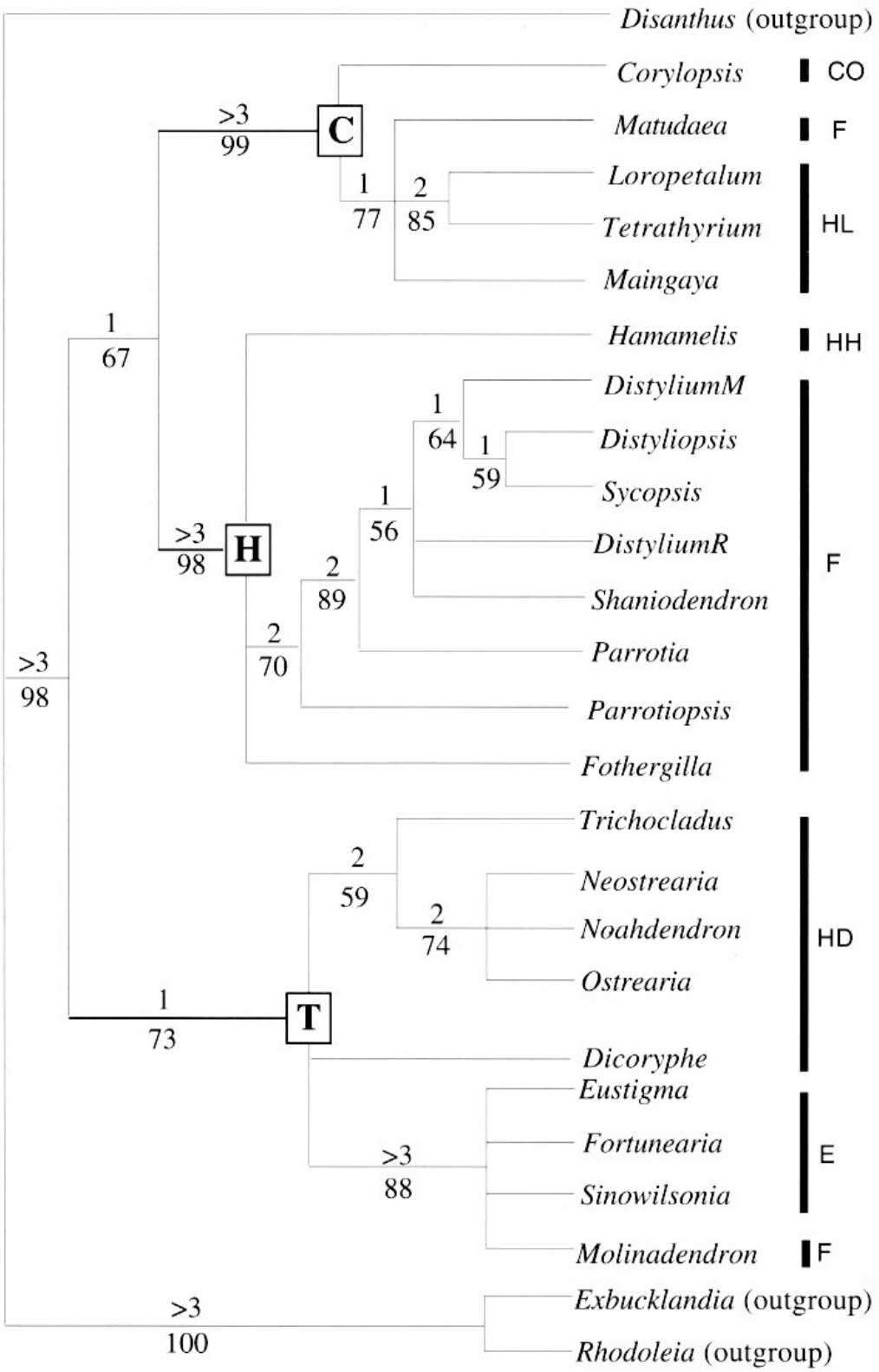


FIGURE 2. The strict consensus of 26 most parsimonious trees of 205 steps based on combined sequences of the non-coding regions of chloroplast DNA using gaps as missing data; CI = 0.88, RC = 0.77. Numbers above and below branches are decay indices and bootstrap percentages, respectively. Boxed letters indicate three major clades, C = *Corylopsis* lineage, H = *Hamamelis* lineage, and T = *Trichocladus* lineage. Groups indicated by black bars follow Endress (1989c). CO = Corylopsideae, HH = Hamamelidinae (Hamamelideae), HL = Loropetalinae (Hamamelideae), HD = Dicoryphinae (Hamamelideae).

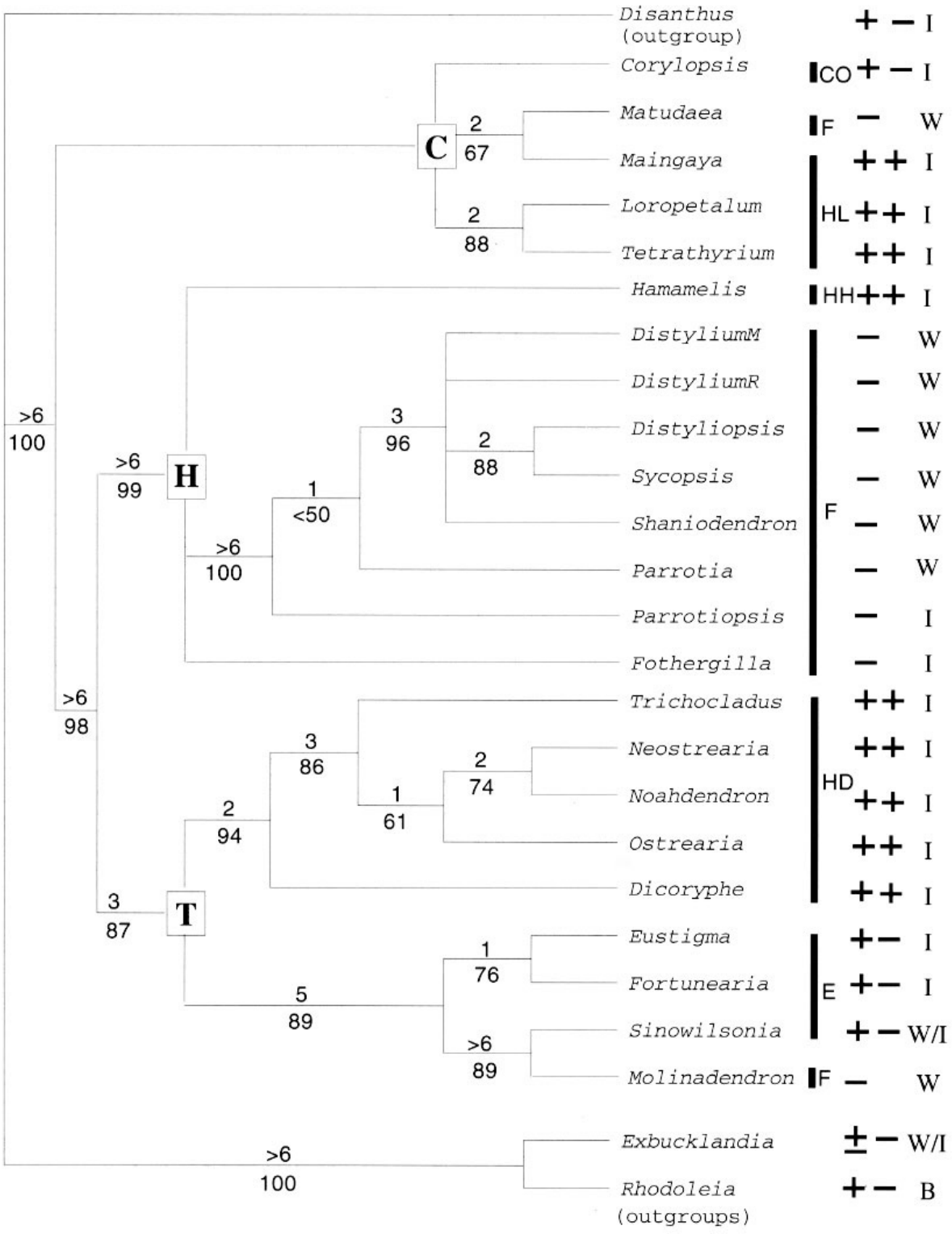


FIGURE 3. The strict consensus of eight shortest trees of 394 steps based on sequences of the non- coding regions of chloroplast DNA using gaps as a fifth character state; CI = 0.79, RC = 0.65. Symbols as in Fig. 2. The three columns on the right represent three morphological characters and their states: 1. Apetaly, 2. Strap-shaped petal, and 3. Pollination: wind (W), insect (I), bird (B).