

Revised infrafamilial classification of Symplocaceae based on phylogenetic data from DNA sequences and morphology

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Phylogenetic analyses were conducted with 51 parsimony-informative morphological characters and previously generated DNA sequence data from five genic regions (ITS, *trnL-trnF*, *rpl16*, *matK*, *trnC-trnD*) to revise the classification of Symplocaceae in accordance with ranked monophyly. Observed conflict between the morphological and molecular estimates is interpreted as a consequence of convergent features of the androecium among two clades of the family, possibly influenced by the advent of hummingbird pollination in the largest New World lineage. All nine taxa above the species level in the revised classification (two genera, and within *Symplocos* two subgenera, three sections, and two series) are based on clades with $\geq 90\%$ bootstrap support values and Bayesian posterior probabilities of 1.00 in molecular analyses. *Symplocos* section *Cordyloblaste* (two species) is elevated to the genus level on the basis of both its position as sister to all other *Symplocos* species and morphological differences that have been used to delineate genera in other Ericalean families. Optimization of the morphological characters onto one of the trees from the combined morphological and molecular analysis suggests that all nine recognized taxa correspond to clades that have at least two morphological synapomorphies, although for two of these clades support is provided by only ambiguous characters. All 318 species of *Symplocos*, as currently recognized in the literature, are assigned to subdivisions. The assignment of 90 of these is based on molecular and morphological data, and that of the rest (as yet unsampled for DNA sequence characters) on morphological attributes alone. The ranks of two taxa are changed (to *Symplocos* subgenus *Palura* and *Symplocos* series *Urbaniocharis*), several lectotypes are designated, and a key to genera and subdivisions of *Symplocos*, descriptions, and complete synonymy are provided.

KEYWORDS: classification, *Cordyloblaste*, phylogenetics, Symplocaceae, *Symplocos*

INTRODUCTION

The flowering plant family Symplocaceae comprises over 300 species of primarily montane trees and shrubs of the Americas, eastern Asia, and Australasia. Current molecular evidence groups Symplocaceae with 22 other families of order Ericales, as sister to a clade comprising Diapensiaceae and Styracaceae (Schönenberger & al., 2005). The family is distinguished from other members of Ericales by the combination of sympetalous, actinomorphic flowers; epipetalous, united, and usually numerous stamens with spheroid thecae; an inferior, incompletely locular ovary; a simple style; unitegmic ovules; and a drupaceous fruit (Nooteboom, 1975, 2003).

Early treatments of Symplocaceae, especially those with a regional focus, often recognized two to several genera within the family (e.g., Adanson, 1763; Aublet, 1775; Linné, 1781; Loureiro, 1790; Don, 1825; Vellozo,

1825). L'Héritier (1791) was the first to place the genera of Symplocaceae recognized up to that time under the single genus *Symplocos*. This circumscription was taken up by De Candolle (1844) in his global treatment (as tribe Symploceae of Styracaceae) and maintained by Bentham & Hooker (1876). Various subsequent authors of minor works recognized other generic segregates within Symplocaceae, a trend carried to an extreme by Miers (1879), who delimited eleven genera. Brand (1901), in his comprehensive revision of Symplocaceae for Engler's *Das Pflanzenreich*, reverted to the earlier monogeneric concept of the family. With only minor exceptions (e.g., Nakai, 1922, 1927; Hatusima, 1936), Symplocaceae have been treated as comprising a single genus to the present day.

Several workers have provided infrageneric treatments of *Symplocos* above the species level. Don (1837) delimited sections *Alstonia*, *Hopea*, and *Palura* on only vaguely defined characters. De Candolle (1844),

recognizing these and adding section *Ciponima*, based his classification primarily on the degree of corolla lobe fusion and stamen adnation to the corolla, stamen arrangement (monadelphous versus pentadelphous), carpel number, and fruit locule number. With the exception of stamen arrangement, these characters have continued to be emphasized in all subsequent subdivisional classifications of *Symplocos*. Bentham & Hooker (1876) largely retained De Candolle's classification but placed section

Table 1. Comparison of three classifications of *Symplocaceae* above the species level, including that from this paper

Brand (1901)	Nooteboom (1975)
<i>Symplocos</i> subg. <i>Symplocos</i>	} <i>S. subg. Symplocos</i>
<i>S. sect. Symplocos</i>	
<i>S. subsect. Symplocos</i>	
<i>S. subsect. Pseudoalstonia</i>	
<i>S. sect. Cordyloblaste</i>	
<i>S. subg. Epigenia</i>	} <i>S. subg. Hopea</i>
<i>S. sect. Barberina</i>	
<i>S. sect. Pseudosymplocos</i>	
<i>S. subg. Hopea</i>	
<i>S. sect. Palaeosymplocos</i>	
<i>S. sect. Bobua</i>	
<i>S. subsect. Lodhra</i>	
<i>S. subsect. Palura</i>	
<i>S. subg. Microsymplocos</i>	
<i>S. sect. Neosymplocos</i>	
<i>S. sect. Urbaniocharis</i>	
This paper	Taxon equivalents of this paper sensu Brand (1901)
<i>Cordylolablaste</i>	<i>S. sect. Cordyloblaste</i>
<i>Symplocos</i>	<i>S. subgg. Epigenia, Hopea, Microsymplocos, and sect. Symplocos</i>
<i>S. subg. Palura</i>	<i>S. subsect. Palura</i> in part (<i>S. paniculata</i>)
<i>S. subg. Symplocos</i>	<i>S. subgg. Epigenia and Microsymplocos, subg. Hopea</i> in part, and <i>sect. Symplocos</i>
<i>S. sect. Lodhra</i>	<i>S. subg. Hopea</i> in part
<i>S. sect. Barberina</i>	<i>S. subg. Hopea</i> in part (<i>S. tinctoria</i>) and <i>subg. Epigenia</i>
<i>S. sect. Symplocos</i>	<i>S. subg. Microsymplocos</i> and <i>sect. Symplocos</i>
<i>S. series Urbaniocharis</i>	<i>S. sect. Urbaniocharis</i>
<i>S. series Symplocos</i>	<i>S. sects. Symplocos and Neosymplocos</i>
<i>Neosymplocos</i>	<i>S. sect. Neosymplocos</i>

Palura under section *Hopea* and added the Asian section *Cordylolablaste*, which they reduced from the genus level as originally proposed by Moritz (1848). Brand (1901) revised and further expanded Bentham and Hooker's infrageneric classification, largely to accommodate morphological variation observed in more recently discovered Neotropical species. Brand recognized subgenera *Symplocos*, *Epigenia*, *Hopea*, and *Microsymplocos*; each of these in turn contained two sections (*Symplocos* and *Cordylolablaste*; *Barberina* and *Pseudosymplocos*; *Bobua* and *Palaeosymplocos*; and *Neosymplocos* and *Urbaniocharis*, respectively). In addition to the characters noted above, Brand's classification was based primarily on leaf midvein elevation, various other stamen features, sexual expression (hermaphroditism versus dicliny), and embryo morphology. Because Brand's classification remains the most recent infrageneric classification of *Symplocos* provided as part of a comprehensive taxonomic revision of the genus, we use it as the primary context for assessing the results of the present work (Table 1).

Various modifications of Brand's classification have been proposed, all for revisionary studies of Asian and Australasian species of *Symplocos*. Nooteboom (1975) placed subgenera *Epigenia* and *Microsymplocos* under subgenus *Hopea* based on palynological and phytochemical data, foregoing finer-scale subdivisions (Table 1). In a revision of the Japanese species of *Symplocos*, Nagamasu (1989a, b, 1993) recognized subgenus *Microsymplocos* and placed subgenus *Epigenia* under subgenus *Hopea*, also based on palynological characters. Of Brand's sections, only those in subgenus *Hopea* have been reexamined (Handel-Mazzetti & Peter-Stibal, 1943; Wu, 1986a, b, 1987; Nagamasu, 1993), and only in the context of the Chinese and Japanese species of *Symplocaceae*. No clear consensus has been established for sectional classification.

Most infrafamilial classifications of *Symplocaceae* above the species level suffer from a lack of clearly contrasting keys and descriptions with which to recognize taxa. The more recent infrageneric treatments of the family (e.g., Nooteboom, 1975; Wu, 1987; Nagamasu, 1993; see Table 1), although improving on older treatments by the incorporation of clear keys and descriptions, have nonetheless still been limited by the lack of an explicit phylogenetic framework with which to discover shared derived character states and monophyletic groups. They are further hampered by a focus on only partial (Old World) revisionary studies of the family.

Recent studies (Soejima & Nagamasu, 2004; Wang & al., 2004; Fritsch & al., 2006) have collectively established a firm phylogenetic estimate with DNA sequence data upon which to reconsider infrafamilial classification of *Symplocaceae*. Still needed, however, is an estimate based solely on morphological characters with which to properly compare the results of the analyses based on molecular

data. The objectives of this study are to construct a dataset of morphological characters of Symplocaceae and to conduct a morphologically based phylogenetic analysis of the genus. This will allow us to examine the evolution of morphological characters in Symplocaceae, combine morphological and molecular data for a total-evidence phylogenetic estimate, and use the results to revise the infrageneric classification of Symplocaceae so that sections and subgenera correspond to monophyletic groups.

MATERIALS AND METHODS

Fifty one parsimony-informative characters (Appendix 1) were included in the morphological data matrix (Appendix 2 in Taxon online issue). Character data were taken mainly from personal observations of living material and herbarium specimens, or sometimes derived from the literature (Appendix 1, where indicated). Several characters initially included in the matrix (e.g., inflorescence type, presence/absence of hypanthium pubescence, presence/absence of corolla pubescence) were ultimately excluded because of either low confidence in delimiting character states or high within-terminal polymorphism. Chambered pith is known in *Symplocos tinctoria* and we have not been able to detect this character in any other species of *Symplocos*. It thus appears to be an autapomorphy for this species and this character was not included in the matrix. Vouchers for the morphological phylogenetic analysis are included in the Taxonomic Treatment section, where fl = flowering specimen, fr = fruiting specimen, and st = sterile. All vouchers are from CAS unless otherwise indicated.

Phylogenetic analysis of the morphological dataset was conducted by using maximum parsimony (MP) with PAUP* version 4.0b10 (Swofford, 2002). Searches were conducted over 100 random-taxon-addition replicates with tree bisection-reconnection (TBR) branch-swapping, steepest descent, and MulTrees in effect. All characters and states were weighted equally and unordered, terminals with multiple character states were treated as polymorphic, and inapplicable character states were treated as missing data. Only parsimony-informative characters were included in the analysis. Because all runs exceeded buffer capacity, each replicate was initialized manually. Relative support for individual clades was estimated with the MP bootstrap (bt) method (Felsenstein, 1985). One thousand pseudoreplicates were performed with uninformative characters excluded. Ten random-taxon-addition heuristic searches for each pseudoreplicate were performed and no more than 2,000 minimum-length trees were saved per search.

The dataset, comprising 90 ingroup terminals and 12 outgroup terminals, is the same set of ingroup species as those used previously for phylogenetic analyses based

on ITS, *trnL-trnF*, *rpl16*, *matK*, and *trnC-trnD* DNA sequences (Wang & al., 2004; Fritsch & al., 2006). Results based on morphological data could thus be compared directly with those based on molecular data, and the datasets from each could be readily combined. Phylogenetic analysis of Ericales DNA sequences with eleven genic regions supports a clade comprising ten families—Actinidiaceae, Clethraceae, Cyrillaceae, Ericaceae, Roridulaceae, Sarraceniaceae, Theaceae, Symplocaceae, Styracaceae, and Diapensiaceae—with the latter three forming a clade (Schönenberger & al., 2005). On this basis, the following exemplar genera were selected as members of the outgroup: *Saurauia* (Actinidiaceae), *Clethra* (Clethraceae), *Cyrilla* (Cyrillaceae), *Rhododendron* (Ericaceae), *Camellia* (Theaceae), *Alniphyllum*, *Huodendron*, *Pterostyrax*, and *Styrax* (Styracaceae), *Diapensia*, and *Galax* (Diapensiaceae). A member of Pentaphragmaceae (*Ternstroemia*), which forms a trichotomy with the ten-family clade and a clade comprising several other families of Ericales (Schönenberger & al., 2005), was also included to provide additional compatibility with the molecular dataset (see below). Character evolution over one of the equally parsimonious trees was traced under parsimony optimization with MacClade 4.0 (Maddison & Maddison, 2000), with any polytomies arbitrarily resolved.

To provide complete genic region data for *Symplocos longipes*, newly generated *matK*, *trnC-trnD*, and *trnL-trnF* sequences were generated. Sequencing methods followed Wang & al. (2004) and Fritsch & al. (2006). The voucher is *Ramírez-Amezcuca & al. 958* from Guerrero, Mexico (CAS; GenBank accessions EU863158, EU863154, and EU863156, respectively). To provide complete genic region data for *Styrax officinalis*, new *rpl16*, *trnC-trnD*, and *trnL-trnF* sequences were generated (voucher listed in Fritsch, 2001) with methods as above (EU863153, EU863155 + EU863159, and EU863157, respectively), and previously generated ITS (Fritsch, 2001; GenBank accession AF327489) and *matK* (Duangjai & al., 2006; GenBank accession DQ924099) sequences were included.

After the molecular dataset was pruned appropriately to exclude synonyms sensu Nooteboom (1975, 2005) and other sequence duplicates of species, MP and maximum likelihood (ML) analyses were performed on the DNA sequence dataset (90 ingroup terminals and two outgroup terminals; ITS, *trnL-trnF*, *rpl16*, *matK*, and *trnC-trnD*). This was done to assess whether the modifications to the composition of the molecular dataset used by Fritsch & al. (2006) had any substantial effects on the results. *Styrax* and *Ternstroemia* were employed as the members of the outgroup because sequences of all five regions are available.

Sequence alignment was done manually and the analysis was conducted by using MP with the same settings as described above, except that terminals with multiple character states were treated as uncertain and

gap characters were treated as missing values. Because this dataset contained extensive missing data resulting from inability to sequence various species for some of the genic regions, an analysis was conducted over all species with complete data or nearly so for all five genic regions (66-terminal dataset, including *Styrax* and *Ternstroemia*). Bootstrap estimates were calculated from this dataset as described above.

ML analyses were conducted on both the 92-terminal and 66-terminal datasets by using PAUP* with a heuristic search and TBR branch-swapping. The starting tree was obtained by neighbor-joining, and the model of nucleotide substitution was selected by using Modeltest (Posada & Crandall, 1998). The GTR + I + Γ model fit the data best and thus was the model employed in the analysis. The model parameters were all estimated by ML.

Bayesian inference of phylogeny (BI) was conducted with MrBayes version 3.0b4 (Huelsenbeck & Ronquist, 2001) on the 66-terminal dataset by using uniform prior probabilities and estimating base frequencies and the parameters for the GTR + I + Γ model, in accordance with the recommendations of Huelsenbeck & Rannala (2004). Four chains of the Markov chain Monte Carlo were run by beginning with a random tree and sampling one tree every 100 generations for 5,000,000 generations. The first 5,000 samples of the chain were used as burn-in. To estimate the posterior probability (pP) of recovered branches, a 50% majority-rule tree was created.

To provide total-evidence phylogenetic estimates of *Symplocos*, all available morphological and DNA sequence data were combined into a single 92-terminal dataset and an MP analysis was conducted with the same settings as described for the molecular analysis, with *Styrax* and *Ternstroemia* as outgroup. This data file (used for all analyses) includes the other ten outgroup taxa for morphology and is available on request from the first author. An additional MP analysis was conducted on the reduced (66-terminal) dataset.

To infer the evolution of *Symplocos* morphology within a total-evidence phylogenetic framework, the 51 characters employed in the morphological analysis were optimized onto the tree from the combined 92-terminal analysis. Polytomies were resolved arbitrarily. Character evolution was traced under parsimony optimization (ACCTRAN and DELTRAN) as above.

Because we hypothesized that androecial characters and possibly all male function characters (i.e., androecium + corolla; see Wilson, 1979, 1994; Stanton & al., 1986; Ladd, 1994) in *Symplocos* sections *Symplocos* and *Cordyloblaste* have undergone convergent evolution (see Results), we constructed various reduced datasets with these characters included or excluded and compared phylogenetic results based on each. For comparison, we did the same for gynoecial and female function characters

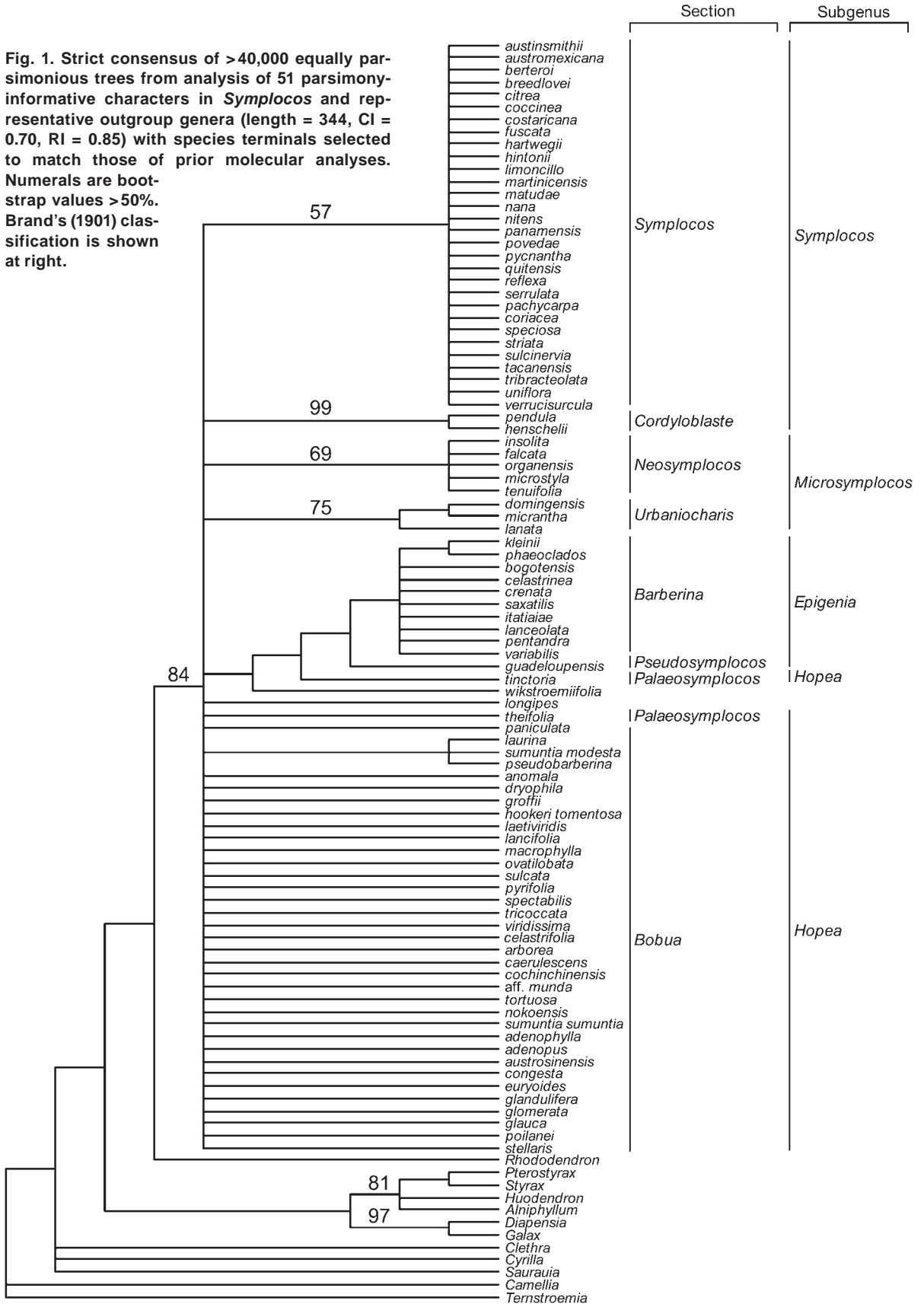
(i.e., gynoecium + fruit). The eight reduced datasets are as follows: (1) all stamen characters excluded (16–31); (2) all stamen and corolla characters excluded (13–31); (3) only stamen characters excluded (16–31); (4) only stamen and corolla characters included (13–31); (5) all gynoecial characters excluded (32–41); (6) all gynoecial and fruit characters excluded (32–49); (7) only gynoecial characters included (32–41); (8) only gynoecial and fruit characters included (32–49). To further test for convergence in androecial characters involving section *Cordyloblaste*, we conducted a morphological analysis with the two species of this section excluded and compared the results to those based on complete-taxon molecular data.

RESULTS

Morphological analysis. — The morphological data matrix contained 238 cells with missing values (4.6%) and 37 cells assigned as inapplicable (0.71%; Appendix 2 in Taxon online issue). The analysis yielded > 40,000 equally parsimonious trees (none of the replicates in the analysis ran to completion) of 344 steps (consistency index, CI = 0.70; retention index, RI = 0.85). In the strict consensus of these trees, *Symplocos* is monophyletic (bt = 84). Within *Symplocos*, the following sections are recovered as individual clades: *Symplocos* (bt = 57), *Cordyloblaste* (bt = 99), *Neosymplocos* (bt = 69), *Urbaniocharis* (bt = 75), and *Barberina* (bt ≤ 50). Subgenus *Epigenia* is monophyletic (bt ≤ 50), with section *Barberina* as sister to the representative of section *Pseudosymplocos* (bt ≤ 50). *Symplocos tinctoria* forms a clade with subgenus *Epigenia* (bt ≤ 50), with *S. wikstroemiifolia* as sister to this clade (bt ≤ 50). Other than three minor clades, no other resolution occurs in the strict consensus. Not apparent from the strict consensus in Fig. 1 is the presence of two islands of equally parsimonious trees resulting from the analysis. In one of these, the main *Hopea* group is placed (as paraphyletic) at the base of the ingroup and section *Cordyloblaste* groups with section *Symplocos*. In the other, section *Cordyloblaste* forms an unresolved polytomy with other clades at the base of the tree and subgenus *Epigenia* groups with the main *Hopea* clade (results not shown).

The following clades are supported by the characters indicated over a representative tree (Fig. 2): *Symplocos*: hypanthium present (9), anthers erect at anthesis (24), anther thecae spheroid (26), fruit indehiscent (42), endocarp with apical pores (46), endocarp with apical depression (47), and seed number/carpel number < 1 (49); section *Cordyloblaste*: pedicel not articulated (8), hypanthium narrowly funnelliform (10), corolla texture coriaceous (adaxially papillose when dry) (15), pollen perforate (27), pollen colpus half-length/diameter > 0.18 (28), ovary partly inferior (33), mesocarp bundles not recessed

Fig. 1. Strict consensus of >40,000 equally parsimonious trees from analysis of 51 parsimony-informative characters in *Symplocos* and representative outgroup genera (length = 344, CI = 0.70, RI = 0.85) with species terminals selected to match those of prior molecular analyses. Numerals are bootstrap values >50%. Brand's (1901) classification is shown at right.



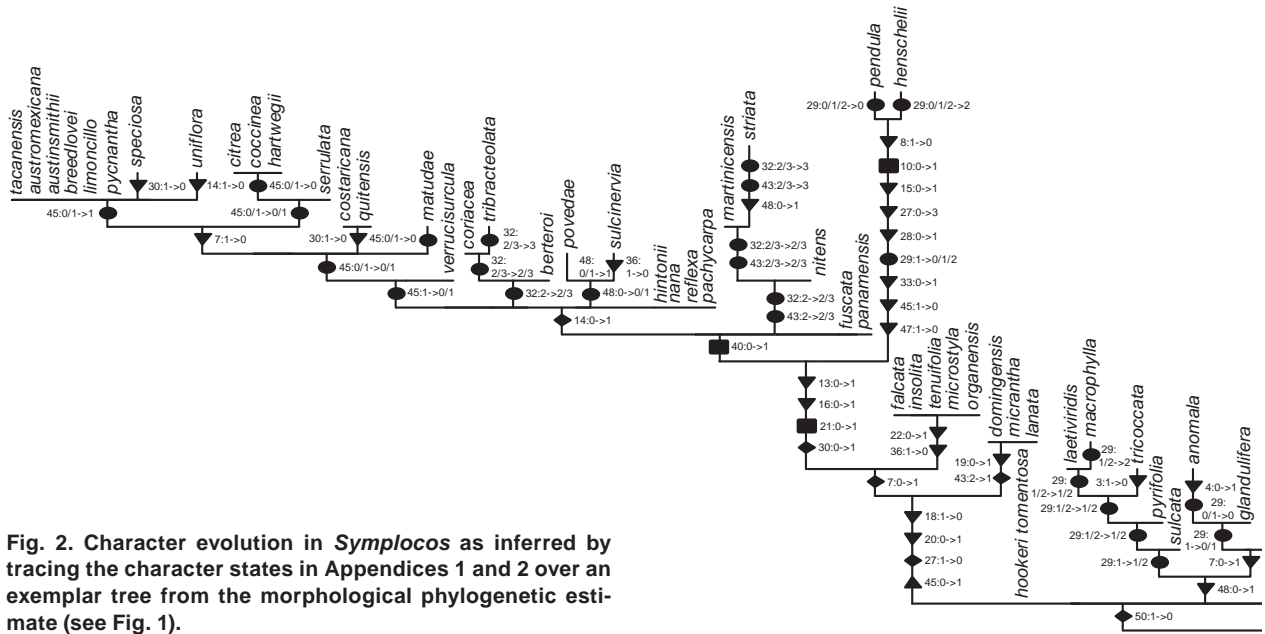


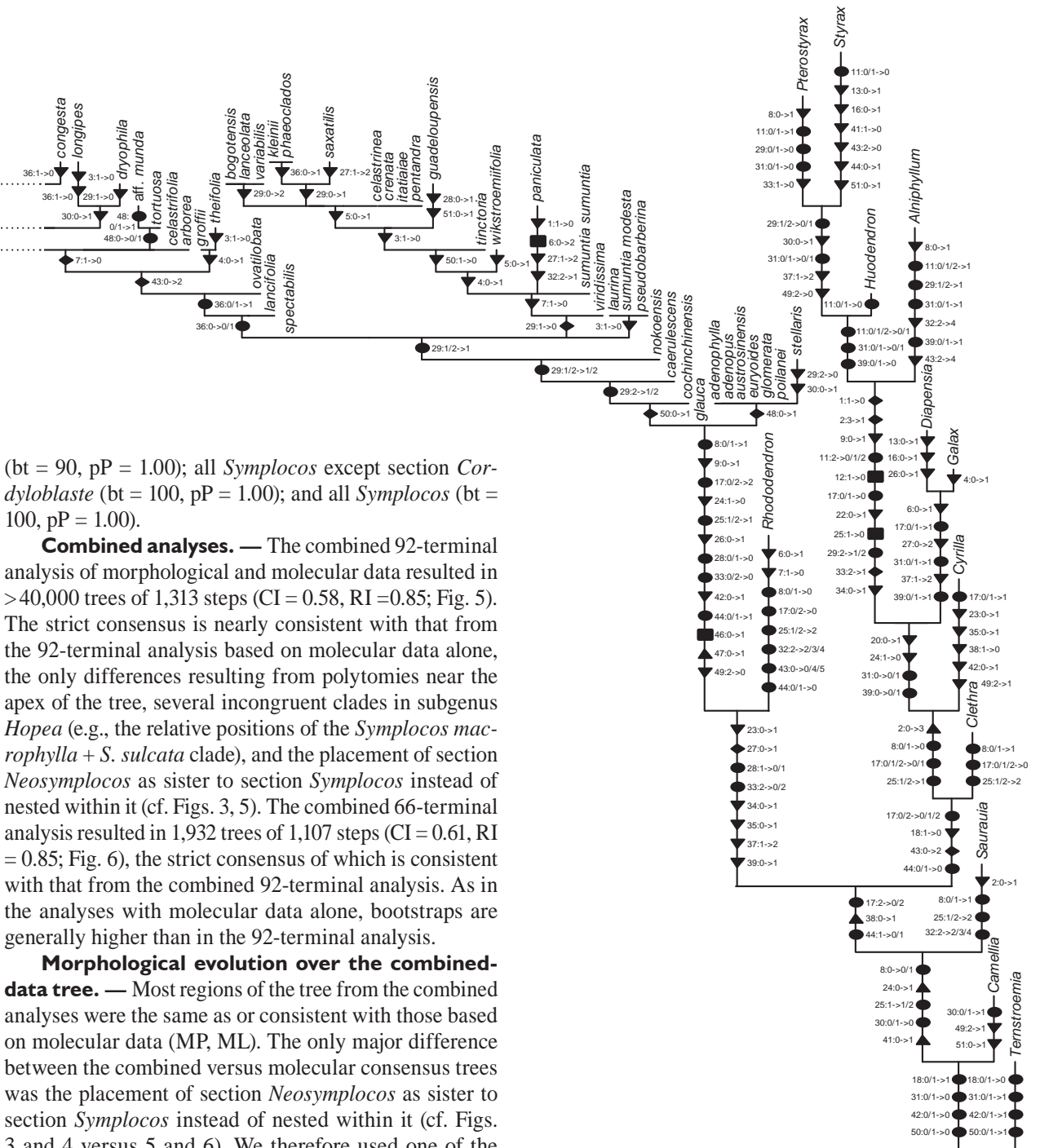
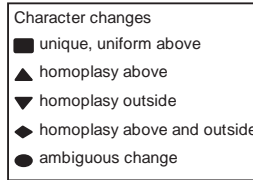
Fig. 2. Character evolution in *Symplocos* as inferred by tracing the character states in Appendices 1 and 2 over an exemplar tree from the morphological phylogenetic estimate (see Fig. 1).

in narrow channels of endocarp (45), and endocarp lacking an apical depression (47); section *Symplocos*: subterminal oil-secreting areas on the style present (40); section *Neosymplocos*: stamen filaments pubescent (22) and nectary disk glabrous (36); section *Urbaniocharis*: all stamens included within corolla (19) and fruit 2-celled (43); subgenus *Epigenia*: mature current-year branchlets green (3); section *Barberina*: sexual expression gynodioecious (5); subgenus *Epigenia* + *S. tinctoria*: embryo straight (50); subgenus *Epigenia* + *S. tinctoria* + *S. wikstroemiifolia*: leaf midvein flat or prominent adaxially (4).

Molecular analysis. — Sequence alignment with all species included regardless of missing data content (92 terminals) resulted in a dataset of 8,197 characters, of which 1,493 (18.2%) were variable and 460 (5.6%) were parsimony-informative. The dataset for MP contained 2.6% gapped positions and 12.9% missing values. MP analysis resulted in >40,000 equally parsimonious trees of 1,182 steps (CI = 0.61, RI = 0.85) and the ML analysis resulted in a single tree (score = 24,617.544; Fig. 3). The MP consensus and ML tree are largely consistent with one another, with the MP consensus more unresolved and conflicting with the ML tree in five places (Fig. 3). In both trees, section *Cordyloblaste* groups as sister to the rest of *Symplocos* (bt = 100), and *S. paniculata* forms the next-diverging lineage above it (bt = 100). A clade comprising most species of subgenus *Hopea* (bt = 98) groups as sister (bt = 87) to a clade comprising subgenus *Epigenia*, section *Symplocos*, subgenus *Microsymplocos*, *S. longipes*, *S. tinctoria*, and *S. wikstroemiifolia* (bt = 70). Section *Urbaniocharis* (bt = 78) groups as sister (bt = 76) to a clade comprising sections *Symplocos* and *Neosymplocos* (bt = 90). The species of section *Barberina* form a clade (bt

= 99), as do those of subgenus *Epigenia* (bt = 100), and these form a trichotomy (bt = 96) with *S. longipes* and a clade comprising *S. tinctoria* + *S. wikstroemiifolia* (bt = 73). Section *Neosymplocos* (bt = 95) nests within section *Symplocos*. Both topologies are largely consistent with a similar (MP) analysis based on the same genic regions but with more terminals included (Fritsch & al., 2006: fig. 3, left tree).

The dataset with complete genic region sequence data (66-terminal) was 8,188 characters long and contained 1,435 (17.5%) variable and 506 (6.2%) parsimony-informative characters. The dataset for MP contained 3.4% gapped positions and 1.5% missing values. MP analysis resulted in 6,719 trees of 1,003 steps (CI = 0.64, RI = 0.85) and the ML analysis resulted in a single tree (score 23,295.156; Fig. 4). The MP strict consensus is completely consistent with the ML tree, and the BI tree is consistent with both the MP and ML trees except for the placement of *S. povedae* and *S. striata*, which group together as sister to *S. costaricana* + *S. limoncillo* (not shown). The ML and BI trees exhibit higher clade resolution than the MP tree (Fig. 4). Bootstraps are generally higher than in the analysis that included all species, likely because of the substantially lower amount of missing data. Support for major clades is as follows: sections *Symplocos* + *Neosymplocos* (bt = 99, pP = 1.00); section *Urbaniocharis* (bt = 100, pP = 1.00); section *Symplocos* + subgenus *Microsymplocos* (bt = 91, pP = 1.00); section *Barberina* (bt = 100, pP = 1.00); subgenus *Epigenia* + *S. longipes* + *S. tinctoria* + *S. wikstroemiifolia* (bt = 96, pP = 1.00); the clade comprising all of the above (bt = 87, pP = 1.00); the main subgenus *Hopea* clade (bt = 100, pP = 1.00); all *Symplocos* except *S. paniculata* and section *Cordyloblaste*



(bt = 90, pP = 1.00); all *Symplocos* except section *Cordyloblaste* (bt = 100, pP = 1.00); and all *Symplocos* (bt = 100, pP = 1.00).

Combined analyses. — The combined 92-terminal analysis of morphological and molecular data resulted in >40,000 trees of 1,313 steps (CI = 0.58, RI = 0.85; Fig. 5). The strict consensus is nearly consistent with that from the 92-terminal analysis based on molecular data alone, the only differences resulting from polytomies near the apex of the tree, several incongruent clades in subgenus *Hopea* (e.g., the relative positions of the *Symplocos macrophylla* + *S. sulcata* clade), and the placement of section *Neosymplocos* as sister to section *Symplocos* instead of nested within it (cf. Figs. 3, 5). The combined 66-terminal analysis resulted in 1,932 trees of 1,107 steps (CI = 0.61, RI = 0.85; Fig. 6), the strict consensus of which is consistent with that from the combined 92-terminal analysis. As in the analyses with molecular data alone, bootstraps are generally higher than in the 92-terminal analysis.

Morphological evolution over the combined-data tree. — Most regions of the tree from the combined analyses were the same as or consistent with those based on molecular data (MP, ML). The only major difference between the combined versus molecular consensus trees was the placement of section *Neosymplocos* as sister to section *Symplocos* instead of nested within it (cf. Figs. 3 and 4 versus 5 and 6). We therefore used one of the

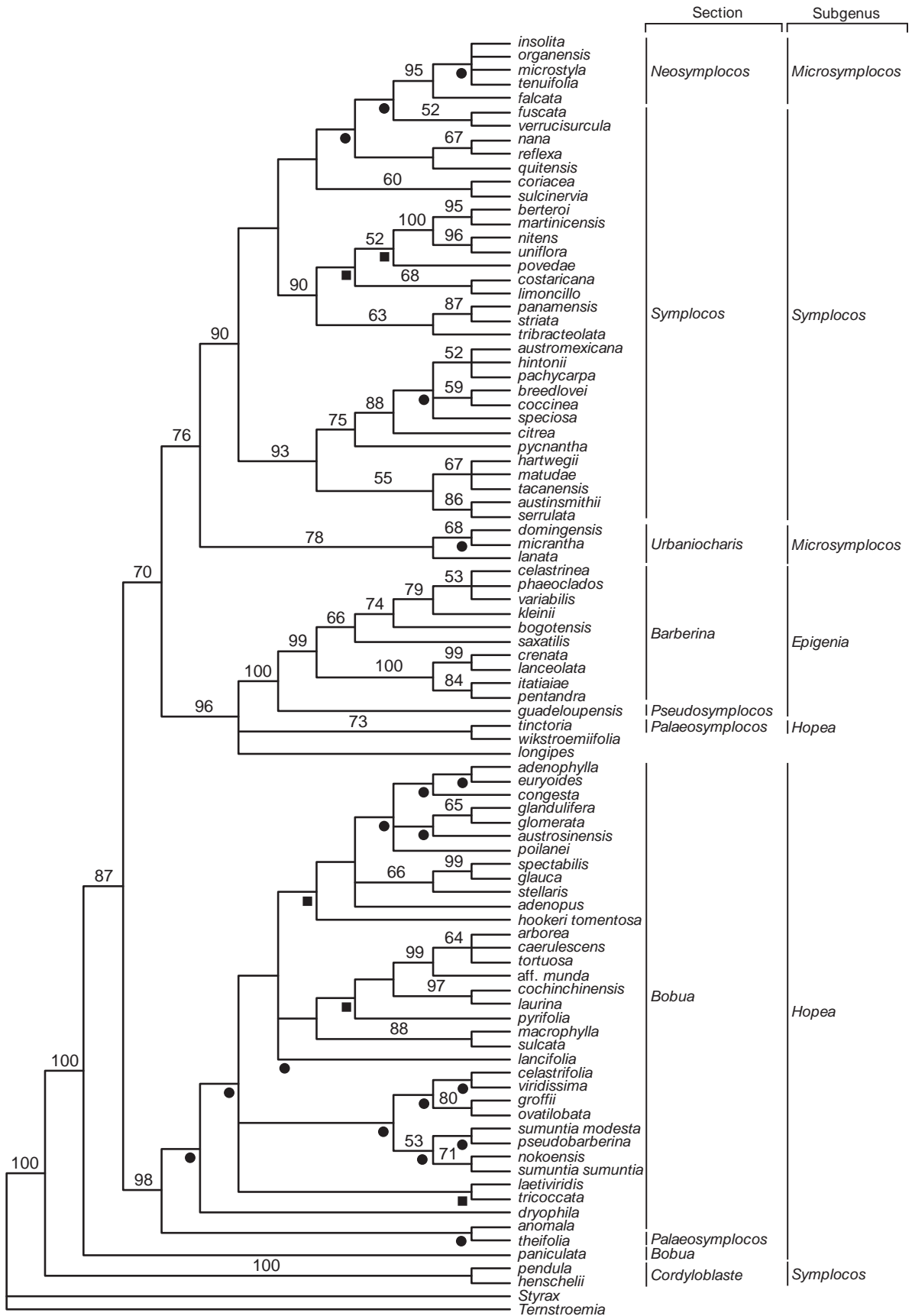


Fig. 4. Maximum likelihood tree from analysis of *Symplocos* DNA sequence data (ITS, *trnL-trnF*, *rpl16*, *matK*, and *trnC-trnD*; score = 23,295.156) that includes only species with complete genic region data (66 terminals). Dots indicate clades that collapse in the strict consensus of the 6,719 equally parsimonious trees from the corresponding MP analysis (length = 1,003, CI = 0.64, RI = 0.85). Numerals above branches are MP bootstrap values >50%; those below branches are Bayesian posterior probabilities. Brand's (1901) classification is shown at right.

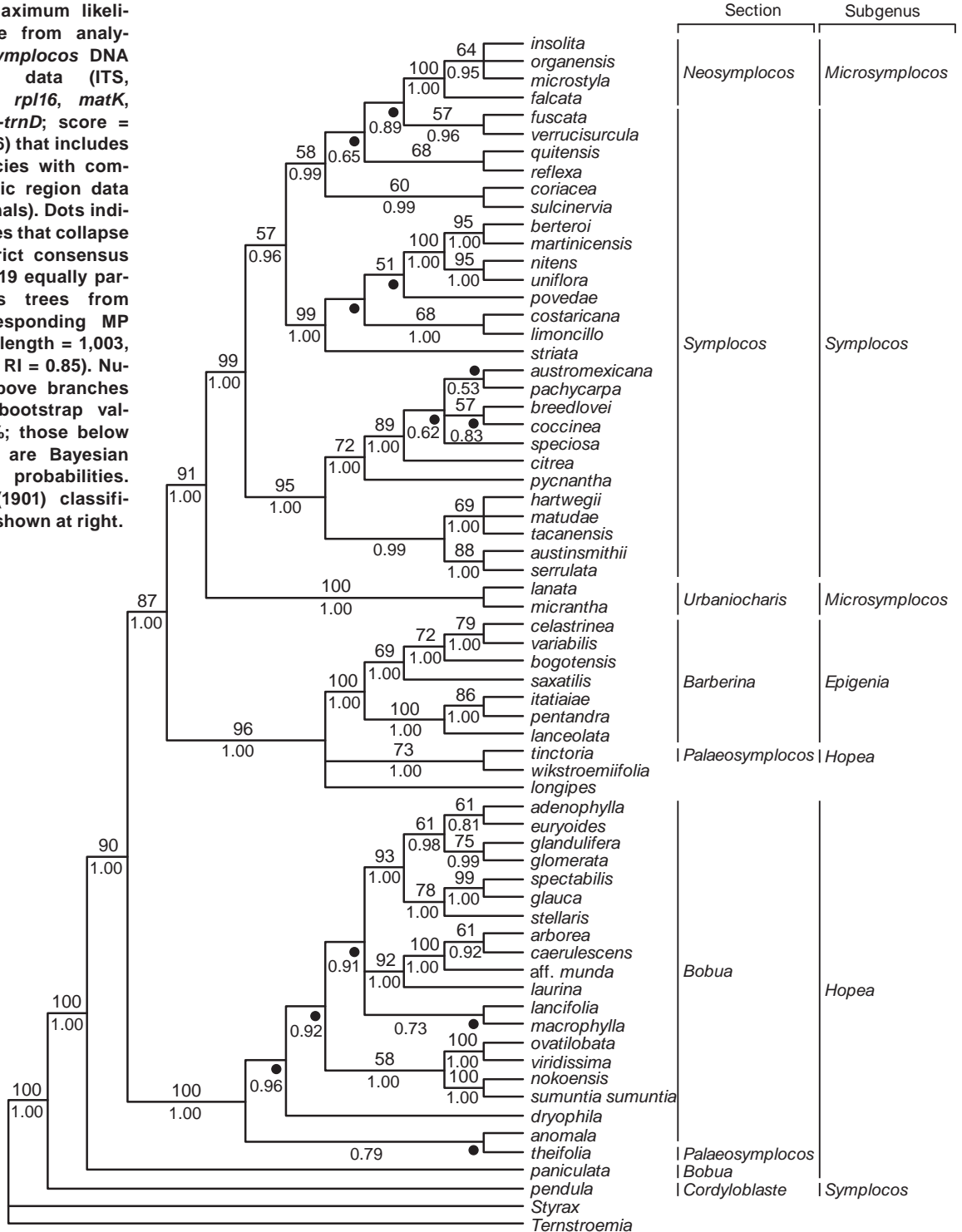
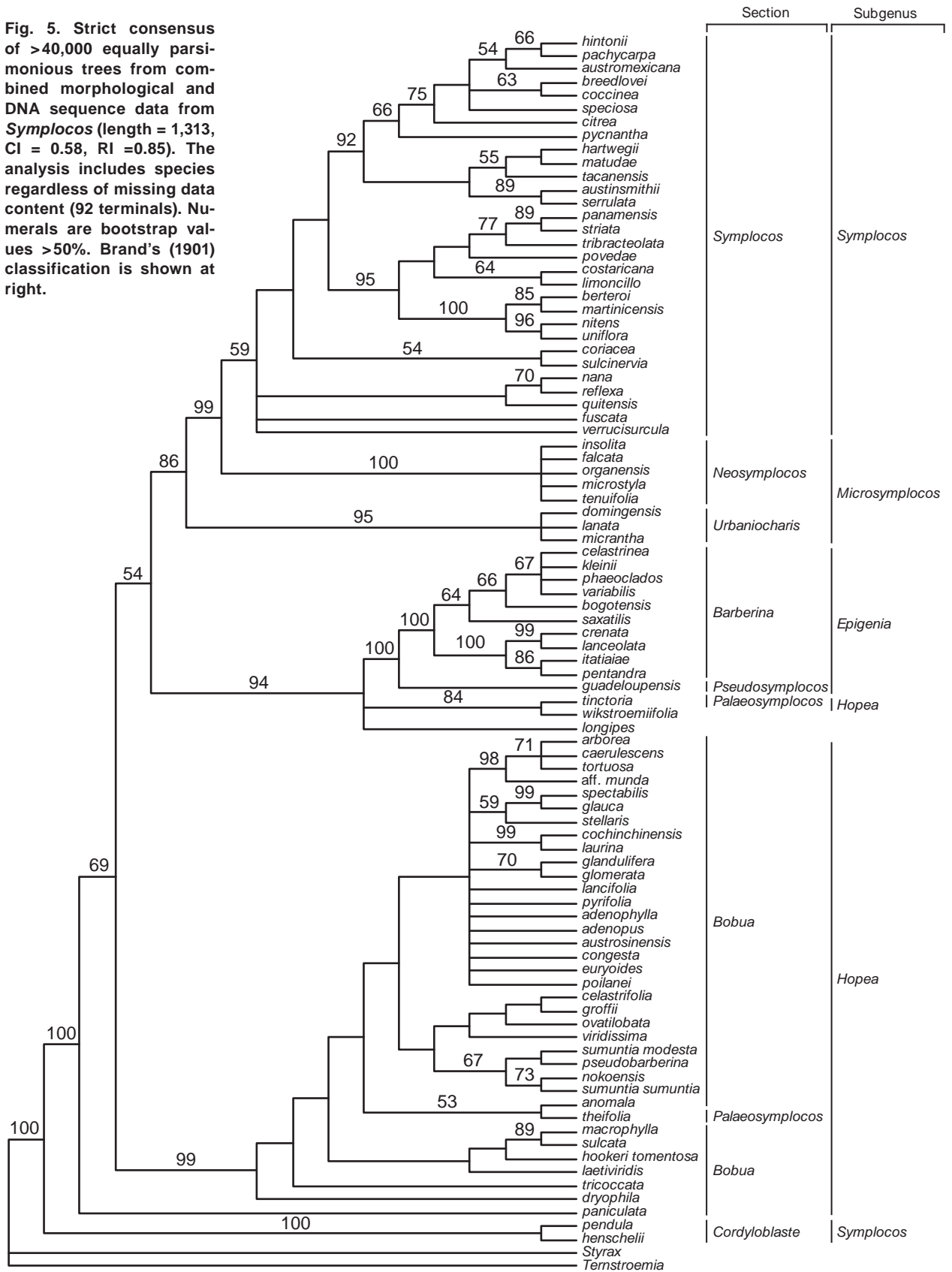


Fig. 3. Maximum likelihood tree from analysis of *Symplocos* DNA sequence data (ITS, *trnL-trnF*, *rpl16*, *matK*, and *trnC-trnD*; score = 24,617.544) that includes species regardless of missing data content (92 terminals). Dots indicate clades that collapse in the strict consensus of the >40,000 equally parsimonious trees from the corresponding MP analysis (length = 1,182, CI = 0.61, RI = 0.85); squares indicate clades from the ML analysis that conflict with those from the MP analysis. Numerals are MP bootstrap values >50%. Brand's (1901) classification is shown at right.

Fig. 5. Strict consensus of >40,000 equally parsimonious trees from combined morphological and DNA sequence data from *Symplocos* (length = 1,313, CI = 0.58, RI = 0.85). The analysis includes species regardless of missing data content (92 terminals). Numerals are bootstrap values >50%. Brand's (1901) classification is shown at right.



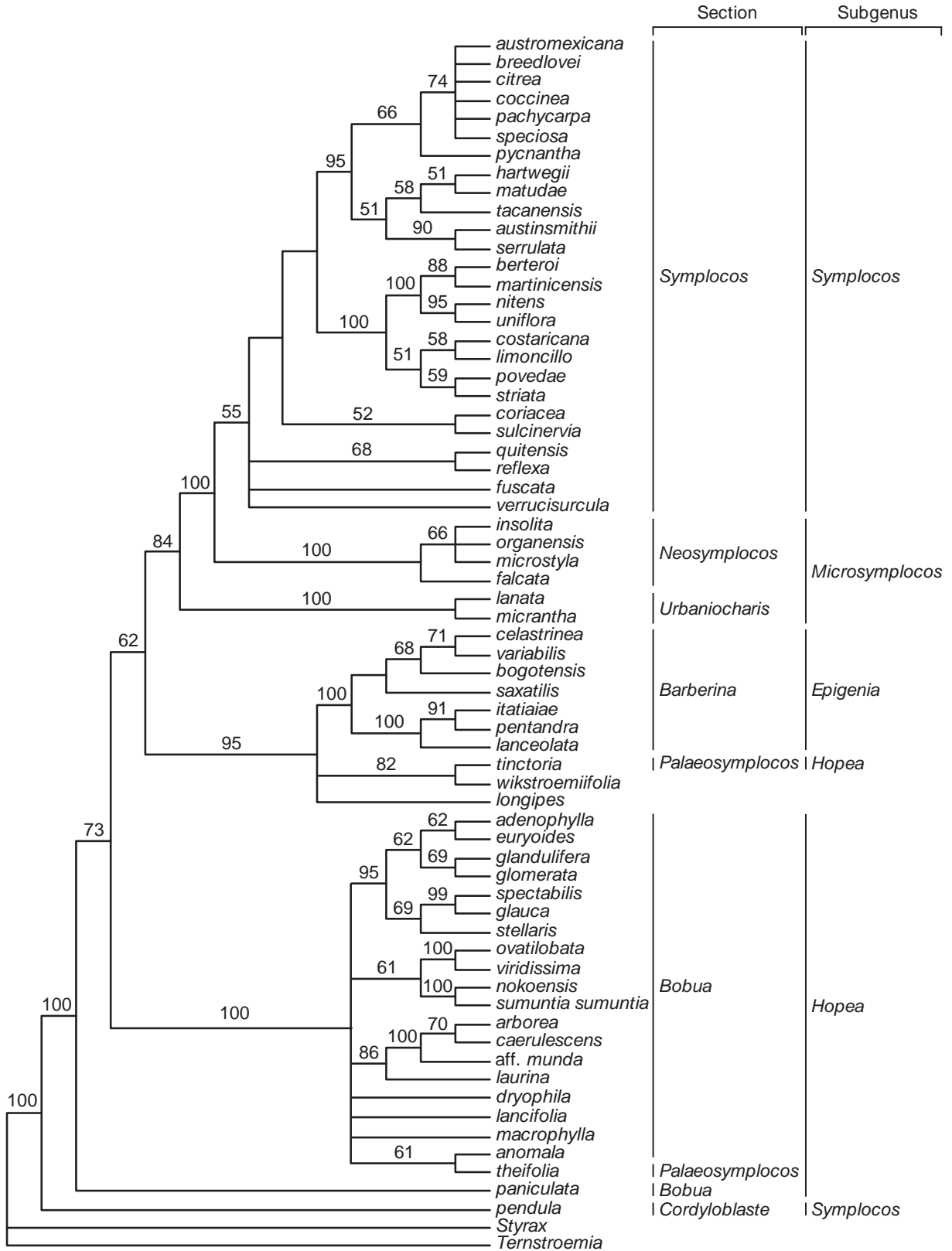
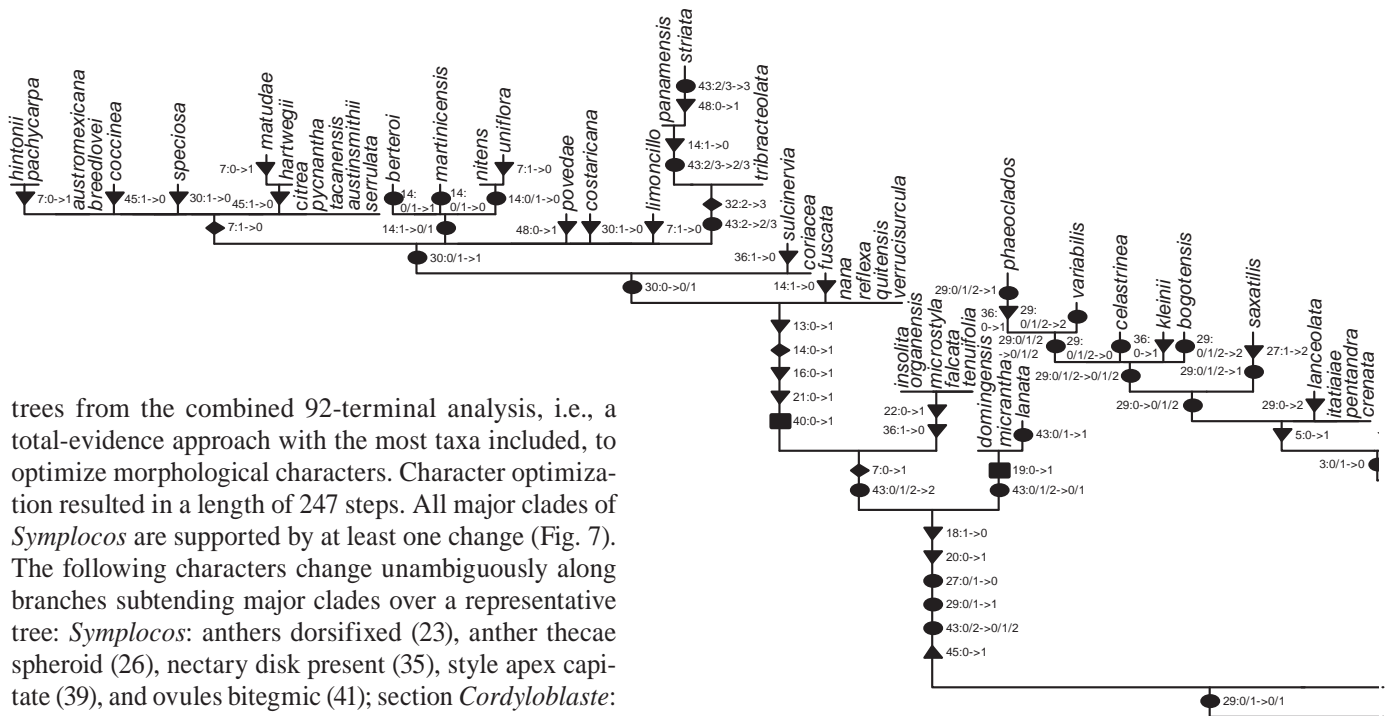


Fig. 6. Strict consensus of the 1,932 equally parsimonious trees from combined morphological and DNA sequence data from *Symplocos* (length = 1,107, CI = 0.61, RI = 0.85). The analysis includes only species with complete data from all five genic regions (66 terminals). Numerals are bootstrap values >50%. Brand's classification (1901) is shown at right.



trees from the combined 92-terminal analysis, i.e., a total-evidence approach with the most taxa included, to optimize morphological characters. Character optimization resulted in a length of 247 steps. All major clades of *Symplocos* are supported by at least one change (Fig. 7). The following characters change unambiguously along branches subtending major clades over a representative tree: *Symplocos*: anthers dorsifixed (23), anther thecae spheroid (26), nectary disk present (35), style apex capitate (39), and ovules bitegmic (41); section *Cordyloblaste*: hypanthium narrowly funnelform (10), corolla texture coriaceous (adaxially papillose when dry) (15), and stamen filaments apically constricted (21); non-*Cordyloblaste* species: bracteoles subtending flowers caducous (7), pedicel articulated (8), stamens non-monadelphous (18), stamen filaments terete (20), pollen colpus half-length/diameter (polar view) ≤ 0.18 (28), pollen diameter (equatorial axis) generally ≤ 30 microns (30), ovary completely inferior (33), and endocarp with apical depression (47); *S. paniculata*: deciduous (1), inflorescences irregularly concaulescent (6), gynoeceum 2-carpellate (32), and embryo curved (50); subgenus *Epigenia* + *S. longipes*, *S. tinctoria*, and *S. wikstroemiifolia*: nectary disk glabrous (36); subgenus *Epigenia* + *S. tinctoria* and *S. wikstroemiifolia*: leaf midvein flat or prominent adaxially (4); section *Barberina*: sexual expression dioecious (5); subgenus *Microsymplocos* + section *Symplocos*: stamens monadelphous (18), stamen filaments tangentially flattened (20), and mesocarp bundles recessed in narrow channels of endocarp (45); section *Urbaniocharis*: all stamens included within corolla (19); section *Symplocos* + section *Neosymplocos*: bracteoles subtending flowers persistent (7); section *Neosymplocos*: stamen filaments pubescent (22) and nectary disk glabrous (36); and section *Symplocos*: petals connate distinctly beyond base (13), corolla pink to lavender (14), androecium adnate to corolla distinctly beyond base (16), stamen filaments apically constricted (21), and subterminal oil-secreting areas on the style present (40). Only ambiguous changes are optimized along the branch subtending the main subgenus *Hopea* clade (*S. glomerata* through *S. dryophila* in Fig. 7), the clade from *S. hintonii* through *S. dryophila* in Fig. 7, the clade from *S. hintonii*

through *S. longipes* in Fig. 7, and subgenus *Epigenia*. These changes all involve one or more of the following characters: mature current-year branchlet color (3), pollen surface sculpturing (27), pollen wall curvature (29), and endocarp locule number (43).

When androecial characters were excluded from the morphological dataset (exclusion set 1), the strict consensus of >40,000 equally parsimonious trees (length = 253, CI = 0.76, RI = 0.85), albeit poorly resolved, was consistent with the results of the molecular analyses except for the positions of *S. wikstroemiifolia* and the species of section *Neosymplocos* (Fig. 8; cf. Figs. 3 and 4). When only gynoecial and fruit characters were included (exclusion set 8), section *Cordyloblaste* was recovered as sister to the remaining (completely unresolved) species of *Symplocos*. All other combinations of excluded characters resulted in either a near-star phylogeny among the ingroup terminals (sets 2 and 7) or, among other areas of nonresolution or incompatibilities with molecular results, a placement of section *Cordyloblaste* as sister to section *Symplocos* (sets 3–6; results not shown). When the two species of section *Cordyloblaste* were excluded from the dataset, the strict consensus of >40,000 equally parsimonious trees (length = 327, CI = 0.71, RI = 0.86; Fig. 9) was consistent with the results of the molecular analyses except for the positions of *S. wikstroemiifolia* and the species of section *Neosymplocos* (Fig. 9; cf. Figs. 3, 4, and 8), as it was in the tree from exclusion set 1 with androecial characters excluded.

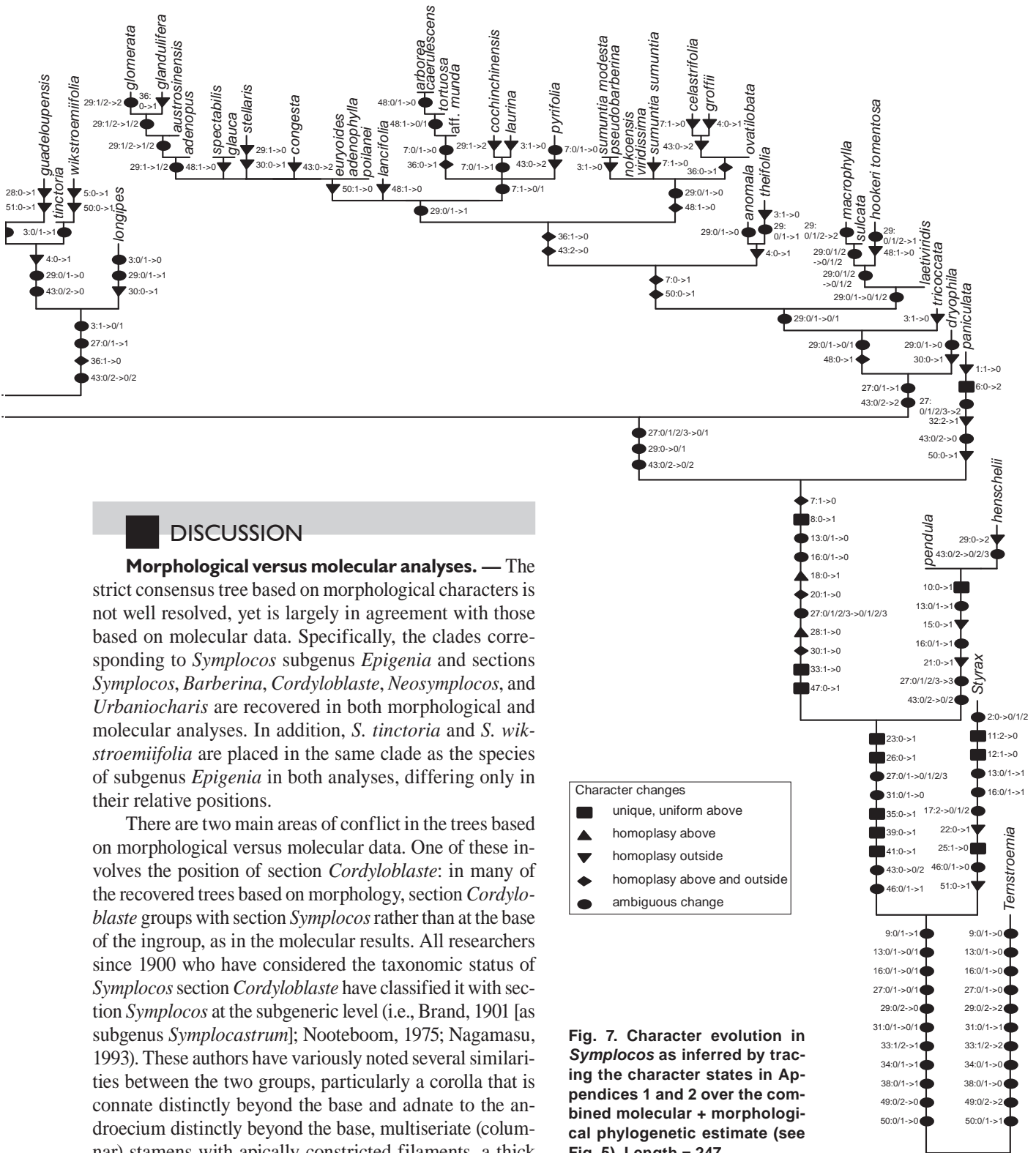


Fig. 8. Strict consensus of >40,000 equally parsimonious trees (length = 253, CI = 0.76, RI = 0.85) from a morphological dataset for *Symplocos* in which androecial characters were excluded. Brand's classification (1901) is shown at right.

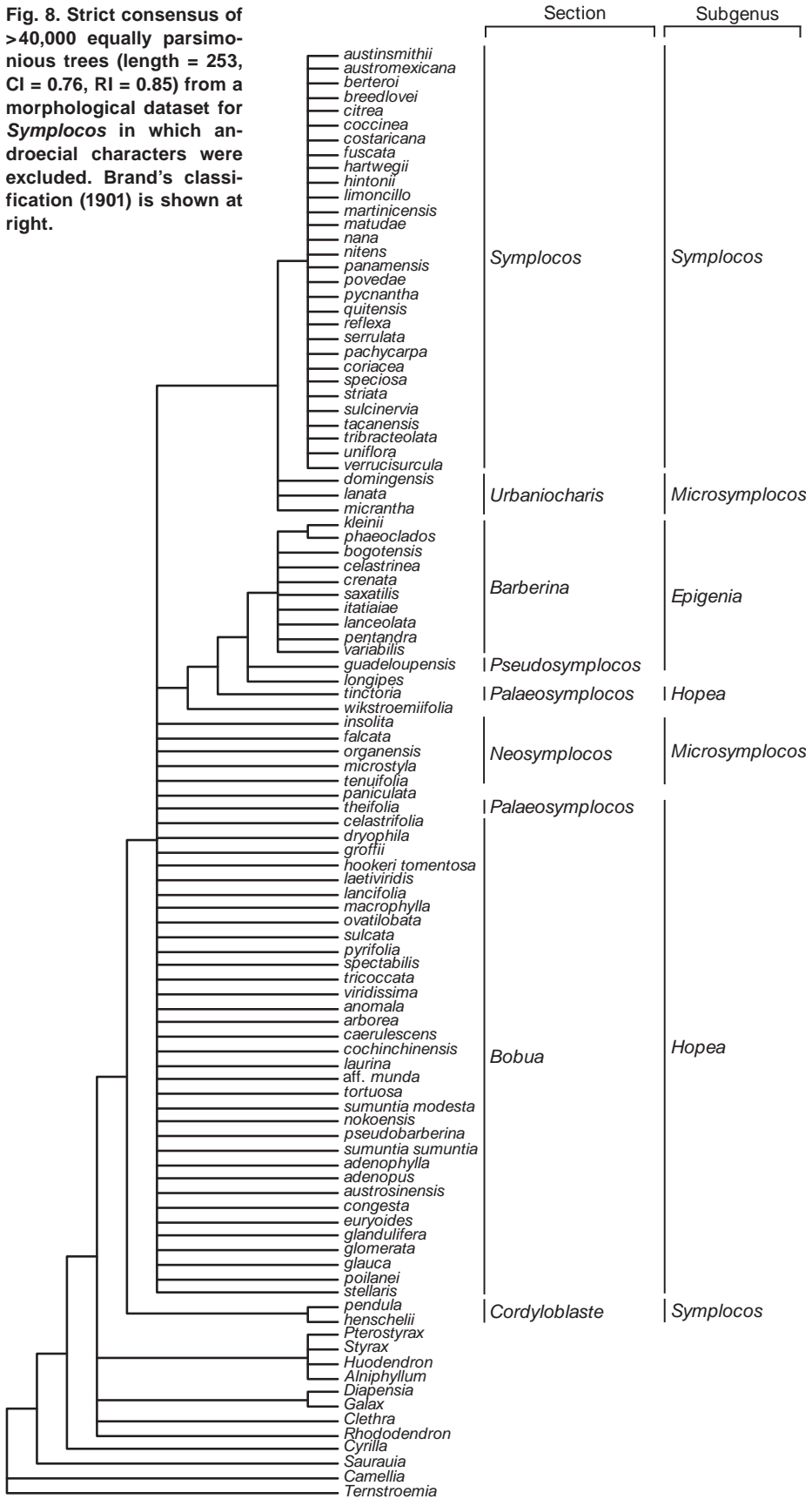
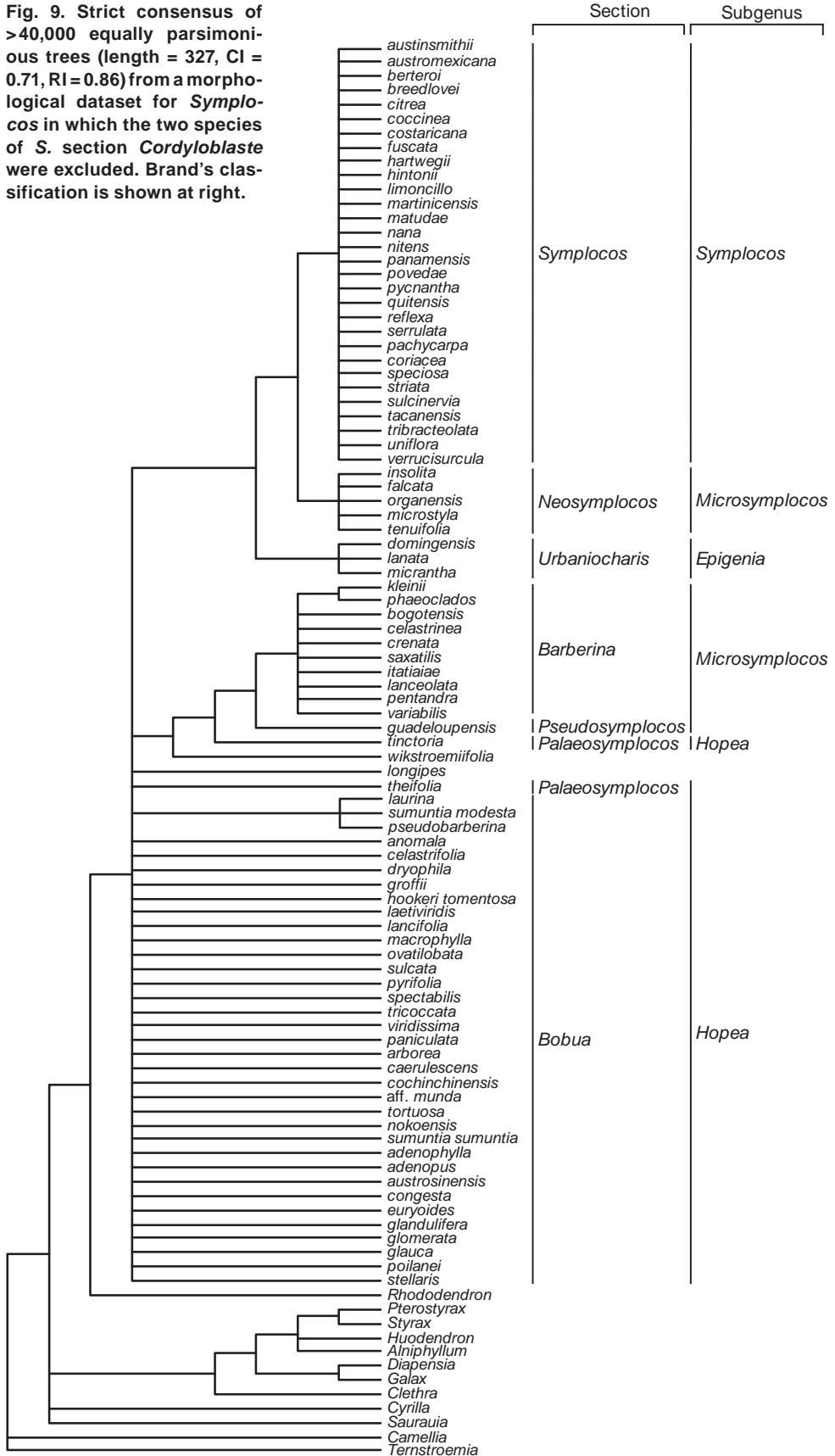


Fig. 9. Strict consensus of >40,000 equally parsimonious trees (length = 327, CI = 0.71, RI = 0.86) from a morphological dataset for *Symplocos* in which the two species of *S.* section *Cordyloblaste* were excluded. Brand's classification is shown at right.



pollen tectum without supracteal processes and with indistinct columellae, and a thick endocarp. The placement of section *Cordyloblaste* as the first-diverging lineage within the genus in the molecular analyses (Wang & al., 2004; Fritsch & al., 2006) was therefore unexpected.

In the morphological analysis, three of the four characters uniting sections *Cordyloblaste* and *Symplocos*, and six of the eight characters placing section *Cordyloblaste* with sections *Symplocos* + *Urbaniocharis*, are androecial. On this basis, we postulated that androecial characters have undergone convergence or parallelism in sections *Symplocos* and *Cordyloblaste*. This is supported by our a posteriori analyses: when either all androecial characters or the two species of section *Cordyloblaste* are excluded from the dataset, the trees from both are largely consistent with those from the molecular analyses. Further, when only gynoecial and fruit characters are included, section *Cordyloblaste* groups as sister to the rest of *Symplocos*, as in the molecular results. This suggests that female characters are a more reliable indicator of relationships than male characters near the first divergence of the phylogeny. The near-star topology recovered when only gynoecial characters were included could possibly result from an insufficient number of characters (only ten were included) to achieve resolution in the consensus tree.

Other groups of plants are known to have strongly convergent androecial characters (e.g., Evans & al., 2003, Commelinaceae; Glover & al., 2004, *Solanum*; Walker & Sytsma, 2006, *Salvia*), thought to often result from similar pollination pressures (D'Arcy, 1996). Our data suggest that the androecium became more distally adnate to the corolla, and the corolla concomitantly more strongly tubular in shape, along the branch subtending the clade of section *Symplocos* (Fig. 7). These changes may have occurred during the advent of pollination by long-tongued bees or hummingbirds in section *Symplocos*. Hummingbird pollination in particular would explain the morphological differences between section *Symplocos* and at least the Asian species of *Symplocos*, because they, like all species of section *Symplocos*, are restricted to the Neotropics. The tubular corolla and androecium with predominantly reddish colors (from an ancestral white condition), as well as the presence of copious nectar produced by the epigynic disk, both strongly suggest the prevalence of hummingbird pollination in this group, although the strongly scented flowers suggest that other animals, such as bees, also serve as pollinators. Information on the pollination biology of species of *Symplocaceae* is scant, but hummingbird visitation has been documented for one pink-flowered species of section *Symplocos* (*S. povedae*; Feinsinger & al., 1987), whereas insect pollination has been observed in at least three (white-flowered) species of the main subgenus *Hopea* clade of Asia (Corlett, 2001, *S. lucida*; Devy & Davidar, 2006, *S. wynadense*; P. Fritsch,

pers. obs., *S. dryophila*). No information is available on the pollination biology of either species of section *Cordyloblaste*. Whether the tubular corollas with adnate stamens arranged in a column in this section are synapomorphic for this clade or ancestral in *Symplocaceae* is ambiguous in our analysis (Fig. 7). Comparative pollination studies among the major clades of *Symplocaceae* would doubtless provide further insight into the evolutionary factors involved in the floral convergence between sections *Symplocos* and *Cordyloblaste* inferred here.

The other difference between the two analyses is the relative placement of section *Neosymplocos*. This section comprises 13 species endemic to southeastern Brazil and Paraguay. Optimization of morphology over the molecular tree yields five reversals in floral characters relative to the branch supporting the clade comprising this section + section *Symplocos* [petals connate at base only (13), corolla white to yellow (14), androecium adnate at base only (16), stamen filaments apically not constricted (21), and subterminal oil-secreting areas on the style absent (40); data not shown]. In this case, the morphological data were influential enough to retain this section as sister to section *Symplocos* in the combined morphological + molecular analyses, rather than place it as nested within section *Symplocos*, as in the molecular analysis (cf. Figs. 3 and 4 versus 5 and 6). Concurrently, the bootstrap support for the nested position of section *Neosymplocos* within section *Symplocos* in the 66-terminal molecular analysis is weak for the four relevant clades in Fig. 4 (all bt < 59), although the posterior probabilities for two of these clades is >0.95.

Although flower size was difficult to score for our phylogenetic analysis and thus was not included in the data matrix, small flowers are a consistent feature among the species of section *Neosymplocos* relative to most species in section *Symplocos*. Although there is virtually no information available on pollination or breeding system biology for the species of section *Neosymplocos*, the data suggest floral reduction in the ancestor of this group, and this would likely have occurred in concert with a pollination shift. Such a shift could involve a greater frequency of self-pollination, as is often seen in groups with small flowers. It could alternatively involve a shift from pollination by hummingbirds, which are known to visit at least one species in section *Symplocos*, to insect pollination. The latter could explain the reversals observed in the most recent common ancestor of section *Neosymplocos* over the molecular topology from predominantly pink or magenta corollas to predominantly white corollas, and from a corolla and androecium united nearly halfway to united only basally.

Four strongly supported clades recovered in our molecular and combined analyses are supported only ambiguously by morphological characters (*Symplocos hintonii* to *S. longipes* in Fig. 7, *S. hintonii* through *S. dryophila* in Fig. 7, main *Hopea*, and subgenus *Epigenia*). The first two

clades have not been circumscribed as taxonomic groups in previous classifications. Although subgenus *Epigenia* was proposed by Brand (1901), the morphological character that ambiguously supports this clade in our analysis (3, mature current-year branchlets green) was not one of those included in Brand's description. Our data suggest that the morphological characters upon which this group was based (petals connate at base only, stamens distinct, filaments terete, ovary 3-locular, style glabrous; Brand, 1901) are not synapomorphies for this clade. Further comparative studies of character variation in Symplocaceae not sampled here (e.g., anatomy, secondary metabolite chemistry) could reveal possible synapomorphies for these clades.

Justification for the revision. — There is strong agreement among systematists that phylogenetic information should be used as the basis for biological classification, but vigorous debate on how this information should be used, and a clear trend in this regard is not yet apparent. The three main approaches currently under debate are (1) acceptance of paraphyletic and monophyletic taxa (e.g., Brummitt, 2002; Nordal & Stedje, 2005), (2) exclusive recognition of monophyletic unranked taxa (e.g., De Queiroz & Gauthier, 1994; Cantino & De Queiroz, 2004), and (3) exclusive recognition of monophyletic ranked taxa (e.g., Potter & Freudenstein, 2005). The first approach conveys hierarchical information but fails to provide an unambiguous grouping criterion. Conversely, the second approach provides an unambiguous grouping criterion but fails to convey hierarchical information. Because the third approach provides both, we consider it to be the most powerful of the three (see discussion in Potter and Freudenstein (2005) for further clarification of this view). It is therefore the approach used here for the infrafamilial classification of the Symplocaceae.

Cordyloblaste was first described at the generic level by Moritzi (1848). Beginning with Bentham & Hooker (1876), this genus was reduced to synonymy under *Symplocos* and has generally remained so until the present, although both Ridley (1923) and Trimen (1931) retained it. We have chosen to recognize *S.* section *Cordyloblaste* sensu Brand (1901) at the level of genus (*Cordyloblaste*), for three reasons. First, the recognition of two genera instead of one eliminates the redundancy in the circumscription of a "monotypic" group, in this case, that of *Symplocos* as the only genus within the Symplocaceae. Second, both the absence of an articulated pedicel and a half-inferior ovary in *Cordyloblaste* versus *Symplocos* s.str. are also differences that delimit genera of the Styrcaceae, a family that forms part of the sister clade (with Diapensiaceae) of Symplocaceae (Schönenburger & al., 2005). Additional characters unique to *Cordyloblaste* within Symplocaceae are a narrowly funnelliform hypanthium, a coriaceous corolla (lobes adaxially papillose when dry), perforate pollen (Nagamasu, 1989a), and

a conical endocarp apex without an apical depression. Third, the endocarps of *Pallioportia*, an extinct genus of Symplocaceae from the Late Oligocene of Europe (Kirchheimer, 1957), have a strongly pitted surface unknown in any other member of Symplocaceae, either fossil or extant, yet it also has an apical depression, like *Symplocos* s.str. but unlike *Cordyloblaste*. If *Pallioportia* is to be retained as a distinct genus, as the unusual pitting in the endocarp would suggest, then the *Cordyloblaste* lineage, apparently falling outside of *Symplocos* s.str. + *Pallioportia*, should also be recognized at least at the genus level.

We agree with Nixon & al. (2003) that a change in the autonym rule of the *International Code of Botanical Nomenclature* (McNeill & al., 2006) should be considered, such that the same epithet would not be required at various taxonomic ranks within a group. In the case of *Symplocos*, the phylogenetic placement of the type of the genus (*S. martinicensis*) as well nested forced us to use the epithet "*Symplocos*" three times at infrageneric ranks (i.e., *S.* subgenus *Symplocos*, *S.* section *Symplocos*, and *S.* series *Symplocos*). A "sequencing convention" would negate the need for replicating epithets, but suffers from a loss of information because many clades that are sister to named clades would remain unnamed. A more desirable alternative would substitute unique epithets for ranks below genus. In this context, we have provided informal unique epithets for the autonoms in our classification.

The classification of *Symplocos* above the species level presented here accords with the best estimate of its phylogeny, i.e., the cladogram from the combined molecular and morphological datasets; Fig. 10). Although support exists from both molecular (Figs. 3 and 4) and morphological data (Figs. 5 and 6) for a clade comprising sections *Symplocos* and *Barberina* (sensu our classification), it is not strong enough to justify formal recognition of this clade. Instead we have chosen to recognize three sections (these two and section *Lodhra*), with the understanding that if more evidence is found to unequivocally support the sister-group relationship between sections *Symplocos* and *Barberina*, then these can be recognized as subsections.

We have also refrained from recognizing lower-level taxa within section *Barberina*. Most species of this section form a well-supported clade easily recognizable morphologically by the androdioecious condition (probably functionally dioecious; J.L.M. Aranha-Filho & al., in press.). These species were formally recognized as section *Barberina* of subgenus *Epigenia* by Brand (1901). There is enough apparent homoplasy in morphology (e.g., midvein prominence, stem color) among the remaining species, however, to obscure the placement of several critical species as yet unsampled for DNA sequence characters (e.g., *Symplocos culminicola*, *S. ovalis*, *S. salicifolia*). Furthermore, *S. longipes* is ambiguously placed as a trichotomy at the base of section *Barberina*.

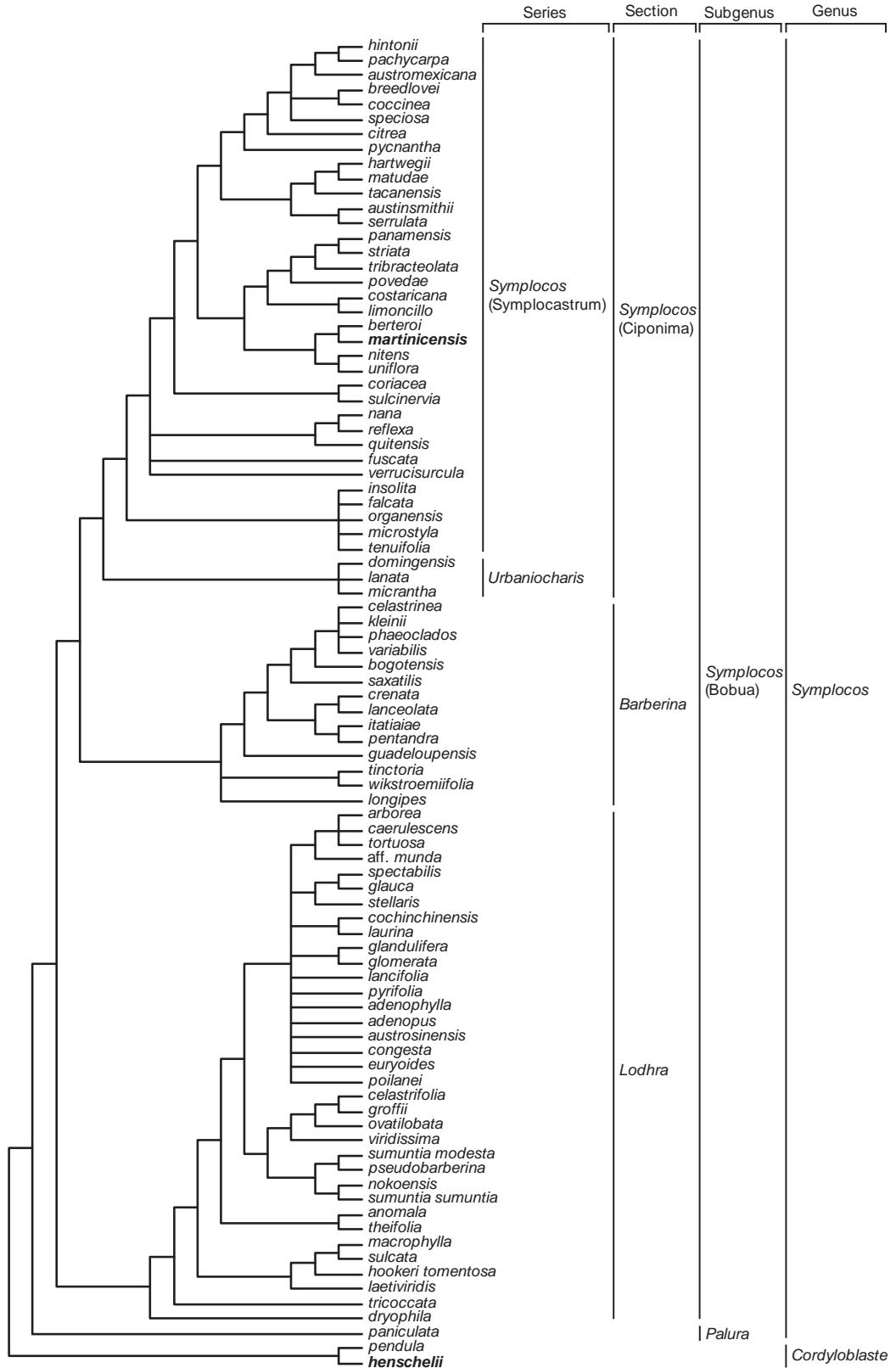


Fig. 10. Revised classification of *Symplocaceae* based on the combined molecular and morphological strict consensus tree in accordance with ranked monophyly. Names in boldface are the types of *Symplocos* and *Cordyloblaste*. Names in parentheses are informal names as proposed substitutes for autonyms.

Section *Neosymplocos* is easily delimited from the rest of *Symplocos* by its pubescent stamen filaments, but its relationship to other groups within the genus are not clear on the basis of our morphological phylogenetic analysis. Our molecular analyses place section *Neosymplocos* as nested within section *Symplocos*, but statistical support for this placement is weak, and morphological character support for the other molecular-based clades in section *Symplocos* is not yet clear. Thus, we have refrained from recognizing additional subdivisions within the clade comprising these sections (*S. series Symplocos* in our reclassification). Further study of morphological characters that are variable within section *Symplocos* (e.g., inflorescence structure, bracteole persistence, endocarp cell number) may provide enough character support to name additional subclades.

All 318 species of *Symplocos*, as currently recognized in the literature, are assigned to subdivisions in the following treatment. The assignment of 90 of these is based on molecular and morphological analyses (Soejima & Nagamasu, 2004; Wang & al., 2004; Fritsch & al., 2006; this paper). Assignments of the rest, as yet unsampled for DNA sequence characters, are based solely on morphological attributes, largely as dictated by synapomorphies as identified on the total-evidence tree. References used to calculate the number of currently recognized species within each subdivision are listed after each geographic distribution statement. Informal epithets used as substitutes for autonyms follow the names, in parentheses.

TAXONOMIC TREATMENT OF SYMPLOCACEAE ABOVE THE SPECIES LEVEL

Symplocaceae Desf. in Mém. Mus. Hist. Nat. 6: 9. 1820, nom. cons. – Type: *Symplocos* Jacq.

Shrubs or trees, usually evergreen, rarely deciduous, often accumulating aluminum, tanniferous; trichomes simple. Vegetative buds with scales or naked. Leaves alternate, spirally or rarely distichously arranged, simple, exstipulate, petiolate, pinnately nerved, often sweet tasting; blade usually with glandular teeth or sometimes entire. Inflorescences axillary and pseudoterminal, or rarely irregularly concaulescent, racemose, spicate, paniculate, fasciculate, or flowers solitary, generally with 1 bract and (1–)2 bracteoles per flower, or sometimes with several bracts and bracteoles in leaf axil through flower abortion. Flowers actinomorphic, bisexual or sometimes unisexual, fragrant. Hypanthium present, adnate to ovary wall; perianth and androecium epigynous; sepals 3–5, basally connate, imbricate; petals (3–)5(–15), connate at base only or to middle, imbricate, lobes oblong; stamens 40–100, or rarely 4–15 especially in dioecious species, adnate to corolla at base only or to middle, distinctly uniseriate or

indistinctly 1–4-seriate, monadelphous or \pm pentadelphous; anthers bilocular, basifixed, erect, introrse, longitudinally dehiscent, much shorter than filaments, thecae generally spheroid; pollen oblate to spheroidal; gynoecium 2–5-carpellate; ovary completely inferior or rarely partly inferior, 2–5-locular and placentation essentially axile but septa incomplete distally; epigynic nectary disk present, sometimes inconspicuous; ovules 2–4 per carpel, unitegmic, tenuinucellar, pendulous, anatropous; style 1 with completely connate stylodia, hollow, filiform or sometimes subulate; stigmas 1, generally capitate. Fruit drupaceous, usually blue, sometimes orange to brown or white, crowned by persistent calyx, mesocarp fleshy to rarely \pm woody; endocarp 1–5-celled, with 1–5 apical pores. Seeds 1–5, brown, ovoid, reniform, ellipsoid, ampulliform, U-shaped, or S-shaped; endosperm copious; seed number/carpel number < 1; embryo straight or curved. $n = 11, 12, 14$, ca. 45.

320 species, Americas, eastern Asia, Australasia.

KEY TO THE GENERA OF SYMPLOCACEAE

1. Pedicel not articulated; hypanthium narrowly funnelliform; corolla lobes coriaceous; pollen perforate; ovary partly inferior; apical depression of endocarp absent; $n =$ ca. 45. 1. *Cordyloblaste*
 1. Pedicel articulated; hypanthium broadly funnelliform; corolla lobes chartaceous to subcoriaceous; pollen variously sculpted but not perforate; ovary completely inferior; apical depression of endocarp present; $n = 11, 12$, or 14. 2. *Symplocos*
1. *Cordyloblaste* Hensch. ex Moritzi in Bot. Zeitung (Berlin) 6: 606. 1848 \equiv *Symplocos* section *Cordyloblaste* (Hensch. ex Moritzi) Benth. & Hook. f., Gen. Pl. 2: 669. 1876 \equiv *Symplocos* subgenus *Cordyloblaste* (Hensch. ex Moritzi) Gamble in J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 74, extra number 17: 248. 1906 – Lectotype (designated by Nooteboom, 1975: 34): *Cordyloblaste henschelii* Moritzi ('*henschelii*').
Evergreen. Mature current-year branchlets brown. Leaf midvein sulcate adaxially. Hermaphroditic. Inflorescences axillary or pseudoterminal; bracteoles subtending flowers persistent; pedicel not articulated. Hypanthium narrowly funnelliform. Petals connate distinctly beyond base; corolla adnate to androecium distinctly beyond base, white to yellow, lobes coriaceous (adaxially papillose when dry). Stamens monadelphous, at least outer exerted from the corolla; filaments tangentially flattened, apically constricted, glabrous; pollen perforate, colpus half-length/diameter (polar view) ca. 0.19–0.24, wall between colpi (polar view) straight to distinctly convex, ca.

35–41 microns in diameter (equatorial axis). Gynoecium 2–4-carpellate; ovary partly inferior; nectary disk pubescent; subterminal oil-secreting areas on style absent. Fruit with mesocarp bundles not recessed in channels of endocarp; endocarp 2–4-celled, apical depression absent, surface curved. Embryo straight, with radicle longer than cotyledons. $n = ca. 45$.

Two species, eastern Asia (Nooteboom, 1975, 2005).

C. henschelii Moritzi (fl: *Maxwell 91-530*; fr: *Maxwell 93-39*), *C. pendula* (Wight) Alston (fl: *Norton 1574*; fr: *Beaman 10358*).

2. *Symplocos* Jacq., Enum. Pl. Carib.: 24. 1760 – Type: *Symplocos martinicensis* Jacq.

Evergreen or deciduous. Mature current-year branchlets green or brown. Leaf midvein sulcate, flat, or prominent adaxially. Hermaphroditic or dioecious. Inflorescences axillary or pseudoterminal, or irregularly concaulescent; bracteoles subtending flowers caducous or persistent; pedicel articulated. Hypanthium broadly funnellform. Petals connate at base only or distinctly beyond base; corolla adnate to androecium at base only or distinctly beyond base, white to yellow or pink to lavender, lobes chartaceous to subcoriaceous (adaxially smooth when dry). Stamens monadelphous or non-monadelphous, exerted from or included within corolla; filaments terete or tangentially flattened, apically constricted or not, glabrous or pubescent; pollen variously psilate, foveolate, rugulate, fossulate, granulate, verrucate, gemmate, echinate, or microreticulate, colpus half-length/diameter (polar view) ca. 0.02–0.25, wall between colpi (polar view) straight to distinctly convex, ca. 18–50 microns in diameter (equatorial axis). Gynoecium 2–5-carpellate; ovary completely inferior; nectary disk glabrous or pubescent; subterminal oil-secreting areas on style present or absent. Fruit with mesocarp bundles recessed in narrow channels of endocarp or not; endocarp 1–5-celled, apical depression present, surface curved, grooved, or ribbed. Embryo straight or curved, with radicle longer or shorter than cotyledons. $n = 11, 12, 14$.

318 species, Americas, eastern Asia, Australasia.

KEY TO INFRAGENERIC TAXA IN SYMPLICOS ABOVE THE SPECIES LEVEL

1. Deciduous; inflorescences irregularly concaulescent; gynoecium 2-carpellate 2.1. *S.* subg. **Palura**
1. Evergreen or rarely (*S. tinctoria*) semi-deciduous; inflorescences axillary or terminal; gynoecium 3–5-carpellate (2–3-carpellate in *S. theifolia*) 2 (2.2. *S.* subg. **Symplocos**)
2. Stamens non-monadelphous; filaments terete; pollen fossulate, granulate, verrucate, gemmate, echinate,

or microreticulate, generally ≤ 30 microns in diameter (equatorial axis); fruit with mesocarp bundles not recessed in channels of endocarp 3

3. Endocarp 1-celled (1–2-celled in *S. wikstroemiifolia*, 1–3-celled in *S. longipes*); leaf midvein flat or prominent adaxially (sulcate in *S. longipes*); nectary disk glabrous (pubescent in *S. kleinii* and *S. phaeocladus*) 2.2.1. *S.* sect. **Barberina**
3. Endocarp (1- to) 3-celled, if 1-celled then leaf midvein sulcate adaxially or nectary disk pubescent (sometimes glabrous in *S. lancifolia*) 2.2.2. *S.* sect. **Lodhra**
2. Stamens monadelphous; filaments tangentially flattened; pollen psilate, foveolate, or rugulate, generally > 30 microns in diameter (equatorial axis); fruit with mesocarp bundles recessed in narrow channels of endocarp or rarely not (*S. coccinea*, *S. hartwegii*, *S. matudae*) 4 (2.2.3. *S.* sect. **Symplocos**)
4. Corolla adnate to androecium at base only; stamens included within corolla; endocarp (1- to) 2-celled (1–3-celled in *S. domingensis*) 2.2.3.1. *S.* ser. **Urbaniocharis**
4. Corolla adnate to androecium distinctly beyond base (at base only in *Neosymplocos*); stamens exerted from corolla; endocarp 3–5-celled (2–4-celled in *Neosymplocos*) 2.2.3.2. *S.* ser. **Symplocos**

2.1. *Symplocos* subgenus **Palura** (G. Don) P.W. Fritsch, **stat. nov.** Basionym: *Symplocos* section *Palura* G. Don, Gen. Hist. 4: 3. 1837 \equiv *Symplocos* subsection *Palura* (G. Don) Benth. & Hook. f., Gen. Pl. 2: 668. 1876 \equiv *Palura* (G. Don) Miers in J. Linn. Soc. Bot. 17: 297. 1879 – Lectotype (designated by Nooteboom, 1975: 34): *Symplocos crataegoides* Buch.-Ham. ex D. Don. (= *Symplocos paniculata* (Thunb.) Miq.).

Deciduous. Mature current-year branchlets brown. Leaf midvein sulcate adaxially. Hermaphroditic. Inflorescences irregularly concaulescent; bracteoles subtending flowers caducous. Petals connate at base only; corolla adnate to androecium at base only, white to yellow. Stamens non-monadelphous, exerted from corolla; filaments terete, apically not constricted, glabrous; pollen microreticulate, colpus half-length/diameter (polar view) ca. 0.12, wall between colpi (polar view) concave to straight, ca. 26–28 microns in diameter (equatorial axis). Gynoecium 2-carpellate; nectary disk glabrous or pubescent; subterminal oil-secreting areas on style absent. Fruit with mesocarp bundles not recessed in channels of endocarp; endocarp 1-celled, surface curved. Embryo curved, with radicle longer than cotyledons. $n = 11$.

One species, eastern Asia (Nooteboom, 1975, 2005; Wu & Nooteboom, 1996).

Symplocos paniculata (Thunb.) Miq. [fl: *Peng 10853*; fr: *Chand 3736* (L)].

2.2. *Symplocos* subg. *Symplocos* (“*Symplocos* subgenus *Eusymplocos* Brand” in Engler, Pflanzennr. 6 (IV, 242): 26, 73. 1901, not validly published – Art. 22.2 & 21.3) (informal name: “*S.* subg. **Bobua**”).

Evergreen or rarely (*S. tinctoria*) semi-deciduous. Mature current-year branchlets green or brown. Leaf midvein sulcate, flat, or prominent adaxially. Hermaphroditic or dioecious. Inflorescences axillary or terminal; bracteoles subtending flowers caducous or persistent. Petals connate at base only or distinctly beyond base; corolla adnate to androecium at base only or distinctly beyond base, white to yellow, or pink to lavender. Stamens monadelphous or non-monadelphous, exerted from or included within corolla; filaments terete or tangentially flattened, apically constricted or not, glabrous or pubescent; pollen variously psilate, foveolate, rugulate, fossulate, granulate, verrucate, gemmate, echinate, or microreticulate, colpus half-length/diameter (polar view) ca. 0.02–0.25, wall between colpi (polar view) straight to distinctly convex, ca. 18–50 microns in diameter (equatorial axis). Gynoecium 3–5-carpellate (2–3-carpellate in *S. theifolia*); nectary disk glabrous or pubescent; subterminal oil-secreting areas on style present or absent. Fruit with mesocarp bundles recessed in narrow channels of endocarp or not; endocarp 1–5-celled, surface curved, grooved, or ribbed. Embryo straight or curved, with radicle longer or shorter than cotyledons. $n = 11, 12, \text{ or } 14$.

317 species, range of the genus.

2.2.1. *Symplocos* (subgenus *Symplocos*) section **Barberina** A. DC., Prodr. 8: 253. 1844. Basionym: *Barberina* Vell., Fl. Flumin.: 235. 1825 and Icon. 5: t. 117. 1835 \equiv *Symplocos* subsection *Barberina* (Vell.) Benth. & Hook. f., Gen. Pl. 2: 668. 1876 – Lectotype (designated by Nootboom, 1975: 33): *Barberina hirsuta* Vell. (? = *Symplocos phaeoclados* (Mart.) A. DC.).

= *Epigenia* Vell., Fl. Flumin.: 183. 1825 and Icon. 4: t. 137–138. 1835, excl. *Epigenia integerrima* Vell. (= *Styrax glabratus* Schott) \equiv *Symplocos* subgenus *Epigenia* Brand in Engler, Pflanzennr. 6 (IV, 242): 25, 26. 1901 – Lectotype (designated here): *Epigenia crenata* Vell. (\equiv *Symplocos crenata* (Vell.) Mattos).

= *Hopea* L., Mant. pl.: 105. 1767 and Syst. Nat. ed. 12. 1767, nom. rej., non Roxb. (1811). *Symplocos* section *Hopea* Benth. & Hook. f., Gen. Pl. 2: 668. 1876 \equiv *Protohopea* Miers in J. Linn. Soc., Bot. 17: 289. 1879 \equiv *Symplocos* subgenus *Hopea* (Benth. & Hook. f.) C.B. Clarke in Hook. f., Fl. Br. India 3: 572. 1882 – Lectotype (designated by Nootboom, 1975: 34): *Hopea tinctoria* L. (\equiv *Symplocos tinctoria* (L.) L'Hér.).

= *Symplocos* section *Pseudosymplocos* Brand in Engler, Pflanzennr. 6 (IV, 242): 25, 30. 1901 – Lectotype (designated here): *Symplocos salicifolia* Griseb.

Evergreen or rarely (*S. tinctoria*) semi-deciduous. Mature current-year branchlets usually green, or rarely brown (*S. culminicola*, *S. ovalis*, *S. salicifolia*, *S. tinctoria*, *S. wikstroemiifolia*). Leaf midvein flat or prominent adaxially, or rarely sulcate (*S. culminicola*). Hermaphroditic or dioecious. Bracteoles subtending flowers caducous. Petals connate at base only; corolla adnate to androecium at base only, white to yellow. Stamens non-monadelphous, exerted from corolla; filaments terete, apically not constricted, glabrous; pollen fossulate, granulate, verrucate, gemmate, or rarely microreticulate (*S. saxatilis*), colpus half-length/diameter (polar view) ca. 0.03–0.15 (ca. 0.25 in *S. guadeloupensis*), wall between colpi (polar view) straight to distinctly convex, ca. 18–29 microns in diameter (equatorial axis) (ca. 46–50 microns in *S. longipes*, ca. 31 microns in *S. salicifolia*). Gynoecium 3-carpellate; nectary disk usually glabrous, rarely pubescent (*S. kleinii*, *S. phaeoclados*); subterminal oil-secreting areas on style absent. Fruit with mesocarp bundles not recessed in channels of endocarp; endocarp usually 1-celled, rarely also 2- (*S. wikstroemiifolia*) or 2–3-celled (*S. longipes*), surface curved. Embryo straight or rarely curved (*S. wikstroemiifolia*), with radicle longer than cotyledons or rarely (*S. guadeloupensis*, *S. ovalis*, *S. salicifolia*) shorter than cotyledons. $n = 14$ (only *S. tinctoria* sampled).

Twenty-five species, eastern Asia (*S. wikstroemiifolia*), Americas (Small, 1933; Aristeguieta, 1957; Nootboom, 1975, 2005; Ståhl 1991, 1993, 1994, 1996; Bidá, 1995; Wu & Nootboom, 1996; Boggan & al., 1997; Steyermark & Berry, 2005; Aranha Filho & al., 2007a; Fritsch & Almeda, unpub. data [Antilles]).

Symplocos bogotensis Brand [fl: Homeier 130; fr: Palacios & Tirado 13074 (MO)], *S. celastrinea* Mart. ex Miq. [fl: Anderson 11162 (DS); fr: Harvey s.n. (DS)], *S. crenata* (Vell.) Mattos (fl: Ratter 3160; fr: Ratter & al. 3331), *S. culminicola* Standl. & Steyermark., *S. debilis* B. Ståhl, *S. denticulata* B. Ståhl, *S. glaberrima* Gontsch., *S. guadeloupensis* Krug & Urb. [fl: Duss 2989 (NY); fr: Howard 18303 (A)], *S. itatiaiae* Wawra [fl: Reitz & Klein 9858 (G)], *S. lanceolata* A. DC. [fl: Anderson 8487 (DS); fr: Dusén 10389 (L)], *S. longipes* Lundell (fl: Breedlove 50675; fr: Breedlove & Almeda 65152), *S. mosenii* Brand, *S. neglecta* Brand, *S. ovalis* C. Wright ex Griseb., *S. pentandra* (Mattos) Occhioni (fl: Hatschbach 30703), *S. phaeoclados* (Mart.) A. DC. (fl: Neto 1339; fr: Neto 1338), *S. pycnophylla* Sleumer, *S. rhamnifolia* A. DC., *S. salicifolia* Griseb., *S. saxatilis* Aranha, P.W. Fritsch & Almeda (fl: Almeda 8936), *S. spruceana* Gürke, *S. tetrandra* Mart. ex Miq., *S. tinctoria* (L.) L'Hér. (fl: Lundell & Lundell 10877; fr: Boufford & Shi 30208), *S. variabilis* Mart. ex Miq. [fl: Glaziou 15204 (G); fr: Mexia 5135], *S. wikstroemiifolia* Hayata (fr: Longxishan Expedition 2510).

Symplocos kleinii A. Bidá, ined. (fl: Kummrow 2298) has not been validly published but is included in the

analyses because it appears to be a good species and has been sampled for molecular characters. It clearly belongs in section *Barberina*.

2.2.2. *Symplocos* (subgenus *Symplocos*) section *Lodhra*

- G. Don, Gen. Hist. 4: 2. 1837 = *Lodhra* Guill. in Ann. Sci. Nat., Bot. 15: 158. 1841 = *Symplocos* subsection *Lodhra* (G. Don) Benth. & Hook. f., Gen. Pl. 2: 668. 1876 – Lectotype (designated by Nootboom, 1975: 34): *Symplocos racemosa* Roxb.
- = *Bobua* Adans., Fam. Pl. 2: 88, 526. 1763; DC., Prodr. 3: 23. 1828 ('*Bobu*') = *Symplocos* section *Bobua* (Adans.) Brand in Engler, Pflanzenr. 6 (IV, 242): 25, 32. 1901 – Lectotype (designated by Nootboom, 1975: 33): *Bobua laurina* (Retz.) DC. (= *Symplocos cochinchinensis* (Lour.) S. Moore).
- = *Decadia* Lour., Fl. Cochinch. 1: 315. 1790 – Lectotype (designated by Nootboom, 1975: 33): *Decadia aluminosa* Lour. (= *Symplocos cochinchinensis* (Lour.) S. Moore).
- = *Dicalix* Lour., Fl. Cochinch. 1: 663. 1790 – Lectotype (designated by Nootboom, 1975: 33): *Dicalix cochinchinensis* Lour. (= *Symplocos cochinchinensis* (Lour.) S. Moore).
- = *Drupastris* Lour., Fl. Cochinch. 1: 314. 1790 – Lectotype (designated by Nootboom, 1975: 33): *Drupastris cochinchinensis* Lour. (= *Symplocos cochinchinensis* (Lour.) S. Moore).
- = *Sariava* Reinw., Syll. Pl. Nov. 2: 12. 1825 – Type: not designated.
- = *Carlea* C. Presl, Epimel. Bot.: 216. 1851 – Lectotype (designated by Nootboom, 1975: 34): *Carlea oblongifolia* C. Presl (= *Symplocos polyandra* (Blanco) Brand).
- = *Baranda* Llanos in Mem. Real Acad. Ci. Madrid 2: 502. 1857 – Lectotype (designated by Nootboom, 1975: 34): *Baranda angatensis* Llanos (= *Symplocos polyandra* (Blanco) Brand).
- = *Chasseloupia* Vieill. in Bull. Soc. Linn. Normandie 10: 101. 1866 – Lectotype (designated by Nootboom, 1980: 411): *Chasseloupia lucida* Vieill. (= *Symplocos flavescens* Brand).
- = *Suringaria* Pierre in Bull. Mens. Soc. Linn. Paris 1: 635. 1886 – Lectotype (designated by Nootboom, 1975: 34): *Suringaria cambodiana* Pierre (= *Symplocos cambodiana* (Pierre) Hallier f.).
- = *Symplocos* section *Palaeosymplocos* Brand in Engler, Pflanzenr. 6 (IV, 242): 25, 30. 1901 – Lectotype (designated by Nagamasu, 1993: 188): *Symplocos phyllocalyx* C.B. Clarke (= *Symplocos theifolia* D. Don).
- = *Symplocos* subgenus *Eosymplocos* Hand.-Mazz. in Beih. Bot. Centralbl., Abt. 2, 62: 4. 1943 – Lectotype (designated by Nootboom, 1975: 34): *Symplocos racemosa* Roxb.

- = *Symplocos* section *Glomeratae* Y.-F. Wu in Acta Phytotax. Sin. 24: 193. 1986 – Type: *Symplocos glomerata* King & Gamble.
- = *Symplocos* section *Singuliflorae* Y.-F. Wu in Acta Phytotax. Sin. 24: 193. 1986 – Type: *Symplocos ovalobata* Noot.
- = *Symplocos* section *Glaucæ* Nagam. in Contrib. Biol. Lab. Kyoto Univ. 28: 191. 1993 – Type: *Symplocos glauca* (Thunb.) Koidz.
- = *Symplocos* section *Lancifoliae* Nagam. in Contrib. Biol. Lab. Kyoto Univ. 28: 190. 1993 – Type: *Symplocos lancifolia* Siebold & Zucc.
- = *Symplocos* section *Okinawenses* Nagam. in Contrib. Biol. Lab. Kyoto Univ. 28: 192. 1993 – Type: *Symplocos okinawensis* Matsum. (= *Symplocos anomala* Brand).

Evergreen. Mature current-year branchlets green or brown. Leaf midvein usually sulcate adaxially, rarely flat or prominent. Hermaphroditic or rarely dioecious. Bracteoles subtending flowers caducous or persistent. Petals connate at base only; corolla adnate to androecium at base only, white to yellow. Stamens non-monadelphous, exerted from corolla; filaments terete, apically not constricted, glabrous; pollen fossulate, granulate, verrucate, gemmate, or echinate, colpus half-length/diameter (polar view) ca. 0.02–0.15, wall between colpi (polar view) straight to slightly convex or rarely distinctly convex, ca. 22–29 microns in diameter (equatorial axis) (ca. 34 microns in *S. dryophila*, ca. 32 microns in *S. stellaris*). Gynoecium 3-carpellate or rarely 2–3-carpellate (*S. theifolia*); nectary disk glabrous or pubescent; subterminal oil-secreting areas on style absent. Fruit with mesocarp bundles not recessed in channels of endocarp; endocarp usually 3-celled, often 1-celled or rarely 1–3-celled (e.g., *S. arborea*), surface curved, grooved, or ribbed. Embryo straight or curved, with radicle longer than cotyledons. $n = 11, 12$.

142 species, eastern Asia, Australasia (Nootboom, 1975, 2005; Wu & Nootboom, 1996; Zhou & al., 2006).

Symplocos adenophylla Wall. ex G. Don [fl: *Clemens* 4222; fr: *Chew* 938 (L)], *S. adenopus* Hance [fl: *Luo* 350; fr: *Teng* 90453 (L)], *S. ambangensis* Noot., *S. anamallayana* Bedd., *S. annamensis* Noot., *S. anomala* Brand [fl: *Boufford & Bartholomew* 24239; fr: *Gibot* 56690 (L)], *S. arborea* Brongn. & Gris [fr: *MacKee* 17752 (L)], *S. atjehensis* Noot., *S. atriolivacea* Merr. & Chun ex H.L. Li, *S. austrosinensis* Hand.-Mazz. (st: *Wang* S208), *S. banaensis* Guillaumin, *S. barisanica* Noot., *S. barringtoniifolia* Brand, *S. batakenensis* Noot., *S. borneensis* Brand, *S. brachybotrys* Merr., *S. bractealis* Thwaites, *S. brandisii* Koord. & Valetton, *S. buxifolia* Stapf, *S. caerulea* (Vieill.) Brongn. & Gris (fr: *Lowry & al.* 5634), *S. calycodactylos* Brand, *S. cambodiana* (Pierre) Hallier f., *S. celastrifolia* Griff. ex. C.B. Clarke [fl: *Beaman* 9433; fr:

Kostermans 9292 (L)], *S. cerasifolia* Wall. ex A. DC., *S. chaoanensis* F.G. Wang & H.G. Yeh, *S. cochinchinensis* (Lour.) S. Moore subsp. *cochinchinensis* (fl: *Toroës* 2678; fr: *Gressitt* 883), *S. c.* subsp. *laurina* (Retz.) Noot. [fl: *Luo* 295; fr: *Maxwell* 86-1040 (L)], *S. colombonensis* Noot., *S. columbuli* Noot., *S. complanata* Brand, *S. composiracemosa* Noot., *S. congesta* Benth. (fl: *Tang* 1410; fr: *Tsang* 25035), *S. cordifolia* Thwaites, *S. coronata* Thwaites, *S. costata* (Blume) Choisy, *S. costatifructa* Noot., *S. crassilimba* Merr., *S. crassipes* C.B. Clarke, *S. crassiramifera* Noot., *S. cuneata* Thwaites, *S. cyanocarpa* C.T. White, *S. cylindracea* Noot., *S. deflexa* Stapf, *S. disepala* Guillaumin, *S. diversifolia* Brand, *S. dolichotricha* Merr., *S. doormannensis* Brand, *S. dryophila* C.B. Clarke (fl: *Grierson & Long* 4608; fr: *Bartholomew & al.* 916), *S. elegans* Thwaites, *S. euryoides* Hand.-Mazz. (st: *Wang* S13), *S. fasciculata* Zoll., *S. flavescens* Brand, *S. foliosa* Wight, *S. fordii* Hance, *S. fukienensis* Ling, *S. gambliana* Brand, *S. gigantifolia* Noot., *S. glabriramifera* Noot., *S. glandulifera* Brand (fl, fr: *Wang* S217), *S. glauca* (Thunb.) Koidz. [fl: *Leu* 1062; fr: *Taoda* 3509 (L)], *S. glomerata* King ex C.B. Clarke fl: *Bartholomew* 1648; fr: *Griffith* 3654), *S. goodeniacea* Noot., *S. gracilis* Brongn. & Gris, *S. graniticola* Jessup, *S. groffii* Merr. (fl: *Merrill* 10257), *S. guillauminii* Merr., *S. hainanensis* Merr. & Chun ex H.L. Li, *S. harroldii* Jessup, *S. hayesii* C.T. White & W.D. Francis, *S. heishanensis* Hayata, *S. herzogii* Sleumer, *S. hookeri* C.B. Clarke (fl: *Maxwell* 87-1071; fr: *Shui* S225), *S. hottae* Nagam., *S. huegeliana* Brand, *S. hylandii* Noot., *S. iliaspaiensis* Noot., *S. johniana* Stapf, *S. junghuhnii* Koord., *S. kemiriensis* Nagam., *S. kothayarensis* Sundaresan, Jothi, S. Rajkumar & Manickam, *S. kurgensis* C.B. Clarke, *S. laeteviridis* Stapf [fr: *Baeka* 6010 (L)], *S. lancifolia* Siebold & Zucc. [fl: *Teng* 90071; fr: *Elmer* 7487 (L)], *S. leochaii* P.P.K. Chai, *S. longifolia* Fletcher, *S. macrocarpa* Wight ex C.B. Clarke, *S. macrophylla* Wall. ex A. DC. [fr: *Richdale* 467 (L)], *S. maliliensis* Noot., *S. megalocarpa* Fletcher, *S. menglianensis* Y.Y. Qian, *S. monantha* Wight, *S. montana* (Vieill.) Brongn. & Gris, *S. multibracteata* Noot., *S. nairii* A.N. Henry, Gopalan & M.S. Swaminathan, *S. neocaledonica* (Vieill.) Noot., *S. nivea* Brand, *S. nokoensis* (Hayata) Kaneh. [fl: *Panero* 6527; fr: *Sheng* 13334 (L)], *S. obovatifolia* Merr., *S. obtusa* Wall. ex G. Don, *S. odoratissima* (Blume) Choisy ex Zoll., *S. oligandra* Bedd., *S. olivacea* Merr., *S. ophirensis* C.B. Clarke, *S. ovatilobata* Noot. (fr: *Wang* S17), *S. oxyphylla* Wall. ex A. DC., *S. paucinervia* Noot., *S. paucistaminea* F. Muell. & F.M. Bailey, *S. pedunculata* Noot., *S. pilosa* Rehder, *S. poilanei* Guillaumin [fl: *Lau* 4939; fr: *Tsang* 29913 (L)], *S. polyandra* (Blanco) Brand, *S. pseudobarberina* Gontsch. [fl: *Ning & al.* S233; fr: *Pierre* 5044 (L)], *S. pulchra* Wight, *S. pulvinata* Noot., *S. pyriflora* Ridl., *S. pyrifolia* Wall. ex G. Don [fr: *Koeltz* 29646 (L)], *S. racemosa* Roxb., *S. ramosissima* Wall. ex G. Don, *S. rayae*

Noot., *S. riangensis* Noot., *S. robinsonii* Ridl., *S. rosea* Bedd., *S. rubiginosa* Wall. ex A. DC., *S. salicioides* Noot., *S. singuliflora* Guillaumin, *S. spectabilis* Brand (fr: *Wang* S408), *S. stellaris* Brand (fl: *Lin* 21; fr: *Yao* 11422), *S. sulcata* Kurz [fl: *Maxwell* 93-1327; fr: *Maxwell* 97-184 (L)], *S. sumatrana* Brand, *S. sumuntia* Buch.-Ham. ex D. Don var. *sumuntia* [fl: *Tsang* 23519; fr: *Poilane* 30926 (L)], *S. sumuntia* var. *modesta* (fl: *Wang & Lin* 2065; fr: *Kao* 502), *S. theifolia* D. Don [fl: *Bartholomew & Boufford* 3873; fr: *Amano* 5918 (L)], *S. trichomarginalis* Noot., *S. tricoccata* Noot. [fr: *Gibot* 56682 (L)], *S. trisepala* Merr., *S. uncarpa* Noot., *S. versteegii* Brand, *S. verticillifolia* Noot., *S. vidalii* Rolfe, *S. viridissima* Brand [fl: *Gaoligongshan Biodiversity Survey* 22000; fr: *Poilane* 24266 (L)], *S. whitfordii* Brand, *S. wynadense* (Kuntze) Noot., *S. xylopyrena* C.Y. Wu ex Y.F. Wu, *S. zizyphoides* Stapf.

2.2.3. *Symplocos* (subgenus *Symplocos*) section *Symplocos* ["*Symplocos* section *Symplocastrum* Brand" in Engler, *Pflanzenr.* 6 (IV, 242): 26, 73. 1901, not validly published – Art. 22.2] (informal name: "*S.* section **Ciponima**").

Evergreen. Mature current-year branchlets brown. Leaf midvein sulcate adaxially. Hermaphroditic. Bracteoles subtending flowers caducous or persistent. Petals connate at base only or distinctly beyond base; corolla adnate to androecium at base only or distinctly beyond base, white to yellow, or pink to lavender. Stamens monadelphous, exerted from or included within corolla; filaments tangentially flattened, apically constricted or not, glabrous or pubescent; pollen psilate, foveolate, or rugulate, colpus half-length/diameter (polar view) ca. 0.02–0.18, wall between colpi (polar view) slightly convex, ca. 22–47 microns in diameter (equatorial axis). Gynoecium 3–5-carpellate; nectary disk pubescent or occasionally glabrous; subterminal oil-secreting areas on style present or absent. Fruit with mesocarp bundles recessed in narrow channels of endocarp or rarely not (*S. coccinea*, *S. hartwegii*, *S. matudae*); endocarp 1–5-celled, surface curved or irregularly grooved, or rarely regularly grooved to ribbed (*S. povedae*, *S. striata*). Embryo straight, with radicle longer than cotyledons. $n = 12$ (only *S. micrantha* sampled).

150 species, tropical America.

2.2.3.1. *Symplocos* (subgenus *Symplocos*) section *Symplocos* series **Urbaniocharis** (Brand) P.W. Fritsch, **stat. nov.** Basionym: *Symplocos* section *Urbaniocharis* Brand in Engler, *Pflanzenr.* 6 (IV, 242): 25, 70. 1901 – Lectotype (designated here): *Symplocos lanata* Krug & Urb.

= *Symplocos* subgenus *Microsymplocos* Brand in Engler, *Pflanzenr.* 6 (IV, 242): 25, 70. 1901 – Lectotype (designated here): *Symplocos micrantha* Krug & Urb.

Bracteoles subtending flowers caducous. Petals connate at base only; corolla adnate to androecium at base only, white (rarely tinged with pink). Stamens included within corolla; filaments apically not constricted, glabrous; pollen ca. 25–28 microns in diameter (equatorial axis). Gynoecium 3-carpellate; nectary disk pubescent; subterminal oil-secreting areas on style absent. Fruit with mesocarp bundles recessed in narrow channels of endocarp; endocarp (1–)2-celled (1–3-celled in *S. domingensis*), surface curved or irregularly grooved. $n = 12$ (only *S. micrantha* sampled).

Seven species, Greater Antilles (Mai, 2005; Fritsch & Almeda, unpub. data).

S. ciponimoides Griseb., *S. domingensis* Urb. [fl: *Ekman 5906* (S); fr: *Clase & Peguero 608*], *S. hotteana* Urb. & Ekman, *S. lanata* Krug & Urb. [fl: *Axelrod & Fritsch 12546*; fr: *Alain 9467* (NY)], *S. leonis* Britton & P. Wilson, *S. micrantha* Krug & Urb. (fl: *Axelrod & al. 12554*; fr: *Axelrod & Fritsch 12512*), *S. moaensis* Borhidi.

2.2.3.2. *Symplocos* (subgenus *Symplocos* section *Symplocos*) series *Symplocos* (informal name: “*S. series Symplocastrum*”).

- = *Ciponima* Aubl., Hist. Pl. Guiane.: 567, t. 226. 1775 (“*Siponima*”) [“*Symplocos* section *Ciponima* (Aubl.) A. DC.”, Prodr. 8: 249. 1844; “*Symplocos* subgenus *Ciponima* (Aubl.) C.B. Clarke” in Hook. f., Fl. Br. India 3: 587. 1882, not validly published – Art. 22.2] – Lectotype (designated by Nootboom, 1975: 33): *Ciponima guianensis* Aubl. (= *Symplocos guianensis* (Aubl.) Gürke).
- = *Alstonia* Mutis ex L. f., Suppl. Pl.: 39. 1781, non Scop. (1777), nom. rej., nec R. Br. (1810), nom. cons. [“*Symplocos* section *Alstonia* (Mutis ex L. f.) G. Don”, Gen. Hist. 4: 1. 1837, not validly published – Art. 22.2] = *Praealstonia* Miers in J. Linn. Soc., Bot. 17: 291. 1879 – Lectotype (designated by Nootboom, 1975: 33): *Alstonia theiformis* L. f. (= *Symplocos theiformis* (L. f.) Gürke).
- = *Mongezia* Vell., Fl. Flumin.: 229. 1825 and Icon. 5: t. 105–106. 1835 – Lectotype (designated here): *Mongezia pilosa* Vell. (= *Symplocos pubescens* Klotzsch ex Benth.).
- = *Stemmatosiphum* Pohl, Pl. Bras. Icon. Descr. 2: 86, t. 157–159. 1831 – Lectotype (designated here): *Stemmatosiphum platyphylla* Pohl (= *Symplocos platyphyllum* (Pohl) Benth.).
- = *Hypopogon* Turcz. in Bull. Soc. Imp. Naturalistes Moscou 31: 246. 1858 – Lectotype (designated by Nagamasu, 1993: 188): *Hypopogon brevipes* Turcz. (= *Symplocos coccinea* Humb. & Bonpl.).
- = *Symplocos* section *Neosymplocos* Brand in Engler, Pflanzenr. 6: 25, 70. 1901 – Lectotype (designated here): *Symplocos tenuifolia* Brand.
- = *Symplocos* subsection *Pseudoalstonia* Brand in Engler,

Pflanzenr. 6 (IV, 242): 26, 73. 1901 – Lectotype (designated here): *Symplocos mapirensis* Brand.

[“*Symplocos* subsection *Ciponimastrum* Brand” in Engler, Pflanzenr. 6 (IV, 242): 26, 78. 1901, not validly published – Art. 22.2].

Bracteoles subtending flowers caducous or persistent. Petals adnate to androecium distinctly beyond base, or rarely at base only (*Neosymplocos*); corolla adnate to androecium distinctly beyond base, or rarely at base only (*Neosymplocos*), white, pink, red, or lavender. Stamens (at least outer) exerted from corolla; filaments apically constricted, or not constricted (*Neosymplocos*), glabrous, or pubescent (*Neosymplocos*); pollen ca. usually ca. 31–47 microns or occasionally ca. 22–29 microns in diameter (equatorial axis). Gynoecium 3–5-carpellate; nectary disk glabrous or pubescent; subterminal oil-secreting areas on style present, or absent (*Neosymplocos*). Fruit with mesocarp bundles recessed in narrow channels of endocarp or rarely not (*S. coccinea*, *S. hartwegii*, *S. matudae*); endocarp 3–5-celled (2–4-celled in *Neosymplocos*), surface curved or irregularly grooved, or rarely regularly grooved to ribbed (*S. povedae*, *S. striata*).

143 species, tropical America (Aristeguieta, 1957; Ståhl, 1991, 1993, 1994, 1995, 1996; Bidá, 1995; Boggan & al., 1997; Kriebel & Zamora, 2004; Kriebel & al., 2004; Steyermark & Berry, 2005; Kelly & Almeda, in press and Web site at <http://www.mobot.org/mobot/fm/>; Almeda, Kelly, & Fritsch, unpubl. data [Mexico]; Fritsch & Almeda, unpubl. data [Antilles]).

Symplocos abietorum Standl. & Steyer., *S. acanensis* Steyer., *S. amplifolia* Brand, *S. andicola* B. Ståhl, *S. apiciflora* B. Ståhl, *S. arechea* L’Hér., *S. austin-smithii* Standl. (fl: *Davidse 24505*; fr: *Haber 761*), *S. austromexicana* Almeda (fl, fr: *Kelly & al. 1304*), *S. badia* B. Ståhl, *S. baehni* J.F. Macbr., *S. berteroi* (A. DC.) Miers (fl: *Clase & al. 1064*; fr: *Clase & al. 3167*), *S. bicolor* L.O. Williams, *S. blancae* B. Ståhl, *S. bolivarana* Aristeg., *S. bombycina* B. Ståhl, *S. breedlovei* Lundell (fl: *Breedlove 11747*; fr: *Ton 875*), *S. canescens* B. Ståhl, *S. carmentitae* B. Ståhl, *S. cernua* Bonpl., *S. chimantensis* Steyer. & Maguire, *S. chloroleuca* B. Ståhl, *S. citrea* Lex. ex LaLlave & Lex. (fl: *Breedlove & Almeda 60478*; fr: *Barriga 7260*), *S. clethriifolia* B. Ståhl, *S. coccinea* Bonpl. [fl: *Kelly & al. 1369*; fr: 1841–1843, *Liebmann s.n.* (S)] *S. colorata* Brand, *S. coriacea* A. DC. (fl: *Øllgaard & Balslev 9749*; fr: *Maguire & Maguire 44446*), *S. costaricana* Hemsl. [fl: *Davidse & al. 35255*; fr: *McPherson 13647* (L)], *S. crassulacea* B. Ståhl, *S. cundinamarcensis* B. Ståhl, *S. decorticans* B. Ståhl, *S. ecuadorensis* Little, *S. elliptica* L. Kelly & Almeda, *S. excelsa* L.O. Williams, *S. fimbriata* B. Ståhl, *S. flosfragrans* M.L. Chaparro, *S. flos-pilosa* Aristeg., *S. fuliginosa* B. Ståhl, *S. fuscata* B. Ståhl [fl: *Clark 7017*; fr: *Øllgaard & Balslev 74325* (MO)], *S. globosa* B. Ståhl, *S. globulifera* B. Ståhl, *S. guianensis* (Aubl.) Gürke, *S.*

hartwegii A. DC. (fl: Kelly & al. 1339; fr: Breedlove & Almeda 15168), *S. hiemalis* Lingelsh., *S. hintonii* Lundell (fl: Hinton 14276; fr: Breedlove & Almeda 65018), *S. incahuasensis* Sagást. & M.O. Dillon, *S. jauaensis* Steyererm. & Maguire, *S. johnsonii* Standl., *S. jurgensenii* Hemsl., *S. lasseri* Steyererm., *S. latifolia* Krug & Urb., *S. laxiflora* Benth., *S. lehmannii* Brand, *S. limoncillo* Bonpl. (fl: Sousa 9341; fr: Hamilton & al. 973), *S. lutescens* Brand, *S. magdalenae* B. Ståhl, *S. mapiriensis* Brand, *S. martinicensis* Jacq. [fl: Duss 1494 (NY); fr: Barrier 4432 (S)], *S. matudae* Lundell [fl: Lundell & Contreras 18931; fr: Lundell & Contreras 21169 (LL)], *S. melanochroa* Sleumer, *S. mezii* Szyszyl., *S. morii* Almeda & L. Kelly, *S. mucronata* Bonpl., *S. nana* Brand (fl, fr: Camp E-5151A & B), *S. naniflora* L. Kelly & Almeda, *S. neblinae* Maguire & Steyererm., *S. neei* B. Ståhl, *S. nitens* (Pohl) Benth. (fl: Hatschbach 35055; fr: Romero & al. 5737), *S. nivalis* Linden ex Brand, *S. novogaliciana* L.M. González, *S. nuda* Bonpl., *S. octopetala* Sw., *S. oreophila* Almeda, *S. pachycarpa* L.M. Kelly & Almeda (fl: Breedlove 61963; fr: Kelly 1309), *S. panamensis* McPherson (fl: McPherson 8447; fr: McPherson 13647), *S. parvifolia* Benth., *S. patazensis* Mansf., *S. peruviana* (Szyszyl.) Brand, *S. phaeoneura* B. Ståhl, *S. pichindensis* Cuatrec., *S. pittieriana* Steyererm., *S. platyphylla* (Pohl) Benth., *S. pluribracteata* B. Ståhl, *S. polyphylla* B. Ståhl, *S. povedae* Almeda (fl: Bello 551; fr: Poveda 1179), *S. psiloclada* B. Ståhl, *S. pubescens* Klotzsch ex Benth., *S. pycnantha* Hemsl. (fl: Kelly & al. 1380; fr: Rico & al. 372), *S. pycnobotrya* Mart. ex Miq., *S. quindiuensis* Brand, *S. quitensis* Brand [fl: Palacios & van der Werff 3906; fr: Solomon & Nee 17917 (MO)], *S. ramuliflora* B. Ståhl, *S. reflexa* A. DC. [fl: Lewis & Lozano 86104 (MO); fr: Homeier 97], *S. retusa* Kriebel, J.A. González, & E. Alfaro, *S. rhomboidea* B. Ståhl, *S. rigidissima* Brand, *S. rimbachii* B. Ståhl, *S. rimosa* B. Ståhl, *S. robinfosteri* B. Ståhl, *S. robusta* B. Ståhl, *S. sandemanii* B. Ståhl, *S. sandiae* Brand, *S. sararensis* Cuatrec., *S. scabra* J.F. Macbr., *S. schomburgkii* Klotzsch ex Brand, *S. serculata* Bonpl. (fl: Fernández 25; fr: Utley & Utley 2514), *S. silverstonei* B. Ståhl, *S. sousae* Almeda, *S. speciosa* Hemsl. (fl: Kelly & al. 1307; fr: Breedlove & Mahoney 72302), *S. striata* Kriebel & N. Zamora (fl: Sperry 817; fr: Wilbur 63552), *S. strigillosa* Krug & Urb., *S. suaveolens* Klotzsch, *S. subandina* Ståhl, *S. subcuneata* (Herzog) Ståhl, *S. sulcinervia* B. Ståhl [fl: Madsen 85854 (MO); fr: Homeier 1239], *S. tacanensis* Lundell (fl: Matuda 2976; fr: Breedlove 65754), *S. tamana* Steyererm., *S. theiformis* (L. f.) Gürke, *S. trachycarpus* Brand, *S. trianae* Brand, *S. tribracteolata* Almeda (fl, fr: Haber 331), *S. tristis* Brand, *S. truncata* B. Ståhl, *S. ulei* Brand, *S. umbellata* Brand, *S. uniflora* (Pohl) Benth. [fl: Kummrow 705; fr: Wasum 1687 (L)], *S. urbaniana* Brand, *S. vatteri* Standl. & Steyererm., *S. venulosa* Cuatrec., *S. verrucisurcula* B. Ståhl (fl: Clark 8119), *S. yapacanensis* Steyererm.

Informal group “**Neosymplocos**” within *Symplocos* series *Symplocos*

Bracteoles subtending flowers persistent. Petals adnate to androecium at base only; corolla adnate to androecium at base only, white. Stamen filaments not constricted, pubescent; pollen ca. 22–27 microns in diameter (equatorial axis). Gynoecium 3-carpellate; nectary disk pubescent or glabrous; subterminal oil-secreting areas on style absent. Endocarp 2–4-celled.

Thirteen species, eastern South America (southeastern Brazil, Paraguay; Bidá, 1995; Aranha & al., 2007b).

Symplocos aegrota Brand, *S. altissima* Brand, *S. angulata* Brand, *S. corymbocladus* Brand, *S. densiflora* Brand, *S. falcata* Brand (fl: Glaziou 20212 (G); fr: Almda & al. 8782), *S. glanduloso-marginata* Hoehne, *S. glaziovii* Brand, *S. insolita* Aranha (fl: Almeda & al. 8910), P.W. Fritsch & Almeda, *S. microstyla* Aranha, P.W. Fritsch & Almeda (fl: Almeda & al. 8878), *S. nitidiflora* Brand, *S. organensis* Brand (fl, fr: Almeda & al. 8792), *S. tenuifolia* Brand [fl: Cervi & Hatschbach 3008; fr: Smith & Klein 11262 (L)].

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Appendix 1. List of characters and their states used in the phylogenetic and optimization analyses. Characters were assessed from personal observations except where indicated with literature sources.

- Deciduous (0); evergreen (1). All species of Symplocaceae are evergreen, with the exception of *Symplocos paniculata* and *S. tinctoria*, the latter of which is scored as polymorphic for this state because it is reported to be deciduous in the northern part of its range and evergreen in the southern portion (Elias, 1980). Otherwise, this character is variable only among outgroup taxa.
- Trichomes simple (0); trichomes stellate (1); trichomes peltate (2); trichomes absent (3).
- Mature current-year branchlets green (0); mature current-year branchlets brown (1). The state “brown” includes various shades of brown, including grayish brown and reddish brown.
- Leaf midvein sulcate adaxially (0); leaf midvein flat or prominent adaxially (1).
- Sexual expression hermaphroditic (0); sexual expression dioecious (1); sexual expression gynodioecious (2). Coding for *Ternstroemia* and *Styrax* (both polymorphic) follows Luna & Ochoterena (2004) and Fritsch (2004), respectively. Morphologically androdioecious species in *Symplocos* section *Barberina* are here considered to be functionally dioecious on the basis of studies by Aranha-Filho & al. (in press).
- Inflorescences axillary or terminal (0); inflorescences strictly terminal (1); inflorescences irregularly concaulescent (2). The inflorescences of *Symplocos paniculata* are unique among Symplocaceae in being concaulescent, i.e., each is borne above the subtending node along the stem (Nagamasu, 1993).
- Bracteoles subtending flowers caducous (0); bracteoles subtending flowers persistent (1). Bracteoles in Symplocaceae can be caducous in flower or in fruit (e.g., Nootboom, 1975), but this distinction is often not clear within species. Persistent bracteoles are defined here as those that are still present when fruits are on the plant.
- Pedicel not articulated (0); pedicel articulated (1). The articulation is located distally on the pedicel, immediately below the hypanthium or sepals.
- Hypanthium absent (0); hypanthium present (1). All species of Symplocaceae have a hypanthium that is fully adnate to the ovary wall. The genera of Styracaceae also have a hypanthium, and this may be fully or only partially adnate to the ovary wall (Fritsch, 2004).
- Hypanthium broadly funnellform (0); hypanthium narrowly funnellform (1).
- Sepal aestivation valvate (0); sepal aestivation open (1); sepal aestivation imbricate (2). This character is variable only among outgroup taxa. Styracaceae have valvate or open aestivation (Fritsch, 2004), whereas all other taxa have imbricate aestivation.
- Sepals fully connate (0); sepals distinct or at most basally connate (1). Fully connate sepals are coded only for outgroup genera of Styracaceae, in which the calyx is a campanulate or cupuliform structure beyond its attachment to the other whorls of the flower (Fritsch, 2004). Other taxa in this analysis (including all members of Symplocaceae) have sepals that are distinct or at most basally connate beyond their attachment to the hypanthium (Symplocaceae) or other whorls.
- Petals distinct or connate at base only (0); petals connate distinctly beyond base (1). Most outgroup taxa have petals that are connate at the base (*Ternstroemia* and *Camellia*: Luna & Ochoterena, 2004; *Clethra*: Sleumer, 1967; *Huodendron*, *Alniphyllum*, *Pterostyrax*: Fritsch, 1999), as do many species of Symplocaceae. Nevertheless, because several taxa have petals that have been described as distinct to \pm connate at the base (*Cyrilla*: Kubitzki, 2004; *Galax*: Rönblom & Anderberg, 2002; *Saurauia*: Keller & al., 1996), or polymorphic (*Rhododendron*: Stevens, 2004), we have combined these conditions (distinct versus connate at base only) into a single state. Some

Appendix 1. Continued.

- species of *Symplocos* have petals that are connate well beyond the base, with a tube that is ca. one-half the length of the corolla; even in these species, the margins of the petals often remain distinct toward the base of the corolla.
14. Corolla white to yellow (0); corolla pink to lavender (1). Data are largely derived from specimen labels and literature citations (e.g., Nooteboom, 1975, 1977, 1980).
 15. Corolla texture chartaceous to subcoriaceous (adaxially smooth when dry) (0); corolla texture coriaceous (adaxially papillose when dry) (1). A relatively thick, coriaceous corolla, as in *Symplocos* section *Cordyloblaste*, is evident in the dry state by the presence of conspicuous adaxial papillae.
 16. Androecium not adnate to corolla or adnate at base only (0); androecium adnate to corolla distinctly beyond base (1). The common condition among ericacean outgroup taxa is that stamens are adnate to the base of the corolla or free from the corolla (e.g., Kubitzki, 2004). Many taxa that have both of these conditions were coded as free by Anderberg (1992), and the difference can be difficult to establish. In *Symplocos* all species have adnate stamens and corolla, but there is variation in degree of adnation. Generally, stamens are either attached basally on the corolla, or they are attached near the middle of the corolla.
 17. Androecium diplostemonous (0); androecium haplostemonous (1); stamens numerous (2). Outgroup taxa in the Theaceae and Actinidiaceae and all species of *Symplocos* have numerous stamens. In *Symplocos*, the number mostly varies from 40 to 100, but sometimes there are fewer in dioecious species.
 18. Stamen fusion monadelphous (0); stamen fusion non-monadelphous (1). Differences in stamen fusion have been important in the infrageneric taxonomy of *Symplocos*. For example Brand (1901: 25–26) recognized several different states of this character, and used the differences to distinguish among the subgenera, sections, and series that he recognized. For the purposes of this analysis, we were able to recognize two discernible states of this character. Stamens that are monadelphous are clearly fused proximally, by the filaments, into a single tube. The free portions of the filaments of monadelphous stamens are oriented parallel to one another with anthers at different levels. In sections *Cordyloblaste* and *Symplocos*, the outermost filaments are generally straight and the longest, whereas the innermost are generally incurved or inflexed and the shortest. This results in irregularly stacked rings of stamens that encircle the style. The various lengths of filaments emerging at different positions from the tube create the effect of multiple series (e.g., Brand, 1901), but definite numbers of series often are not clearly distinguishable. In section *Urbaniocharis*, the filaments are monadelphous and generally form a single series that more or less rests against the inner surface of a cupuliform corolla. The filaments are generally longer in regions between the corolla lobes, and gradually become shorter toward the central regions of the lobes (e.g., Brand 1901: fig. 2E). In section *Neosymplocos*, the filaments also form a single series, and most or all are incurved.
- In contrast, the state “non-monadelphous” incorporates several different conditions, which often are not clearly distinguished and sometimes vary within species or individuals. These conditions include stamens that are clearly or indistinctly pentadelphous (connate into five discrete clusters), pentadelphous with additional stamens between the clusters, somewhat monadelphous but with a broken, discontinuous tube, or with stamens that appear individually inserted on the corolla. Generally, stamens that are non-monadelphous are divergent from each other and have a brush-like arrangement.
19. At least some stamens exerted from corolla (0); all stamens included within corolla (1).
 20. Stamen filaments terete (0); stamen filaments tangentially flattened (1). The stamen filaments of some species of *Symplocos*, Styracaceae (Fritsch, 2004), and Dipensiaceae (Rönblom & Anderberg, 2002) are thick, fleshy, and tangentially flattened (at least at the base, but often also distally toward the anther sac). In contrast, some species of *Symplocos*, and the remaining outgroup taxa, have filaments that are narrow, filamentous, and terete in cross section for their entire length.
 21. Stamen filaments apically not constricted (0); stamen filaments apically constricted (1). The species of *Symplocos* series *Symplocos* have stamen filaments that are abruptly constricted distally, so that the anthers are borne on a narrow stipe. From our observations a slight constriction seems sometimes apparent in some individuals of *S.* sections *Neosymplocos* and *Urbaniocharis*, but the small size of the flowers of the species in these sections makes it difficult to discern this character clearly. We have consequently followed Brand (1901) in scoring the filaments of *S.* sections *Neosymplocos* and *Urbaniocharis* as unconstricted.
 22. Stamen filaments glabrous (0); stamen filaments pubescent (1). Some species of *Symplocos* have filaments that are densely pubescent with short, soft, unicellular trichomes. These trichomes are normally different from those that are present on other flower parts of the same species.
 23. Anthers basifixed (0); anthers dorsifixed (1).
 24. Anthers erect at anthesis (0); anthers inverted at anthesis (1). Some Ericacean outgroup taxa have anthers that are inverted during ontogeny, with pollen released through a morphologically basal pore that becomes apical after inversion. Coding for outgroup taxa follows Anderberg (1992).
 25. Anthers introrsely dehiscent (0); anthers latrorsely dehiscent (1); anthers porosely dehiscent (2).
 26. Anther thecae bacilliform or ellipsoid (0); anther thecae spheroid (1). Bacilliform or ellipsoid anthers, as in most of the outgroup taxa, are more than two times as long as wide. Spheroid anther thecae, as in *Symplocos*, have approximately the same length and width.
- (27–31). Most data for *Symplocos* across the following five pollen characters are based on an unpublished scanning electron microscopy study by J.L.M. Aranha Filho, P.W. Fritsch, and A. Bruehl (in prep.), with additional data from van der Meijden (1970), Barth (1979, 1982), Mai (1986), and Nagamasu (1989a, b). Data for outgroups were derived from Keng (1962), Dickison & al. (1982), Xi & Tang (1990), Morton & Dickison (1992), Zhang & Anderberg (2002), Wei (2003), Scott (2004), and Weitzman & al. (2004).
27. Pollen psilate, foveolate, or rugulate (0); pollen fossulate, granulate, verrucate, gemmate, or echinate (1); pollen microreticulate (2); pollen perforate (3). There are four distinct classes of wall surface features among species of *Symplocos*: those with a relatively smooth tectum (0), found in, e.g., section *Symplocos*; those with a relatively coarsely sculptured tectum (1), found in, e.g., the Asian *Hopea* species *S. tinctoria*; those with netted sculpturing with relatively large, irregularly shaped pores (2), found in *S. lancifolia*, *S. paniculata*, and

Appendix 1. Continued.

- S. saxatilis*; and those with a distinctly perforate tectum (3) characteristic of section *Cordyloblaste*.
28. Pollen colpus half-length/diameter (polar view) ≤ 0.18 (0); pollen colpus half-length/diameter > 0.18 (1). In polar view, the colpi of the pollen grains of most of the outgroup taxa, the species of *Symplocos* section *Cordyloblaste*, and *S. guadeloupensis* extend toward the pole farther than those of the other species of *Symplocos* sampled.
 29. Pollen wall between colpi (polar view) straight to concave (0); pollen wall between colpi slightly convex (1); pollen wall between colpi distinctly convex (2).
 30. Pollen diameter (equatorial axis) generally ≤ 30 microns (0); pollen diameter generally > 30 microns (1). A notable difference in the size of pollen grains occurs among the species of *Symplocos*. The species of section *Symplocos* have pollen grains that are generally larger than those of other species of *Symplocos*, with several exceptions (*S. dryophila* and *S. stellaris* of the main *Hopea* clade, *S. longipes*, and the species of section *Cordyloblaste*).
 31. Pollen oblate to spheroidal (0); pollen prolate-spheroidal to prolate (1). Species of *Symplocos* have pollen that is either oblate, or at most spheroidal, in shape and thus differ from those with prolate pollen (e.g., many outgroup taxa).
 32. Gynoecium 1-carpellate (0); gynoecium 2-carpellate (1); gynoecium 3-carpellate (2); gynoecium 4-carpellate (3); gynoecium 5-carpellate (4). Most species of Symplocaceae have tricarpellate gynoecia; only *Symplocos paniculata* is exclusively bicarpellate, and many species are polymorphic (most commonly with 3-, 4-, or 5-carpellate gynoecia).
 33. Ovary completely inferior (0); ovary partly inferior (1); ovary superior (2). Partially inferior ovaries, found in Styracaceae (Fritsch, 2004) and in *Symplocos* section *Cordyloblaste* (Nootboom, 1975; Nagamasu, 1993), are adnate to the outer whorls for ca. one-half of their length proximally, and generally maintain this degree of adnation in fruit. Completely inferior ovaries in *Symplocos* may be distally free at anthesis ($<$ one-half of their length), but are fully adnate in fruit (with free portions of sepals persistent at the apex of the fruit).
 34. Ovary completely septate (0); ovary incompletely septate (1). Incomplete septa are found in Styracaceae (e.g., Fritsch, 2004) and Symplocaceae. Ovaries that are incompletely septate have septa that are united along a central axis until the septa begin to diverge distally. The result is an ovary that is partially compartmentalized proximally and continuous distally with the ridged and angled styler canal.
 35. Nectary disk absent (0); nectary disk present (1). All species of Symplocaceae have a nectary disk on top of the inferior ovary. The nectary tissue is highly vascularized, densely cytoplasmic, and provided with an abundance of stomata. The disk surrounds the free apical portion of the ovary at anthesis, and is often evident in fruit as a light-colored proliferation that may or may not project beyond the persistent sepals. At anthesis, the nectary disk varies from flat to pulviniform or coroniform, and may be angled or lobed. The different shapes were not coded as separate states because of continuous variation, and because of variation within species. There is some question as to whether nectar secretion from the lower part of the ovary in *Clethra* constitutes tissue homologous with a nectary disk (Brown, 1938); we have coded the nectary disk absent in *Clethra* because this tissue lacks the structural features of the disk. Other outgroup taxa mostly lack nectaries, with the exception of *Cyrilla* and Ericaceae (e.g., Gilg, 1892; Palser, 1961).
 36. Nectary disk glabrous (0); nectary disk pubescent (1). The nectary disk in many species of Symplocaceae is pubescent. Taxa that lack nectaries are inapplicable for this character.
 37. Stylodia distinct (0); stylodia partly connate (1); stylodia completely connate (2). Several outgroup terminals are polymorphic. All members of Symplocaceae have fully connate styles, with an irregularly lobed apex.
 38. Style solid (0); style hollow (1). In Symplocaceae and in some of the outgroup taxa, the styles are hollow and fluted in alignment with the locules of the ovary. Coding of outgroups follows Anderberg (1992).
 39. Style apex punctate (0); style apex capitate (1). Many Ericales, and several of the outgroup taxa, have tapered styles that are narrowed distally to a punctate apex. All species of *Symplocos* have uniformly cylindrical styles that are expanded and capitate at the apex.
 40. Subterminal oil-secreting areas on style absent (0); subterminal oil-secreting areas on style present (1). The species of *Symplocos* section *Symplocos* have a subterminal oil-secreting area on the style that appears to function as a mechanism for secondary pollen presentation (Kriebel & al., 2007). Several distantly related angiosperms are known to present pollen secondarily on subterminal regions of the style (e.g., Campanulaceae, Fabaceae, Myrtaceae; see Ladd, 1994). The flowers of *Chamaelucium* (Myrtaceae) are strikingly similar to those of section *Symplocos* in presenting pollen through immersion in oil on a “compact substigmatic ring” (Slater & Beardsell, 1991) but differ from those of *Symplocos* in secreting the oil from the anther theca instead of the style. We refrain from calling the oil-secreting area in *Symplocos* substigmatic for the present, pending further data on stigmatic receptivity.
 41. Ovules unitegmic (0); ovules bitegmic (1). From Cronquist (1981).
 42. Fruit dehiscent (0); fruit indehiscent (1).
 43. Fruit 1-celled (0); fruit 2-celled (1); fruit 3-celled (2); fruit 4-celled (3); fruit 5-celled (4).
 44. Mesocarp absent (0); mesocarp present (1).
 45. Mesocarp bundles not recessed in narrow channels of endocarp (0); mesocarp bundles recessed in narrow channels of endocarp (1).
 46. Endocarp lacking apical pores (0); endocarp with apical pores (1).
 47. Endocarp lacking an apical depression (0); endocarp with an apical depression (1). Most species of *Symplocos* have a depression at the apical portion of the endocarp, such that the apex of the central canal is lower than the surrounding walls. In the species of section *Cordyloblaste*, however, the apex is more or less low-conical, with the germination pores situated on the sides of the cone.
 48. Endocarp surface curved or irregularly grooved (0); endocarp surface regularly grooved or ribbed (1). As supplemented by Nootboom (1975).
 49. Seed number/carpel number < 1 (0); seed number/carpel number 1–2 (1); seed number/carpel number > 2 (1).
 50. Embryo straight (0); embryo curved (1). From Wood & Chanell (1960), Nootboom (1975), and Nagamasu (1993).
 51. Embryo with radicle longer than cotyledons (0); embryo with radicle shorter than cotyledons (1). From Brand (1901).

Appendix 2. Morphological data matrix for phylogenetic analysis of Symplocaceae. See Appendix 1 for character list.

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	2	2	2	
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>Symplocos adenophylla</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. adenopus</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. anomala</i>	1	0	1	1	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. arborea</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. austinsmithii</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. austromexicana</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. austrosinensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. berteroi</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. bogotensis</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. breedlovei</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. caeruleascens</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. celastrifolia</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. celastrinea</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. citrea</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. coccinea</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. cochinchinensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. congesta</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. coriacea</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. costaricana</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. crenata</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. domingensis</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	0	1	1	0	0
<i>S. dryophila</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. euryoides</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. falcata</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	0	0	1	0	1
<i>S. fuscata</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. glandulifera</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. glauca</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. glomerata</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. groffii</i>	1	0	1	1	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. guadeloupensis</i>	1	0	0	1	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. hartwegii</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. henschelii</i>	1	0	1	0	0	0	1	0	1	1	2	1	1	0	1	1	2	0	0	1	1	0
<i>S. hintonii</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. hookeri</i> var. <i>tomentosa</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. insolita</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	0	0	1	0	1
<i>S. itatiaiae</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. kleinii</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. laetiviridis</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. lanata</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	0	1	1	0	0
<i>S. lanceolata</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. lancifolia</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. laurina</i>	1	0	0	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. limoncillo</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0

Dashes indicate non-applicable characters. Question marks indicate missing data.

2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1
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1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	0	1	1	0	1	0	1	1	1	0	0	0
1	0	1	1	1	0	0	0	0	2	0	1	1	1	2	1	1	0	1	1	2	1	0	1	1	1	0	01	0
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	012	1	0	1	1	0	0	1	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	0	1	1	0	1	0	1	1	1	0	0	0
1	0	1	1	?	?	?	?	?	234	0	1	1	1	2	1	1	1	1	1	234	1	1	1	1	0	0	0	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	01	2	1	1	0	1	1	0	1	0	1	1	0	0	1	0
1	0	1	1	?	?	?	?	?	2	0	1	1	01	2	1	1	0	1	1	2	1	0	1	1	0	0	1	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	1	1	1	2	1	?	1	1	0	0	0	0
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1	0	1	1	1	0	1	0	0	2	0	1	1	0	2	1	1	0	1	1	2	1	0	1	1	1	0	0	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	0	1	1	0	1	0	1	1	?	0	0	0
1	0	1	1	0	?	1	?	?	2	0	1	1	0	2	1	1	0	1	1	2	1	1	1	1	0	0	0	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	1	1	1	2	1	1	1	1	0	0	0	0
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1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	0	1	0	1	1	0	0	0	0
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	2	1	0	1	1	1	0	0	0
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1	0	1	1	1	0	1	0	0	2	0	1	1	01	2	1	1	0	1	1	0	1	0	1	1	01	0	1	0
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Appendix 2. Continued.

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>S. longipes</i>	1	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. macrophylla</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. martinicensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. matudae</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. micrantha</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	0	1	1	0	0
<i>S. microstyla</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	0	0	1	0	1
<i>S. aff. munda</i>	1	0	?	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. nana</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. nitens</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. nokoensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. organensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	1	2	0	0	1	0	1
<i>S. ovatilobata</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. pachycarpa</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. panamensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. paniculata</i>	0	0	1	0	0	2	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. pendula</i>	1	0	1	0	0	0	1	0	1	1	2	1	1	0	1	1	2	0	0	1	1	0
<i>S. pentandra</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. phaeocladus</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. poilanei</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. povedae</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. pseudobarberina</i>	1	0	0	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. pycnantha</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. pyrifolia</i>	1	0	?	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. quitensis</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. reflexa</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. saxatilis</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. serrulata</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. speciosa</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. spectabilis</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. stellaris</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. striata</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0
<i>S. sulcata</i>	1	0	1	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. sulcinervia</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. sumuntia</i> var. <i>modesta</i>	1	0	0	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. sumuntia</i> var. <i>sumuntia</i>	1	0	0	0	0	0	1	1	0	2	1	0	0	0	0	0	2	1	0	0	0	0
<i>S. tacanensis</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. tenuifolia</i>	1	0	1	0	0	0	1	1	1	0	2	1	0	0	0	0	2	0	0	1	0	1
<i>S. theifolia</i>	1	0	0	1	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. tinctoria</i>	0	1	1	0	0	0	1	1	0	2	1	0	0	0	0	0	2	1	0	0	0	0
<i>S. tortuosa</i>	1	0	?	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. tribracteolata</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. tricoccata</i>	1	0	0	0	0	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. uniflora</i>	1	0	1	0	0	0	0	1	1	0	2	1	1	0	0	1	2	0	0	1	1	0

	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9	4 0	4 1	4 2	4 3	4 4	4 5	4 6	4 7	4 8	4 9	5 0	5 1			
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1	0	1	1	?	?	?	?	?	234	0	1	1	1	2	1	1	1	1	1	1	234	1	1	1	1	1	0	0	0	0		
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1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	1	1	1	1	2	1	?	1	1	0	0	0	0	0		
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1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	0	1	1	1	0	0	0	
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1	0	1	1	?	?	?	?	?	234	0	1	1	1	2	1	1	1	1	1	1	234	1	?	1	1	1	0	0	0	0	0	
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1	0	1	1	1	0	0	1	0	2	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	0	1	1	1	0	0	0	
1	0	1	1	?	?	?	?	?	3	0	1	1	1	2	1	1	1	1	1	1	3	1	?	1	1	1	1	0	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	0	1	1	2	1	0	1	1	1	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	1	1	1	1	2	1	?	?	?	?	0	0	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	0	1	1	0	0	1	0	
1	0	1	1	1	0	0	0	0	2	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	0
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	1	1	1	1	2	1	1	1	1	1	0	0	0	0	0	
1	0	1	1	0	0	1	0	0	2	0	1	1	0	2	1	1	0	1	1	0	1	1	23	1	1	1	1	0	0	0	0	
1	0	1	1	1	0	1	0	0	12	0	1	1	1	2	1	1	0	1	1	0	1	1	12	1	0	1	1	0	1	0	1	0
1	0	1	1	1	0	0	0	0	2	0	1	1	0	2	1	1	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	?	1	0	1	1	?	0	1	?	0	1	0	
1	0	1	1	0	0	1	1	0	3	0	1	1	1	2	1	1	1	1	1	1	23	1	1	1	1	1	0	0	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	0	1	1	0	1	1	2	1	0	1	1	1	0	0	0	0
1	0	1	1	0	0	1	1	0	234	0	1	1	1	2	1	1	1	1	1	1	234	1	1	1	1	1	0	0	0	0	0	

Appendix 2. Continued.

	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
<i>S. variabilis</i>	1	0	0	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. verrucisurcula</i>	1	0	1	0	0	0	1	1	1	0	2	1	1	1	0	1	2	0	0	1	1	0
<i>S. viridissima</i>	1	0	0	0	0	0	1	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>S. wikstroemiifolia</i>	1	0	1	1	1	0	0	1	1	0	2	1	0	0	0	0	2	1	0	0	0	0
<i>Saurauia</i>	1	1	1	0	0	0	1	1	0	-	2	1	0	0	0	0	2	1	0	0	0	0
<i>Clethra</i>	0	0	1	0	0	0	-	1	0	-	2	1	0	0	0	0	0	0	0	0	0	0
<i>Cyrilla</i>	1	3	1	0	0	0	1	0	0	-	2	1	0	0	0	0	1	-	0	0	0	0
<i>Diapensia</i>	1	3	1	0	0	1	1	0	0	-	2	1	1	0	0	1	1	0	0	1	0	0
<i>Galax</i>	1	3	1	1	0	1	1	0	0	-	2	1	0	0	0	0	1	0	0	1	0	0
<i>Rhododendron</i>	0	0	1	0	0	1	0	0	0	-	2	1	0	0	0	0	0	1	0	0	0	0
<i>Alniphyllum</i>	0	1	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1
<i>Huodendron</i>	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
<i>Pterostyrax</i>	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1
<i>Styrax</i>	0	1	1	0	0	0	1	0	1	0	0	0	1	0	0	1	0	0	0	1	0	1
<i>Ternstroemia</i>	1	0	1	0	0	0	0	0	-	2	1	0	0	0	0	2	0	0	0	0	0	0
<i>Camellia</i>	1	0	1	0	0	0	0	0	-	2	1	0	0	0	0	2	1	0	0	0	0	0

	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	5	5	
	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1						
1	0	1	1	1	0	2	0	0	2	0	1	1	0	2	1	1	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	1	2	1	1	1	1	1	1	?	1	?	?	?	?	?	0	0	0	0	0	0	0	0
1	0	1	1	1	0	0	0	0	2	0	1	1	0	2	1	1	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0	
1	0	1	1	?	?	?	?	?	2	0	1	1	01	2	1	1	0	1	1	01	1	0	1	1	0	0	1	0	0	1	0	0	0	0	
0	1	2	0	01	1	2	0	01	34	2	0	0	-	01	0	0	0	1	01	-	1	0	-	-	-	-	2	0	0	0	0	0	0	0	
0	1	2	0	01	1	12	0	0	2	2	0	0	-	12	1	0	0	1	0	2	0	-	0	0	0	2	0	0	0	0	0	0	0	0	
1	1	1	0	0	1	12	0	0	123	1	0	1	0	1	0	0	0	1	1	12	0	-	0	0	0	1	0	0	0	0	0	0	0	0	
0	0	1	1	2	1	2	0	1	2	2	0	0	-	2	1	1	0	1	0	2	0	-	0	0	-	2	01	0	0	0	0	0	0	0	
0	0	1	0	2	1	2	0	1	2	2	0	0	-	2	1	1	0	1	0	2	0	-	0	0	-	2	01	0	0	0	0	0	0	0	
1	1	2	0	1	01	12	01	-	34	012	1	1	0	2	1	1	0	1	0	45	0	-	0	0	0	2	0	0	0	0	0	0	0	0	
0	0	0	0	0	1	1	0	1	4	1	1	0	-	1	1	1	0	1	0	4	0	-	0	0	0	2	0	0	0	0	0	0	0	0	
0	0	0	0	0	1	12	0	01	23	1	1	0	-	1	1	0	0	1	0	23	0	-	0	0	0	2	0	?	0	0	0	0	0	0	
0	0	0	0	01	1	0	1	0	23	0	1	0	-	2	1	0	0	1	0	12	0	-	0	0	01	0	0	0	0	0	0	0	0	0	
0	0	0	0	01	1	01	1	01	2	1	1	0	-	2	1	0	0	0	01	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
0	0	1	0	0	1	2	01	1	012	2	0	0	-	12	0	0	0	0	1	0	1	0	-	-	0	2	1	0	0	0	0	0	0	0	0
01	0	1	0	0123	1	012	1	0	234	2	0	0	-	01	0	0	0	0	0	0-4	1	0	0	0	0	1	0	1	0	1	0	1	0	1	