

A Morphological Cladistic Analysis of Olacaceae

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ABSTRACT. A cladistic study based on morphological characters is presented for all 28 genera of Olacaceae as well as 26 representative genera from five other families of Santalales: Loranthaceae, Misodendraceae, Opiliaceae, Santalaceae, and Viscaceae. The data matrix consists of 80 macro-morphological, palynological, and anatomical characters. The phylogenetic trees obtained show a paraphyletic Olacaceae with four main clades. Some of these clades are congruent with previously recognized tribes, but all of subfamilies are para- or polyphyletic. Examination of character transformations confirms several assumptions of evolutionary trends within Olacaceae and Santalales, but others appear to be more complex than expected. Optimization of trophic mode on the consensus tree shows that root hemiparasitism had a single origin in Santalales. Whatever the optimization procedure used, the basal-most clade of Olacaceae consists of 12 genera, among which five are known to be autotrophs, whereas the remaining three clades (15 genera) contain four genera known to be root parasites.

Olacaceae (ca. 28 genera and 200 species) constitute a small family of tropical, woody, autotrophic or root hemiparasitic plants (Breteler et al. 1996). Two genera, *Erythralum* and *Octoknema*, are sometimes considered to belong to this family or to represent the monogeneric families Erythralaceae and Octoknemaceae. Together with Loranthaceae, Misodendraceae, Opiliaceae, Santalaceae (including Eremolepidaceae, Nickrent et al. 1998), and Viscaceae, Olacaceae belong to the order Santalales and are considered the basalmost family in this order (Engler and Gilg 1924; Fagerlind 1948; Kuijt 1968, 1969). Such a basal position is supported by molecular phylogenies for Santalales proposed by Nickrent and Franchina (1990), Nickrent and Duff (1996), Nickrent et al. (1998), Nickrent and Malécot (2001), and in phylogenies of all angiosperm (Savolainen et al. 2000; Soltis et al. 2000).

In the first edition of "Natürlichen Pflanzenfamilien" (Engler 1897), the family included three subfamilies and six tribes and since this publication, modification of the infrafamilial classification consists primarily of newly described genera as listed by Sleumer (1984b) and Breteler et al. (1996) (Table 1). The main distinction between the subfamilies Anacolosoideae (formerly known as Dysolacoideae), Olacoideae, and Schoepfioideae, was the presence or absence of ovule integuments and the micropyle position, but according to Sleumer (1984b), the sampling on which these observations were made was too limited to justify the use of these characters at such a level of classification. Moreover, Bouman and Boesewinkel (in Breteler et al. 1996) showed that numerous observations of integument number in the literature were doubtful, and

probably erroneous. Tribes as defined by Engler (Anacoloseae, Aptandreae, Couleae, Heisterieae, Olaceae, Ximenieae) are distinguished mainly by the type of endosperm reserve (starch or lipid) and by the degree of fusion of the stamens. But as with ovule integument number, the endosperm reserve character (composed of just two states, either starch or lipid) is too simplistic, plus this feature is not known for about 20% of the genera in the family. Given these facts, previous authors have regularly expressed doubts on the validity of this classification (Gagnepain 1910; Reed 1955; Sleumer 1984b), and some have suggested that Olacaceae be split (Kuijt 1969) or have actually split it into several families (van Tieghem 1896; Gagnepain 1910; Hutchinson 1969; Takhtajan 1997). Specific studies of palynology (Feuer 1977; Lobreau-Callen 1980), leaf anatomy (Baas et al. 1982), and wood anatomy (van den Oever 1984), resulted in groupings that differed considerably from older classifications and highlighted the huge diversity of characters among the various genera of this family. More recently, molecular phylogenetic studies of Santalales, using nuclear small-subunit (SSU) ribosomal DNA (rDNA) sequences alone (Nickrent and Duff 1996) or together with the chloroplast-encoded gene *rbcl* (Nickrent et al. 1998), revealed the polyphyletic nature of the family. These studies sampled relatively few genera, hence no classification was suggested for the entire family. A broader sampling (17 genera of Olacaceae and 58 species of Santalales) was used by Nickrent and Malécot (2001), in a phylogenetic study based on SSU rDNA and *rbcl*, but incomplete sampling similarly prevented proposing a classification for the entire family.

TABLE 1. Intrafamilial classification of Olacaceae based on Engler (1897) with modification and additions by Sleumer (1984b) and Breteler et al. (1996).

Subfamily <i>Anacolosoidae</i> Airy-Shaw
Tribe 1. <i>Couleae</i> Engl.
<i>Coula</i> Baill.
<i>Maburea</i> Maas
<i>Minquartia</i> Aubl.
<i>Ochanostachys</i> Mast.
Tribe 2. <i>Heisterieae</i> Dumort.
<i>Chaunochiton</i> Benth.
<i>Heisteria</i> Jacq.
Tribe 3. <i>Anacolosae</i> Engl.
<i>Anacolosia</i> (Blume) Blume
<i>Brachynema</i> Benth.
<i>Cathedra</i> Miers
<i>Diogoia</i> Exell and Mendonca
<i>Engomegoma</i> Breteler
<i>Phanerodiscus</i> Cavaco
<i>Scorodocarpus</i> Becc.
<i>Strombosia</i> Blume
<i>Strombosiopsis</i> Engl.
<i>Tetrastylidium</i> Engl.
Tribe 4. <i>Ximenieae</i> Engl.
<i>Ximenia</i> L.
Subfamily <i>Olacoidae</i> Sond.
Tribe 5. <i>Olacae</i> Horan.
<i>Curupira</i> G.A.Black
<i>Douradoa</i> Sleumer
<i>Dulacia</i> Vell.
<i>Malania</i> Chun and S.K.Lee
<i>Olax</i> L.
<i>Ptychopetalum</i> Benth.
Tribe 6. <i>Aptandreae</i> Engl.
<i>Aptandra</i> Miers
<i>Harmandia</i> Pierre ex Baill.
<i>Ongokea</i> Pierre
Subfamily <i>Schoepfioideae</i> Engl.
Tribe 7. <i>Schoepfieae</i> Miers
<i>Schoepfia</i> Schreb.
Dubious affinities
<i>Erythralpalum</i> Blume
<i>Octoknema</i> Pierre

Distinguishing genera in the family is relatively straightforward owing to the monographic studies of Sleumer for Asia (Sleumer 1980), Malaysia (Sleumer 1984a) and Latin America (Sleumer 1984b), as well as those of African Olacaceae by Michaud (1962, 1966). Among the 28 genera, 13 are monospecific, and only six consist of more than ten species. Moreover, four genera have been described within the last 20 years: *Malania* from China (Lee 1980), *Douradoa* from Brazil (Sleumer 1984b), *Maburea* from Guyana (Maas et al. 1992), and *Engomegoma* from Gabon (Breteler et al. 1996). Some genera show disjunct distributions (afro-american, afro-asiatic or asiatic-american) and consideration of morphological, anatomical, and chemical characters suggest an origin of the family during the Lower Cretaceous (Ling 1982) or Upper Cretaceous

(Sleumer 1984b; Haron and Ping 1997). This biogeographic hypothesis is reinforced by the presence of fossil pollen from the Maestrichtian assigned to the pollen form genus *Anacolosidites*, which is similar to pollen of the current genera *Anacolosia*, *Cathedra*, and *Phanerodiscus* (Krutzschn 1989; Askin 1989; Malécot 2002).

The goal of this work is to use a cladistic approach to examine the phylogeny of Olacaceae and putatively related taxa using morphological, palynological, and anatomical (leaf and wood) characters. To take into account the risk associated with the study of a probable paraphyletic or polyphyletic group (Nickrent and Duff 1996; Nickrent et al. 1998; Nickrent and Malécot 2001), members of other families of Santalales (Loranthaceae, Misodendraceae, Opiliaceae, Santalaceae, and Viscaceae) have been included. A revised classification of the family will not be presented here but will be published after inclusion of results from molecular phylogenetic analyses (see Malécot 2002; Nickrent and Malécot, in prep.). A second objective is to study evolutionary trends in selected characters of the family and order inferred in previously published works.

MATERIALS AND METHODS

Taxa. The studied taxa include all genera that have at one time or another been classified in Olacaceae (Table 1), with the exception of *Brachynema* which is only doubtfully assigned to Santalales. Placentation in Santalales consists of a few ovules inserted on the top of a free-central column (or as a 'mamelon' in Opiliaceae, Loranthaceae, and Viscaceae). Placentation in *Brachynema* is axile in a 4–5 loculate ovary, i.e. clearly not santalaceous. In addition, other morphological characters such as glandular toothed leaves, apiculate stamen connectives, and convolute aestivation, are unknown in Santalales. For these reasons, *Brachynema* was excluded from this analysis and may be best placed among Ericales (Malécot 2002).

In addition to Olacaceae, six genera of Opiliaceae, one genus of Misodendraceae, four genera of Loranthaceae, 11 genera of Santalaceae, and four genera of Viscaceae were included. For a few genera where some characters show variability between species (e.g., *Heisteria*, *Phoradendron*, *Viscum*), two species have been included as terminal taxa for this cladistic analysis. When character state variability (polymorphism) existed among species of a genus, both states were recorded in the data matrix.

Recent molecular phylogenetic analyses (Savolainen et al. 2000; Soltis et al. 2000) have suggested various putative sister clades for Santalales, in particular Saxifragales and Caryophyllales. Therefore, *Daphniphyllum*, a primitive member of Saxifragales, and *Rhabdodendron* from Caryophyllales were chosen as outgroups.

Characters. Macromorphological characters for all taxa were scored from specimens housed in various herbaria (e.g., K, KUN, L, MO, P), or taken from previously published descriptions (e.g., *Malania*, *Douradoa*, and *Curupira*). Voucher information is included in Lobreau-Callen (1980, 1982), Baas et al. (1982), and Koek-Noorman and van Rijckevorsel (1983). Palynological characters were taken from Feuer (1977), Lobreau-Callen (1980, 1982, in Sleumer 1984b), as well as new observations by Lobreau-Callen. Leaf anatomical characters for Olacaceae have been obtained from Baas et al. (1982) and Baas and Koel (1983), whereas those for Opiliaceae were taken from Koek-Noorman and van Rijckevorsel (1983). Wood anatomical characters were obtained from publications by van den Oever (1984) and van den Oever et al. (1993) for Olacaceae, and from Koek-Noorman and van Rijckevorsel (1983) for Opiliaceae. Most of the data (morphology, palynology, leaf and wood anatomy) for *Engomegoma* and *Maburea* were taken from the very comprehensive papers by Breteler et al. (1996) and Maas et al.

(1992), respectively. Data for other Santalales and the outgroup genera were obtained from herbarium samples or were gleaned from the literature (particularly from Metcalfe 1935; Reed 1955; Metcalfe and Chalk 1957; Puff and Weber 1976; Bhatnagar and Garg 1977; Carlquist 1982, 1985, 2001; Zavada and Dilcher 1986; Norverto 1993; Huang 1996). The 80 characters used for this cladistic analysis are described in Appendix 1. Data matrices are available on TreeBASE (study accession number S1022, matrix accession number M1730). Parasitism was not included as a character in this cladistic analysis because the available data for Olacaceae were too poor and because we wished to study this character by optimizing it on the consensus tree obtained.

Data Analysis. Cladistic analysis of the data was conducted using PAUP* (Swofford 2000). Heuristic searches for most parsimonious trees used 100 random addition sequences and TBR branch swapping. Characters were unweighted and character state transformations of binary and multistate characters were unordered. Node specific support was assessed using bootstrap analysis (Felsenstein 1985) with 1,000 replications and "Bremer support" (Bremer 1988, 1994; Donoghue et al. 1992) was calculated using Autodecay (Eriksson 1999). MacClade (Maddison and Maddison 1997) and Winclada (Nixon 1999) were used to optimize character state distributions.

RESULTS

A total of 80 parsimony informative characters was identified for use in this cladistic analysis of Santalales. The data matrix consisted of 58 binary and 22 multistate characters. Of these, 32 were derived from anatomy, 14 from palynology, and 34 from floral and vegetative morphology, with 9.1% of the cells coded as missing. The data matrix used for this cladistic analysis is presented in Appendix 2.

Maximum parsimony analysis resulted in 33 most parsimonious trees (length = 457 steps, consistency index (CI) = 0.33, retention index (RI) = 0.69). The strict consensus of those trees is presented in Fig. 1. Relatively few nodes showed bootstrap (BS) values above 50%. Bremer support values above one are commonly associated with nodes that had bootstrap values above 50%. Santalales are monophyletic (BS 90%), with a clade of 13 Olacaceae genera sister to the remaining Santalales. As a family, Olacaceae are paraphyletic and four lineages (Clades 1–4 on Fig. 1) can be identified. Clade 1 is composed of 13 genera including members of tribe Couleae (*Coula*, *Ochanostachys*, *Minuartia*, *Maburea*), Heisterieae (*Heisteria*), Anacoloseae sensu Breteler et al. (1996) (*Diogoia*, *Engomegoma*, *Strombosia*, *Strombosiopsis*, *Tetrastylidium*), as well as two problematic genera *Erythralum* and *Octoknema*. Clade 2 consists of four genera: *Ximenia* (tribe Ximenieae), *Curupira*, *Douradoa*, and *Malania*, the latter three genera doubtfully placed in tribe Olaceae by Sleumer (1984b). Clade 3 is composed of ten olacaceous genera from tribes Olaceae, Aptandreae, Anacoloseae (in part) and *Chaunochiton*. This clade is sister to one with *Schoepfia* and the remaining Santalales families: Misodendraceae, Opiliaceae, Loranthaceae, Santalaceae, and Viscaceae. Clade 4 consists solely of the genus *Schoepfia* which appears as sister to the other families of Santalales. A clade consisting of Misodendraceae plus Op-

iliaceae is sister to a clade that includes Loranthaceae, a paraphyletic Santalaceae, and Viscaceae. Opiliaceae are monophyletic (BS 64%), as are Loranthaceae (BS 85%).

DISCUSSION

In general, the relationships obtained from this cladistic analysis of Santalales are quite similar to those obtained following analyses of SSU rDNA and *rbcL* sequences (Nickrent and Malécot 2001), despite differences in taxon sampling. This study also demonstrates the paraphyly of Olacaceae as first suggested by molecular analyses (Nickrent and Duff 1996; Nickrent et al. 1998; Nickrent and Malécot 2001). As traditionally circumscribed, Olacaceae is paraphyletic, but four groups (clades) can be recognized (Fig. 1). A Templeton test (as implemented in PAUP*) in which the monophyly of the four clades of Olacaceae was constrained shows that this hypothesis was significantly worse than the most parsimonious trees.

Comparison to Previous Subfamilial and Tribal Delimitations. Neither of the two multigeneric subfamilies recognized by Sleumer (1984b) and Breteler et al. (1996), Anacoloioideae and Olacoideae (Table 1), are monophyletic and indeed Olacoideae are polyphyletic. Three genera of tribe Olaceae, *Curupira*, *Douradoa*, and *Malania*, are placed in a clade with *Ximenia* of tribe Ximenieae (subfamily Anacoloioideae). The remaining six genera of subfamily Olacoideae (*Aptandra*, *Dulacia*, *Harmandia*, *Olox*, *Ongokea*, *Ptychopetalum*), together with *Chaunochiton* (tribe Heisterieae) and *Anacolsa*, *Cathedra*, and *Phanerodiscus* of tribe Anacoloseae, constitute Clade 3. As with Olacoideae, subfamily Anacoloioideae is thus polyphyletic and is not the basalmost subfamily as suggested by Ling (1982). Most members of Anacoloioideae form a clade at the base of Santalales, including the two genera with doubtful affinities: *Erythralum* and *Octoknema*.

Only some of the tribes defined by Engler (1897) appear to be monophyletic, such as Couleae (*Coula*, *Minuartia*, *Ochanostachys*), Aptandreae (Aptandraceae of Takhtajan = *Aptandra*, *Ongokea*, *Harmandia*), and Olaceae (*Olox*, *Ptychopetalum*, *Dulacia*). However, other genera that were included within this last tribe by Sleumer (1984b), e.g., *Malania*, *Curupira*, and *Douradoa*, or *Maburea*, placed in tribe Couleae by Maas et al. (1992), are excluded. Tribes Ximenieae (*Ximenia*) and Schoepfieae (*Schoepfia*) were both monogeneric, but Ximenieae are included here in a larger clade with *Malania*, *Douradoa*, and *Curupira*. Tribe Heisterieae, composed of *Heisteria* and *Chaunochiton*, is polyphyletic, as already suggested by Reed (1955). Members of tribe Anacoloseae are scattered in various positions on the tree with members in both Clades 1 and 3 (Fig. 1). Baas et al. (1982), Lobreau-Callen (1980), and van den Oever (1984) have already highlighted this heterogeneity,

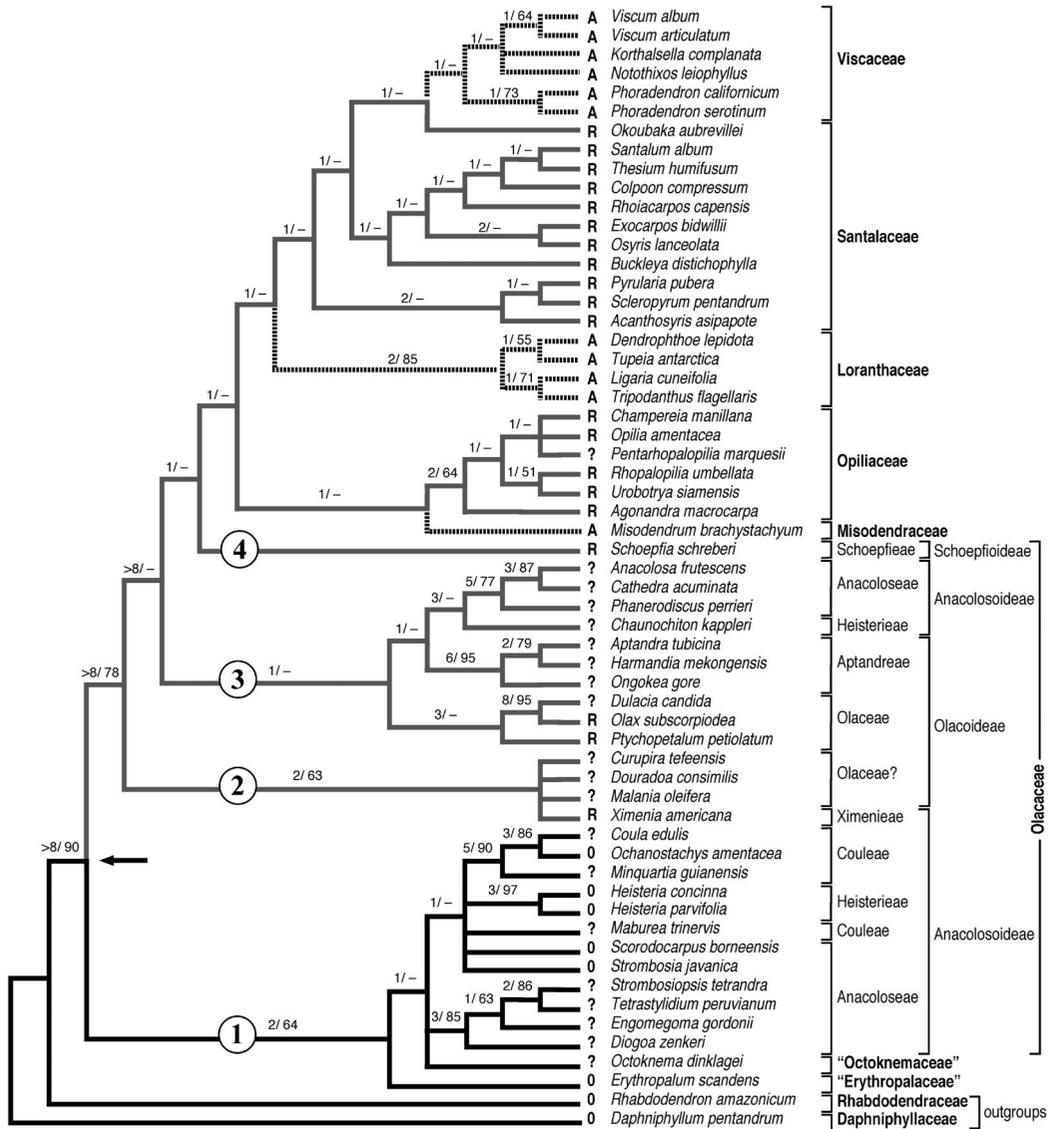


FIG. 1. Phylogenetic relationships of Olacaceae and Santalales based on anatomical and morphological characters. Branch support is given above the branches in the following format: decay index / bootstrap percentage (1000 replications). Circled numbers indicate major clades of Olacaceae (see text). For nutritional mode character state transformations (using either ACCTRAN or DELTRAN optimizations): black = hemiparasitism absent; grey = root hemiparasitism; black dashed = aerial hemiparasitism. For trophic conditions: ? = trophic status unknown; 0 = autotrophs; R = root hemiparasites; A = aerial hemiparasites. The subfamilial and tribal names for Olacaceae correspond to the infrafamilial classification shown in Table 1.

which is confirmed here. Relationships within and among the clades as shown on Fig. 1 will be discussed in the following section.

Clades of Olacaceae. The basalmost member of Clade 1 is *Erythralpalum*, a genus with doubtful olacaceous affinity based on anatomy (Reed 1955; Baas et al. 1982) but whose embryology clearly place it in Santalales (Fagerlind 1946, 1948). Its wood structure (van den Oever, unpublished) and pollen morphology suggest an affinity with Santalaceae (Lobreau-Callen

1982). Ling (1982) considered this genus as the most derived subfamily of Olacaceae (Erythralpaleae).

The remaining genera of Clade 1 form a polytomy of three poorly to well-supported clades. One of these consists of *Octoknema*, which is frequently placed in its own family, Octoknemaceae. Fagerlind (1948) showed that the genus has typical santalaceous placentation and proposed a relationship with tribe Couleae. From its wood anatomy, Reed (1955) linked it to *Heisteria* and Couleae. The same relationship has been proposed

by Feuer (1977) on the basis of palynology, whereas, according to Lobreau-Callen (1982), its pollen is similar to Opiliaceae. The second clade of the polytomy received strong support (BS 85%, Bremer support = 3) and is composed of *Diogoia*, *Engomegoma*, *Tetrastylidium*, and *Strombosiosis* (hereafter the *Diogoia* clade). Unambiguous changes for this clade are the occurrence of epidermal druse crystals and a constricted furrow in the pollen ectoaperture. In most previous classifications (Reed 1955; Feuer 1977; Lobreau-Callen 1980; Baas et al. 1982), a group was recognized that included not only these genera (minus *Engomegoma*, then undescribed) but also *Strombosia* and several other genera in tribe Anacoloseae. In another case (van den Oever 1984), two groups were distinguished, one with *Diogoia* and *Strombosiosis*, the other with *Tetrastylidium* and *Strombosia*. Molecular analyses of Nickrent and Malécot (2001) showed that *Diogoia* and *Strombosiosis* are associated with *Strombosia* and *Scorodocarpus*, with strong support (BS > 90%). This relationship is not supported here, but nodes between these genera are also not well supported. Breteler et al. (1996), who described the genus *Engomegoma*, indicated rather ambiguous affinities within Olacaceae near *Diogoia*, *Strombosia*, *Strombosiosis*, and *Tetrastylidium*. This relationship is supported here.

The third subclade of the polytomy of Clade 1 is composed of seven genera. For the genera or clades included in this polytomy, different patterns of relationships have been proposed based on different organs or on molecular data. For *Maburea*, wood anatomical data link it to *Heisteria* (Maas et al. 1992), leaf anatomy to *Scorodocarpus* and *Brachynema* (Maas et al. 1992) and the pollen apertures (analyzed by Hiepko and Lobreau-Callen, in Maas et al. 1992) to *Minquartia*, *Coula*, and *Heisteria*. On the basis of both palynology and anatomy, *Strombosia* is placed near *Diogoia* and *Scorodocarpus* (Feuer 1977; Lobreau-Callen 1980; Baas et al. 1982; van den Oever 1984). Molecular analyses by Nickrent and Malécot (2001) indicated a strong relationship (BS > 90%) among *Diogoia*, *Strombosia*, *Strombosiosis*, and *Tetrastylidium*. According to wood anatomy, *Scorodocarpus* is closest to Couleae (van den Oever 1984). Leaf anatomy links it to members of the *Diogoia* clade and *Strombosia*, but also to *Heisteria* (Baas et al. 1982). Palynology suggests a relationship with *Strombosia* (Feuer 1977; Lobreau-Callen 1980). The genus *Heisteria* has been considered the most primitive member of Olacaceae by Reed (1955), mainly on the basis of wood anatomical features. In his wood anatomical study of the family, van den Oever (1984) placed this genus in the same group as *Brachynema*, likely because of shared ancestral features. The rather homogeneous tribe Couleae (*Coula*, *Minquartia*, *Ochanostachys*) has long been recognized (van Tieghem 1899a, 1899b; Stauffer 1961). Fagerlind (1948) suggested a basal po-

sition of this tribe within the family, a relationship that was supported by Michaud (1962, 1966) but not the present study. Couleae are unique among all dicotyledons because they possess both laticifer and secretory cavities in their leaves. Unambiguous changes in this tribe also include the acquisition of libriform fibers (also in *Scorodocarpus*), two or more cycles of stamens, and thyrsoid inflorescences.

The composition of Clade 2 (*Ximenia*, *Malania*, *Curupira*, and *Douradoa*; BS = 63%, Bremer support = 2) is exactly the same as proposed by van den Oever (1984). According to Sleumer (1984b), *Ximenia* constitutes a monogeneric tribe (Ximenieae) within subfamily Anacolosoideae, whereas *Curupira*, *Malania*, and *Douradoa* were doubtfully placed within tribe Olaceae of subfamily Olacoideae. An affinity between *Malania* and *Ximenia* corresponds with the proposal made by Lee (1980) in his generic description, and was found by Nickrent and Malécot (2001) in their molecular study. This association was supported by Ling (1982), but was never pointed out in the later synthesis by Sleumer (1984b) and Breteler et al. (1996). *Curupira* was placed close to *Ptychopetalum* because of the absence of staminodes or an accrescent calyx (Black and Murça Pires 1948). In the present study, the clade composed of *Ximenia* and *Malania* as well as the two Brazilian genera *Curupira* and *Douradoa* can be attributed to their shared umbellate inflorescences, flowers with two stamen cycles, lipid reserves in the fruit, and several wood anatomical features.

Clade 3 received less support (<50% BS, Bremer support = 1) but is here composed of ten genera, arranged in three major subclades. Three members of one subclade (*Olox*, *Ptychopetalum*, and *Dulacia*) have long been recognized for their morphological (Sleumer 1984b), anatomical (Reed 1955; Baas et al. 1982; van den Oever 1984), and palynological (Feuer 1977; Lobreau-Callen 1980) homogeneity. This group was strongly supported (100% BS) in the molecular analysis of Nickrent and Malécot (2001). According to van Tieghem (1896), this group is equivalent to family Olacaceae *sensu stricto*. Unambiguous character changes for this clade include heterogeneous type I rays, a pollen foot-layer in masses, and the loss of endexine in the mesocolpium of the pollen. Bootstrap support for a clade composed of the three genera coinciding with tribe Aptandreae (*Harmandia*, *Aptandra*, and *Ongokea*) was strong (BS 95%, Bremer support = 6). The homogeneity of this group has long been known, and indeed van Tieghem (1896), Pierre (1897), and Gagnepain (1910) all suggested that these genera be recognized at the family level (Aptandraceae). Several morphological features link these three genera, particularly the very peculiar fused androecium and the anthers that dehisce by means of flaps. Molecular data (Nickrent and Malécot 2001) provide strong support

(BS = 82%) for a relationship between two representatives of this group (*Aptandra* and *Ongoeka*). The third component of Clade 3 (*Chaunochiton*, *Phanerodiscus*, *Cathedra*, and *Anacolosa*) received BS support below 50% but Bremer support = 3. A clade minus *Chaunochiton* received higher support (BS = 77%, Bremer support = 5), thus in agreement with the assignment of the three genera to tribe Anacoloseae *sensu stricto* as recognized by Reed (1955) and Baas et al. (1982). Floral features of this smaller clade include petals inserted on the top of a disk and poricidal stamens. *Chaunochiton* has been more commonly associated with Aptandreae ("Chaunochitoneae" of Fagerlind 1948), based on ovary morphology. The molecular analysis by Nickrent and Malécot (2001) also supported a clade composed of *Chaunochiton* and Aptandreae (BS = 81%). Relationships between Anacoloseae s.s. and Aptandreae have been proposed by Baas et al. (1982) on the basis of leaf anatomy. Despite an early association with tribe Heisterieae (Engler 1897), affinities of *Chaunochiton* are clearly not with *Heisteria* as stated by Fagerlind (1948) and subsequent workers (Feuer 1977; Lobreau-Callen 1980; Baas et al. 1982; van den Oever 1984, 1990).

Engler (1894) placed the genus *Schoepfia* in its own tribe in Olacaceae (Schoepfieae) and later (Engler 1897) proposed a monogeneric subfamily (Schoepfioideae). This genus was previously assigned to Loranthaceae (de Candolle 1830). Van Tieghem (1896) and Gagnepain (1910) both proposed raising this genus to the family level (Schoepfiaceae). According to wood anatomy, Reed (1955) noted that this genus was the most specialized among all Olacaceae, noting further that its pollen was comparable to that of some Santalaceae. In molecular phylogenetic analyses (Nickrent and Duff 1996; Nickrent et al. 1998; Nickrent and Malécot 2001), *Schoepfia* was separated from other Olacaceae and placed in a clade together with *Misodendrum* and Loranthaceae. In our study, this genus occurs in Clade 4 and is sister to all the remaining Santalales families.

Compared to the traditional infrafamilial classification of Olacaceae, these results suggest that relatively few characters can be used to distinguish subfamilies Olacoideae and Anacoloideae, such as integument number (1 or 2 for Anacoloideae, 0 for Olacoideae) and an accrescent calyx (absent in Anacoloideae, mostly present in Olacoideae) (Sleumer 1984b). Moreover, some genera have been assigned to subfamily based on erroneous data (e.g., Bouman and Boeswinkel in Breteler et al. 1996, comments on ovule integument number). Aside from those genera described after 1948, tribal characteristics appear more pertinent, except for tribes Anacoloseae and Heisterieae, in which genera were grouped based on non-homologous characters. For the genera described during the second part of the 20th century, some tribal assignments may have

been the consequence of the absence of data (e.g. *Curupira* placed in Olacaceae because it lacks an accrescent calyx and staminodes). Moreover, some genera were classified based on data not initially used for delimitating the tribes, such as *Douradoa* and *Malaria*, which were placed in Olacaceae because they are morphologically close to *Curupira*, and *Maburea*, which was placed in Couleae based on flower morphology.

Other Santalalean Families. Of the major clades sister to *Schoepfia*, the first is Opiliaceae, a monophyletic and moderately well-supported family (BS 64%, Bremer support = 2). This family was recognized as distinct from Olacaceae by Valetton (1886) and it is commonly divided into two tribes: Agonandreae and Opilieae. According to Sleumer (1935), the first tribe contains *Agonandra* and *Gjellerupia*, whereas Hiepko (1984) includes only *Agonandra* therein, placing *Gjellerupia* with *Urobotrya* and *Lepionurus*. Anatomical data presented by Koek-Noorman and van Rijckevorsel (1983) place these latter three genera together in one group and *Champereia*, *Melientha*, *Opilia*, and *Rhopalopilina* (and possibly *Cansjera*) in another group; *Agonandra* showed uncertain affinities. Molecular results support a monophyletic Opiliaceae but the topology differs from the above treatments. According to the combined analysis of SSU rDNA and *rbcl* by Nickrent and Malécot (2001), *Lepionurus* is basalmost in the family followed by *Agonandra* and the four other genera in the family (*Champereia*, *Cansjera*, *Opilia*, and *Pentarrhopalopilina*). Although additional sampling is called for, the presence of *Agonandra* near the base for the family is supported by this morphological cladistic analysis because this genus has the highest number of plesiomorphies. Dividing the family into two tribes seems premature at this time, even though six characters state transformations (characters 2, 42, 50, 75, 76, 78) separate *Agonandra* from the remaining Opiliaceae.

Misodendrum of the monogeneric mistletoe family Misodendraceae is placed here as sister to Opiliaceae. The genus has a large number of autapomorphies, such as wood features (peculiar/highly modified rays, fibers and parenchyma), or palynological characters (polyporate, echinulae) (Skottsberg 1914; Metcalfe and Chalk 1957; Feuer 1981; Carlquist 1985). This position as sister to Opiliaceae is not stable as indicated by a BS value of less than 50% (Bremer support = 1) for this clade. Molecular data (Nickrent and Soltis 1995; Nickrent and Duff 1996; Nickrent et al. 1998; Nickrent and Malécot 2001) always link *Misodendrum* and *Schoepfia*, a relationship also recovered in some morphological cladistic analyses (data not shown) where fewer genera of Santalaceae and Loranthaceae were used.

The four genera sampled from Loranthaceae (*Dendrophthoe*, *Ligaria*, *Tripodanthus*, and *Tupeia*) are monophyletic and this well-supported (BS 85%, Bremer sup-

port = 2) clade is sister to Santalaceae and Viscaceae. Santalaceae appear paraphyletic in this study. One clade consists of members of tribe Thesieae of Pilger (*Acanthosyris*, *Scleropyrum*, *Pyrularia*) and is relatively similar in composition to Santalaceae clade *c* of Nickrent and Malécot (2001). *Okoubaka*, also considered to belong to this tribe based on habit, fruit morphology, wood anatomy, and palynology (Stauffer 1957; Lobreau-Callen 1982; Hallé 1987), is here placed as sister to Viscaceae, an anomalous position supported by a single character (37, long ray cells). The remaining Santalaceae form a poorly-supported clade that includes members of Santalaceae clades *d*, *e* and *f* of Nickrent and Malécot (2001), mainly from tribes Santaleae and Antholobeae. The four genera of Viscaceae are monophyletic, but with low BS support Bremer support = 1, thus few intergeneric relationships are resolved.

Character Transformations. This discussion of character transformations will concentrate mostly on Olacaceae, although some characters more particularly concern the other families. The unambiguous character optimizations are presented in Fig. 2. Alternate (character 1) and developed (character 3) leaves are plesiomorphic within Santalales, and opposite and/or squamate leaves appear independently derived several times in non-olacaceous families (Loranthaceae, Misodendraceae, Santalaceae, Viscaceae). Such evolution appears consistent with morphological reduction associated with the parasitic habit. The presence of tomentum, whether on twigs (character 2) or leaves (characters 7, 8), is a derived feature. Dendritic leaf hairs is a synapomorphy of tribe Couleae. Regarding venation, the variability of the states for the outgroups prevent any decision regarding plesiomorphic and apomorphic features as secondary (character 4) and tertiary (character 5) venation distinguish Clade 1, (with camptodromous leaves and reticulate tertiary venation) from the remaining clades (Clades 2, 3, 4). Mesh shape (character 6) is primarily polygonal and flabellate meshes are a synapomorphy for *Coula* and *Ochanostachys*.

Evolution of leaf anatomical features commonly follows the assumptions of Baas et al. (1982), with derived features being sclerification or lignification of epidermal cells (character 9), lignification of guard cells (character 10), wide lumina of stomata (character 11), and the presence of cuticular ledges on guard cells (character 12). Occurrence of paracytic (character 13) or cyclocytic (character 15) stomata separate Clade 1 (cyclocytic stomata) from the remaining Santalales (with paracytic stomata). However, according to Baas et al. (1982), the presence of paracytic stomata may be plesiomorphic. Regarding stomatal features, Couleae strangely show a reversal compared with other members of Clade 1. Contrary to Baas et al. (1982), the presence of laticifers (character 17) is a derived feature,

whereas schizogenuous cavities (character 16) are a synapomorphy of Couleae, in agreement with them. The presence of druses in epidermal cells (character 18), silicified walls of mesophyll and epidermal cells (character 19), mesophyll sclereids (character 20), and leaf cystoliths (character 21) are all apomorphic within Santalales. The presence of mechanical tissues of the vascular system, e.g. sclerenchyma fibers (character 22) and astrosclereids (character 23) in the petiole and median vein, appear to be plesiomorphic within Santalales, in agreement with Baas et al. (1982); the absence of such mechanical tissue is a specialization achieved through reduction.

General trends for wood anatomical features mostly conform to the hypotheses put forth by Bailey (1957), but occurrence of the derived state does not imply a close relationship. For example, ray organization (character 36) follows Bailey's hypothesis, with heterocellular rays being plesiomorphic, whereas homocellular rays are apomorphic. Clade 1 consists only of taxa with heterocellular rays with several rows of erect or square cells. Clades 2 and 3 consist of taxa with heterocellular rays with a single row of erect or square cells. For the remaining santalalean families the picture is not so clear and several reversals from homocellular to heterocellular rays (whether with one or several rows of erect or square cells) have occurred in the Opiliaceae and *Exocarpos/Santalum* clades. Presence of wood cystoliths (character 38) is a possible synapomorphy for two genera of Opiliaceae (*Champereia* and *Opilia*), and the presence of silica bodies (character 39) is a synapomorphy for the three genera of tribe Olacaceae (*Ptychopetalum*, *Olox*, *Dulacia*).

Tetramerous (character 44) flowers with oval buds (character 43), partially fused sepals (character 45), accrescent calices (character 46), fused petals (character 47) and pubescent petals (character 48) occur commonly in a few unrelated clades, thus suggesting that parallel morphological evolution may be linked with pollination syndromes. The primitive androecial condition appears to be five (character 49), epipetalous (character 51) stamens organized in a single (character 50) cycle. Such an organization contradicts the hypothesis of Michaud (1962, 1966) who proposed that the two-cycled androecium as occurs in *Heisteria* and tribe Couleae is primitive. Duplication of the androecium occurs independently in Clade 1 (Couleae, *Heisteria*, *Scorodocarpus*, *Maburea*), Clade 2 (all genera except *Douradoa*), and Clade 3 (tribe Olacaceae). The presence of staminodia (character 52), of fused filaments (character 53), or of a modified anther connective (character 54) are all synapomorphies of small clades, commonly regarded as tribes within Clades 1 or 3. Anthers are primitively basifixed (character 55) with a transformation to dorsifixed in Clade 1, and to oblique in Clade 3. Anther dehiscence mode (character 56) and

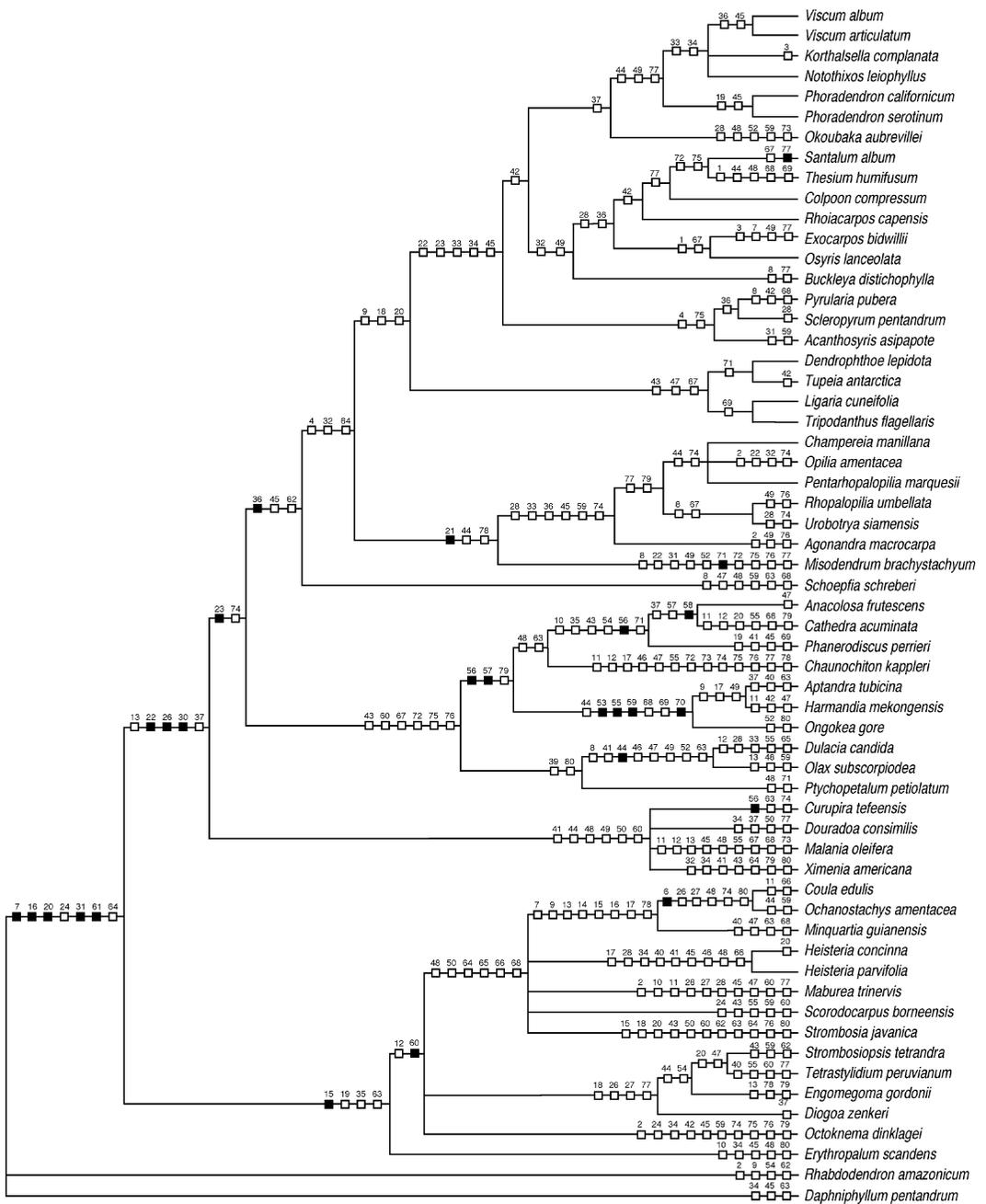


FIG. 2. Optimization of morphological characters on cladogram given in Fig. 1. Open boxes indicate homoplastic characters, filled boxes non-homoplastic characters.

orientation (character 57) appear to be linked, with longitudinal and introrse (or lateral) anther dehiscence as plesiomorphies. In contrast, extrorse dehiscence is almost always associated with porous or valvate dehiscence, as occurs in *Chaunochiton* and tribes Aptandreae and Anacoloseae of Clade 3.

The accrescent disk (character 58) is a synapomorphy of *Anacolsa* and *Cathedra* within Clade 3. The

glandular tissue (character 59) is primitively located between the stamens and ovary. Its location between the stamens and petals is a synapomorphy for members of Aptandreae. The absence of glandular tissue occurs in several independent lineages. A short cylindrical style (character 60) seems to be plesiomorphic within Santalales. Style shape modifications are common in Clade 1, but are uninformative. Conversely,

long conical styles appear as a clear synapomorphy for Clade 2 and a long cylindrical style as a synapomorphy for Clade 3.

The inferior ovary (character 62) is a synapomorphy of non-olacaceous families and *Schoepfia*, but within Olacaceae, semi-inferior ovaries arose several times independently. The ovary locule number of two (character 63) is plesiomorphic within Clade 1, and increases (to four or five) in the *Diogoia* clade. For the remaining Santalales (Clades 2, 3 etc.), the plesiomorphic state is a single locule, with an increase of up to two in Anacoloseae, or to three in *Olax*. Such patterns contradict common assumptions on the prevalence of reduction in locule number evolution in Santalales (Sleumer 1984b), but new observations may be necessary for some taxa as some reports date to Valeton (1886).

Breviaxial pollen (character 67) is a synapomorphy for Clade 3, whereas heteropolarity (character 68) has occurred independently in various groups. A concave mesocolpium (character 69) and concave apocolpium (character 70) are synapomorphies for members of Aptandreae, the former occurring also in a few unrelated genera. Apertures are primitively three or four and zonoaperturate (character 71); duplication of the number occurs independently in *Ptychopetalum* and in Anacoloseae s.s. (*Anacolosia*, *Cathedra*, *Phanerodiscus*). Round or elliptic ectoapertures (character 73) are a synapomorphy for Clade 3 (with a reversal for *Chaunochiton*), as stated by Lobreau-Callen (1980). The occurrence of granules on the apertural membrane (character 73) does not constitute a synapomorphy for any group of Olacaceae, but granules in the endoaperture (character 76) are synapomorphies of Clade 3. The endoaperture and ectoaperture of identical size (character 75) are mainly synapomorphies of Clade 3, with few independent occurrences in other Santalales. Mesocolpium ornamentation (character 77) is primitively smooth or microperforate, but derived states occur several times independently. The presence of granules in the infractectum (character 78) is a synapomorphy for members of Couleae and Opiliaceae, but this feature appears to be independently derived in these two groups. Formation of a columella in the infractectum (character 79) also appears independently in a few clades (Aptandreae and Anacoloseae s.s.; Opiliaceae p.p.) suggesting these features are not always homologous. A smooth foot layer (character 80) is plesiomorphic in Santalales, but contrary to the assumptions of Lobreau-Callen (1980), an irregular foot layer surface is not homologous in all Olacaceae. An irregular foot-layer is a synapomorphy for two groups, Couleae (*Coula*, *Ochanostachys*) and Olacaceae (*Ptychopetalum*, *Dulacia*, *Olax*).

Parasitism. The occurrence of root hemiparasitic and autotrophic taxa in Olacaceae has been known for decades, but the evolution of this ecological specialization remains poorly understood. Only four genera of

Olacaceae are known to contain species that possess haustoria on their roots: *Ximenea* (Heckel 1899), *Olax* (Barber 1907), *Schoepfia* (Piehl 1973; Werth et al. 1979), and *Ptychopetalum* (Anselmino 1932). The absence of haustoria has been documented only for *Heisteria* (Kuijt 1969), *Ochanostachys*, *Strombosia*, *Scorodocarpus*, and *Erythralium* (Ping 1997). No data are available for the remaining 19 genera in the family. Haustoria have been recorded for eight of the ten genera of Opiliaceae. *Gjellerupia* and *Pentarthopalopilia* are the only genera for which parasitism has not yet been confirmed, but all Opiliaceae are assumed to be root parasites (Kubat 1987). All Santalaceae are considered to be either aerial or root hemiparasites, including *Okoubaka*, a 40 meter high African tree whose parasitic mode was only recently reported (Veenendaal et al. 1996). Hemiparasitism has been documented in *Acanthosyris* (Barroso 1969), *Colpoon* (Visser 1981), *Pyrularia* (Leopold and Muller 1983), *Scleropyrum* (van Rheede 1688; Arnott 1836; Nicolson et al. 1988) and for *Santalum*, *Thesium*, *Exocarpos*, *Osyris*, and *Buckleya* (see references in Kuijt 1969). Among the 11 genera of Santalaceae used in this study, documentation of parasitism is lacking only for *Rhoiacarpus*. The three genera of Loranthaceae included here are all aerial hemiparasites (mistletoes), as is *Misodendrum* and all Viscaceae. On the basis of molecular results, Nickrent (2002) showed that aerial hemiparasitism arose independently in Santalales at least five times, but the evolution of root hemiparasitism was not addressed.

Positive documentation of hemiparasitism and non-parasitism have been plotted on the tree obtained from this cladistic analysis (Fig. 1). When those taxa with an unknown parasitic state are coded with "?", root hemiparasitism arises only once in Santalales, in the common ancestor of Clade 1 (Olacaceae) and its sister group (remaining Santalales). This result is obtained using both ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) optimization strategies. Aerial hemiparasitism appears in three independent lineages among the taxa studied here: Misodendraceae, Loranthaceae and Viscaceae (an aerial parasite from Santalaceae was not included). Moreover, an additional appearance of root parasitism can be assumed at the base of Loranthaceae (*Atkinsonia*, *Gaiadendron*, and *Nuytsia*, none of which were sampled here). If taxa coded as unknown are considered root parasites or autotrophs ("R" or "0"), ancestral states for Santalales are ambiguous, thus leaving the possibility open that root parasitism arose numerous times.

From the topology of the tree shown in Fig. 1, it may be assumed that, in addition to the five olacaceous genera documented as lacking haustoria, eight other genera are autotrophs: *Coula*, *Diogoia*, *Engomogoma*, *Minquartia*, *Maburea*, *Octoknema*, *Strombosiopsis*, *Tetrastylidium*. Furthermore, eleven genera not known to be

parasites may, based on our optimizations, be root hemiparasites: *Anacolosia*, *Aptandra*, *Cathedra*, *Chaunochiton*, *Curupira*, *Douradoa*, *Dulacia*, *Harmandia*, *Malania*, *Ongokea* and *Phanerodiscus*. If the tree topology is correct, and any of these genera are later found to be autotrophic, such cases would represent reversals from the parasitic mode. Such reversals, however, have never been reported for any parasitic plant and seem unlikely given the selective advantage conferred by this trophic mode.

Perspectives. Several previous works based on morphological or molecular data suggested a paraphyletic or polyphyletic Olacaceae. The present study reaches the same conclusion, but the positions of genera such as *Maburea*, *Strombosia*, and *Scorodocarpus* remain uncertain when compared with available molecular data. This cladistic analysis demonstrates that the infrafamilial classification of the family is in need of revision. The existing classification is based on the work of Engler from the 19th century (Engler 1894, 1897). Subsequent work during the last century mainly provided amendments, such as the description of new taxa, but the overall structure of the classification remained relatively unchanged. In the present analysis, the subfamilies Olacoideae and particularly Anacoloideae are polyphyletic and only a few of the named tribes appeared monophyletic. A revised classification of the family will not be presented here but will be published after consideration of results from molecular phylogenetic analyses (Nickrent and Malécot, in prep.). Regarding parasitism, if states are inferred for unknown taxa, this study suggests a single origin of root hemiparasitism within Santalales, whereas aerial hemiparasitism appeared independently in at least three of the lineages sampled here. The evolution of hemiparasitism appears to have been a major event in Olacaceae, one that can be used to distinguish two groups in the family. Character optimization for parasitism allows a prediction, for the first time, of the nutritional mode for nineteen genera of Olacaceae.

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APPENDIX 1

List of characters used in this cladistic analysis of Olacaceae with discussion of character state assignments.

Stem

- Phyllotaxy: alternate (0): opposite (1). All species of Olacaceae have alternate phyllotaxy, but various Santalaceae and Loranthaceae have opposite leaves. In rare cases (e.g., *Okoubaka*), phyllotaxy varies near the proximal ends of shoots within an individual, thus such species were coded as polymorphic.
- Twig tomentum: none (0): simple hairs (1): stellate hairs (2). According to Reed (1955), *Coula* and *Minuartia*, as well as *Octoknema*, could be allied by the presence of branched hairs on the young branches. Diverse Opiliaceae also have pubescent young branches, albeit with simple hairs. We interpreted the pubescence on young growth among Opiliaceae and Couleae as non-homologous and coded the states accordingly.

Leaf

The majority of foliar anatomical characters result from work of Baas et al. (1982) who studied infrageneric variation in leaf anatomical characteristics of Olacaceae. They also proposed assumptions as for the homology and the taxonomic utility of these attributes while taking into account the other families of Santalales. For Opiliaceae, Koek-Norman and van Rijkvorsel (1983) did similar work.

3. Leaf size: developed (0); squamate (1).
4. Secondary venation: camptodromous (0); brochidodromous (1). The venation of the leaves of Olacaceae shows some diversity. The secondary venation is always pinnate, either of a festooned brochidodromous, or a festooned eucamptodromous type (Mouton 1972). In the genera with three clear basal veins (*Maburea*, *Curupira*, etc.), the secondary veins are widely spaced at the base, and much closer towards the top, and the type of secondary venation remains identifiable starting from these final veins.
5. Tertiary venation: plagiodromous (parallel) (0); reticulate (1). The tertiary venation is of a simple plagiodromous type (parallel veins between them, at oblique angles to the secondary veins), or reticulate and irregular.
6. Quarternary venation (areolation): meshes flabellate (0); meshes polygonal (1). The meshes (areolae) are either flabellate in a direction parallel with the tertiary veins or polygonal.
7. Leaf dentritic hairs: absent (0); present (1). Baas et al. (1982) recognized three types of hairs: dendritic, unicellular, and uniseriate. The simultaneous presence of hairs of two types in certain genera (e.g. *Ochanostachys*) led us to independently code for each hair type rather than to use only one character with four states (hairs absent, dendritic, unicellular, uniseriate). Moreover, according to Baas et al. (1982), the presence of uniseriate hairs does not make it possible to characterize any genus of Olacaceae, and this character varies between leaves of the same individual. Consequently, only two characters will be defined, one for dentritic hairs and a second one (character 8) for unicellular hairs.
8. Leaf unicellular hairs: absent (0); present (1).
9. Epidermal cell lignification: none (0); weakly lignified (1); lignified (2). The secondary walls of the "ordinary" epidermal cells (excluding guard cells and stomatic cells) can be sclerified—a very rare phenomenon in angiosperms (Baas et al. 1982). Such cells are found on the entire abaxial surface of the leaves of the genera of tribe Couleae, as well as occasionally on the leaves of *Heisteria* p.p., *Harmandia*, and *Aptandra*. For these last three genera, a very weak sclerification is observed, thus the phenomenon may not be homologous with that observed in Couleae. Thus weakly lignified epidermal cells was treated as distinct.
10. Guard cell lignification: not lignified (0); lignified (1). According to Baas et al. (1982), there is no link between the sclerification of the epidermal cells and the lignification of the guard cells. The majority (more than 60%) of the guard cells are lignified in the genera *Aptandra*, *Cathedra*, *Maburea*, and *Phanerodiscus*. Taking into account the small percentage (lower than 10%) of lignified guard cells mentioned for *Heisteria* p.p., *Chaunochiton*, *Harmandia* and *Dulacia*, these genera were scored with a question mark.
11. Lumina of guard cells: narrow (0); wide (1). Seen in cross section, the guard cells of the stomata are of very different form and size in Olacaceae. Two extreme types were defined by Baas et al. (1982): 1) guard cells with a broad lumen and equally thick walls above and below and 2) guard cells with a narrow lumen with the inner wall (facing the mesophyll) much thicker than the outer wall. They found that the guard cells with broad lumens are constantly associated with marked cuticular ledges, whereas the guard cells with narrow lumens generally occur (but not always) in the species with paracytic stomates. However, exceptions to this relationship exist. Thus, two characters will be defined, one corresponding to the size of the lumen of the guard cells, the other to the presence of cuticular ledges (character 12).
12. Cuticular ledges of guard cells: inconspicuous (0); thick (1).
13. Paracytic stomata: absent (0); present (1). Olacaceae show a great diversity of stomate types (Baas et al. 1982), and different types can be present on the same individual. Thus, in an effort to avoid using a polymorphic characters, each stomatal type was coded independently (characters 13–15) except anomocytic stomata which occur in all genera.
14. Cyclocytic stomata: absent (0); present (1).
15. Anisocytic stomata: absent (0); present (1).
16. Schizogenous cavities in leaf: absent (0); present (1).
17. Laticiferous channel in leaf: absent (0); present (1). The laticifers present in the leaves of certain species of Olacaceae are not ramified, and have a diameter ranging between 8 and 45 μm (Baas et al. 1982). Their presence has been used to delimit tribe Couleae (Sleumer 1935), however, they are also present in species of *Heisteria*, *Chaunochiton*, *Harmandia*, and *Aptandra*.
18. Druses in epidermal cells: absent (0); present (1). Druses are considered by Baas et al. (1982) to be an apomorphy for the genera *Diogo*, *Strombosia*, *Strombosiopsis*, and *Tetrastylidium*. Other types of crystals listed by Baas et al. (1982) were recorded in only some species of the same genus, thus only druses will be used in this phylogenetic analysis.
19. Silicified walls of mesophyll and epidermal cells: absent or extremely infrequent (0); present (1). In various genera of Olacaceae and the majority of the other families of Santalales the walls of certain cells of the mesophyll and epidermis are silicified, more particularly those associated with the stomatal complex or vein endings. Baas et al. (1982) consider that this is a derived condition in Olacaceae.
20. Mesophyll sclereids: absent (0); present (1). Idioblastic sclereids are morphologically variable in the species of *Heisteria* (Baas et al. 1982; Baas and Kool 1983), but not so in the other genera of the family. Only the presence of this type of mesophyll sclereid will be coded here.
21. Leaf cystoliths: absent (0); present (1). Mesophyll cystoliths are observed only for Opiliaceae and could constitute an apomorphy for this family (Koek-Noorman and van Rijckevorsel 1983).
22. Petiole and median vein sclerenchyma fibers: absent (0); present (1). Baas et al. (1982) considered that the presence of sclerenchyma fibers is strongly related to the type of vascularization. The presence of such fibers is common in angiosperms, but the linkage with the type of vascularization is not so strong in other families. On the other hand, the absence of sclerenchymatous fibers (more exactly their substitution by collenchyma) as supportive tissue in the median vein is not very common in angiosperms (Baas et al. 1982). Moreover, this absence from the median vein does not automatically correspond to an absence near the other veins. Baas et al. (1982) identified a particular type of nonlignified fiber near the margin of the leaf in *Strombosia*, *Strombosiopsis*, and *Diogo*. The difficulty in observing this type of fiber makes it impossible to determine if its absence in the other families of Santalales is real or simply a lack of observation. Thus, only the presence or absence of sclerenchyma fibers in the petiole and median vein will be coded, but not in other veins.
23. Petiole and median vein astroclereids: absent (0); present (1). With the exception of *Phanerodiscus*, these sclereids are present in the majority of Anacoloseae s.l., such as *Heisteria*, *Maburea*, *Engomogoma*, *Curupira*, and *Douradoa*, and sporadically in *Malania* and *Ximenia* (Baas et al. 1982). These sclereids are morphologically close (groups of isodiametric and slightly ramified sclereids) and have an identical position in the central tissue of the petiole and the median vein (Baas et al. 1982).

Vascularization of nodes and petiole

24. Vascularization of the nodes: unilacunar (0); trilacunar (1); pentalacunar or more (2). The genera for which information is available derives from Reed (1955), otherwise taxa were coded with missing data. A possible correlation (although unconfirmed) between the vascularization of the petiole and the median vein may exist (Baas et al. 1982). Thus, the unilacunar nodes would be generally associated with a simple type of vascularization of the petiole and principal vein. However, trilacunar nodes can be associated with a closed vascular cylinder or a simple arc. For *Oc toknema*, the vascularization of the nodes was described by van Tieghem (1905).
25. Basal petiole vascularization: simple bundle (0); incomplete vascular cylinder (1); simple vascular cylinder (2). This type of

vascularization is constant in a genus and sometimes in a tribe (Baas et al. 1982). Variation exists, however, in the condition of the vascular system between the base of the petiole, the top of the petiole (character 26), and the median vein in the center of the lamina (character 27).

26. Distal petiole vascularization: simple bundle (0); complex vascular cylinder and one or more adaxial or enclosed strands (1); simple vascular cylinder (2).

27. Median vein vascularization: simple bundle (0); complex vascular cylinder and one or more adaxial or enclosed strands (1); simple vascular cylinder (2).

Wood anatomy

The diagnostic characteristics of wood in Olacaceae were outlined by van den Oever (1984). Moreover, Herendeen and Miller (2000) proposed a phylogenetic coding for characters traditionally used for wood anatomical data and this coding will be used here.

28. Vessel grouping: solitary (0); grouped in multiples (1). Vessels can be exclusively solitary, or can be grouped in multiples of two to four (and even up to 15 in *Anacolosa*). A frequency of solitary vessels higher than 60% was coded as wood with solitary vessels, following van den Oever (1984).

29. Perforation plate type: scalariform (0); simple (1). The type of perforation was studied by van den Oever (1984) on mature wood. *Heisteria scandens*, a lianescent species, has simple and scalariform perforations in young wood, then exclusively simple perforations in older wood (van den Oever in prep.). Herendeen and Miller (2000) proposed using a more complex coding that does not have utility in this study. The number of bars of the scalariform perforations could also be introduced into the analysis. Van den Oever (in prep.) mentions that scalariform perforations of the genera *Coula*, *Minuartia*, *Ochanostachys*, *Scorodocarpus*, and *Engomegoma* always have more than ten bars.

30. Vessel member length: below 900 μm (0); over 900 μm (1). Two distinct non-overlapping length classes for vessel elements exist in the wood of Olacaceae (van den Oever 1984; in prep.).

31. Intervascular pits (if present): alternate (0); opposite (1); scalariform (2). Although used by van den Oever (1984), this character may not be independent of character 28. Solitary vessels obviously never have intervacular pits. However, taking into account the occasional presence of two adjacent vessels (and coding "solitary vessels" when at least 60% of them are solitary), the type of intervacular pitting can be easily observed (van den Oever in prep.). This coding corresponds to that recommended by Herendeen and Miller (2000) when character states inapplicable in Santalales are removed.

32. Vascular tracheids associated with the vessels: absent (0); present (1). This character was defined by van den Oever (1984). These tracheids are rare but can be observed in certain cases in macerations. The coding used corresponds to that of Herendeen and Miller (2000).

33. Fibers: fiber-tracheids (0); libriform fibers (1). The terminology used for this character is that of Baas (1986), and coding is that proposed by van den Oever (1984, in prep.). Usually one observes either fiber tracheids or libriform fibers. An exceptional case is the septate libriform fibers in *Octoknema*, which were coded as libriform fibers.

34. Axial parenchyma frequency: abundant (0); rare or absent (1). The abundance of axial parenchyma was recorded by van den Oever (1984; in prep.). This type of tissue is very rare in *Heisteria* and *Maburea* and some other genera.

35. Axial parenchyma strand width: less than seven cells (0); more than seven cells (1). Two classes of axial parenchyma strand width can be distinguished in Olacaceae: less than seven cells broad (narrow bands of axial parenchyma), and greater than seven cells broad (broad bands of axial parenchyma) (van den Oever 1984, in prep.). Taxa with rare or absent axial parenchyma (character 34 state 1) have been coded as inapplicable "-". This coding

corresponds to one of the four characters suggested by Herendeen and Miller (2000) to code parenchyma.

36. Ray type: all cells procumbent (homogeneous) (0); heterocellular, one row of erect cells (1); heterocellular, several rows of erect or square marginal cells (2). Various types of rays can be distinguished that correspond to the heterogeneous rays I, II, III types (van den Oever 1984, in prep.) and with the homogeneous rays of Kribs (1968). Herendeen and Miller (2000) recommend coding the composition of the rays in the following way: first, homogeneous rays, all cells procumbent (homogeneous I II and III of Kribs 1935 = homogeneous of Kribs 1968); second, heterocellular rays, a file of erect cells (heterogeneous I of Kribs 1935 and Kribs 1968); third, ray heterocellular, only one row of erect or square marginal cells (heterogeneous IIA and IIB of Kribs 1935 = heterogeneous II and III of Kribs 1968). Such coding will be used here.

37. Ray height: long (over 1,000 μm) (0); short (below 1,000 μm) (1). The height of the rays varies from 94 μm to 4300 μm , and van den Oever (1984) determined a threshold value equal to 1 mm, making it possible to distinguish two non-overlapping groups within Olacaceae.

38. Wood cystoliths: absent (0); present (1). Various genera of Opiliaceae have cystoliths in the wood rays, that are apparently independent of their presence in leaves (Koek-Noorman and van Rijckevorsel 1983). It is possible that this character could be used to distinguish groups within Opiliaceae.

39. Silica bodies in ray cells: absent (0); present (1). van den Oever (1984) mentions only their presence in three genera, *Olox*, *Ptychopetalum*, and *Dulacia*.

Inflorescence and flowers

40. Inflorescence bracts: absent (0); present (1).

41. Floral and inflorescence trichomes: absent (0); present (1).

42. Flower sexual condition: bisexual (0); unisexual (1).

Perianth

43. Floral bud shape: spherical (0); oval (1). In Olacaceae, floral buds are either spherical, measuring 2–3 mm in diameter (e.g., *Coula*), or lengthened, and reaching more than 5 cm in length (e.g., *Chaunochiton*). The length and width of floral buds before anthesis were measured on rehydrated flowers from herbarium specimens. The flowers for which the length/width ratio was between 0.9 and 1.1 were regarded as spherical, whereas those with values higher than 1.1 were regarded as oval.

44. Flower merosity: five (0); four (1); six (2). The number of parts per floral cycle was determined directly or obtained from the literature (*Douradoa*). The number of stamens was not used to code this character because of the simultaneous and variable presence, in certain genera, of stamens and staminodes. Within a genus, the number of parts per cycle does not vary, except for *Phanerodiscus* and *Olox* spp. Sometimes the number of floral parts per flower varies on the same branch. *Olox* is often regarded as having only three petals (Linné 1753; Sleumer 1984a, 1984b), but the anatomical studies of Argawal (1963) and Patil and Pai (1984), the observations of Capuron (1968), and our own observations of herbarium samples indicate that these flowers are pentamerous with varying degrees of fusion between the more or less distinct petals.

45. Sepals: developed, partially fused (0); developed, completely fused (1); calyculus (2); absent (3). Among genera of Olacaceae, the petals are more or less fused. In Opiliaceae, Santalaceae, Viscaceae, and Loranthaceae various and contradictory interpretations of the floral parts have been proposed. Here we scored Misodendraceae and Opiliaceae as lacking a calyx (a 'torus' is present in Opiliaceae according to Hiepko 2000), whereas we interpreted Santalaceae and Viscaceae as having only a developed calyx (Eichler 1878; Kuijt 1968). In Loranthaceae, a calyculus is generally present. Among Olacaceae, *Schoepfia* and *Octoknema* were regarded

as lacking a calyx, although very small sepals are present on the female flowers of *Octoknema orientalis*.

46. Accrescent calyx: absent (0); present (1). Identification of an accrescent structure around the fruit was based on the study of herbarium samples of ripe and unripe fruits. Taking into account the problems of homology and the difficulty in considering the development relative to certain organs, each tissue that can be accrescent was coded independently, and only the accrescence of the calyx and of the disc/receptacle (character 58) were taken into account. In *Erythrophalum*, one observes no accrescent structure around the fruit, but at maturity the mesocarp tears into four to five parts, revealing a black, sclerified endocarp, and a bright red, internal mesocarp face. This structure has sometimes been regarded as an accrescent calyx (particularly given its radial pseudo-symmetry), but it is not at all homologous. In santalaceous families treated here as lacking a calyx (character 45 state 3) this character was coded as inapplicable.

47. Corolla connation: apopetalous (0); sympetalous at base only (1); sympetalous with a floral tube (2). If one considers that Santalaceae have only one cycle of floral parts (monochlamydous) and this is interpreted to represent the calyx, the present character cannot be coded for that family, and was scored as inapplicable. For our purposes, we considered petals fused by less than half their length to be connate at their base, whereas those fused by more than half their length to have a floral tube. In the case of variation in the degree of fusion between petals of the same flower (*Olax*), we took account of the measured minimal value.

48. Petal pubescence: petal glabrous (0); petal with hairs in upper third (1); petal with 1 row of hairs (2). Pubescence is particularly variable on the external as well as the internal surfaces of the petals. External pubescence was very variable on the same individual at anthesis and was thus not taken into consideration. The exact nature of the trichomes occupying the internal face was not established with precision but in *Anacolosia*, *Cathedra*, and *Phanerodiscus* they appear as two types. Those adjacent to the stamens are likely glandular (but were not coded here), whereas the uniserial trichomes were coded.

Androecium

49. Stamen number: three (six including staminodes) (0); four (eight including staminodes) (1); five (ten including staminodes) (2); twelve to twenty (3).

50. Stamen whorls: one (0); two (1); three (2). The number of staminal cycles was calculated by taking into account possible staminodes and the merosity of the flowers. In the case of *Olax*, the total number of stamens and staminodes is in general not proportional to the number of petals (five), but always lies between seven and ten. The flowers of this genus were regarded as having an androecium composed of two cycles.

51. Stamen position relative to corolla: alternate and opposite (0); opposite only (1). For Olacaceae we tried to identify epipetalous stamens and alternipetalous stamens, but, in various genera this distinction proved to be impossible to realize in the absence of fresh material and a study of floral development. Thus, for flowers of *Scorodocarpus*, two stamens are fused with each petal and are placed at equal distance from the edges of the petal. For *Olax*, a similar phenomenon is observed, which becomes complicated because of the probable absence of certain parts of the androecium. In these last two cases, stamens were regarded as only opposite.

52. Staminodia: absent (0); present (1). The presence of staminodia provides a means of distinguishing the genera of tribe Olacaceae. Other genera (e.g. *Ongokea*) have at the base of the staminal column either staminodia or a divided disc, depending upon interpretation. Similarly, the condition in Opiliaceae can be interpreted as staminodia (Kuijt 1969) or a divided disc (Hiepko 2000). In all such cases, our coding follows the latter interpretation.

53. Filament: free (0); fused (1). The mutual fusion of the fila-

ments of stamens (synadelphous or monadelphous) is characteristic of a small number of genera: *Aptandra*, *Harmandia*, and *Ongokea*.

54. Anther connective: typical (0); prolonged to a point or thickened (1). The top of the stamen connective is generally blunt and without excrescences, but for *Anacolosia* and *Cathedra* it is pubescent, whereas for *Diogoia*, *Tetrastylidium*, and *Engomegoma* it is pointed.

55. Anther attachment: dorsifixed (0); basifixed (1); oblique (2); other (3). The state "oblique" was applied to the very short anther of *Chaunochiton* whereas "other" was applied to members of tribe Aptandreae where stamens are fused by their filaments.

56. Anther dehiscence: slit (0); pores (1); flaps (2); disaggregation (3). Anther dehiscence is generally longitudinal but poricidal for tribe Aptandreae. For Anacoloseae and *Chaunochiton*, dehiscence is valvate. *Curupira* has a curious short longitudinal dehiscence that does not appear to be the result of mechanical tearing but a disaggregation of the tissue that exposes the interior of the thecae.

57. Direction of anther dehiscence: introrse or lateral (0); extrorse (1).

Gynoeceum

58. Accrescent disk: absent (0); present (1). The disc corresponds either to glandular tissue surrounding the ovary (*Strombosia*), or located below it (*Olax*), or with a cup into which the petals and stamens are inserted (*Anacolosia*, *Cathedra*, *Phanerodiscus*). Thus, the disc is a descriptive term used to indicate an often glandular structure of the flower (see also character 59). Accrescence of the "disk" applies only to a cup into which the corolla and androecium are inserted. For *Phanerodiscus*, Capuron (1968) and Malécot et al. (2003) showed that neither the calyx nor the disk are accrescent, but a structure indiscernible in the flower at anthesis.

59. Glandular tissue (disk): between stamens and ovary (0); between stamens and petals (1); none (2). In this analysis, we code only glandular tissue that correspond to structures of reduced size, that are separate from the ovary (not fused as in *Strombosiosis*), and that are not being used as support for the stamens and the petals (as in *Anacolosia*, *Cathedra*, and *Phanerodiscus*) (see also character 58).

60. Style shape: long conical (0); cylindrical short (1); cylindrical long (2); short conical (3). Although style shape may be influenced by the position of the ovary (inferior or superior), the relative length of the style was established by taking into account the relationship between the distance from the top of the locules of the ovary to the stigma and the diameter below the stigma. When this ratio is lower than six, the style was regarded as short. The values used were measured on rehydrated floral material at anthesis (long-styled flowers in the case of the genera with heterostylous flowers). Heterostyly is mentioned or supposed for several genera of Olacaceae (Michaud 1966; George 1984; Sleumer 1984a, 1984b), in which case only longistylous material was used for coding.

61. Stigma length: small globular (0); elongated (1). The length of the stigmas was measured on the same material used for coding character 60. The elongated character state occurs only in the out-group (stigmas of more than 1 mm in length). The micromorphology of the stigmas was not studied.

62. Ovary position: hypogynous (0); epigynous (1); half inferior (2). The position of the ovary was observed on rehydrated flowers obtained from herbarium samples or was determined from the literature (*Douradoa*). *Schoepfia*, sometimes described as having a half inferior ovary, was regarded as having an inferior one.

63. Ovary locule number: five (0); four (1); three (2); two (3); one (4). The number of locules at the base of the ovary is based on the data available in the literature, in particular Fagerlind (1946, 1947, 1948) and Sleumer (1984a, 1984b). The reliability of this information is doubtful for some and unknown for other genera.

64. Integument number: two (0); one (1); none (2). Given varying accounts in the old literature, only the indications provided by Bouman and Boesewinkel (in Breteler et al. 1996) were used in coding. The genera for which variation exists (cf. Sleumer 1984b) were coded as polymorphic.

Fruit

65. Starch in fruit: absent (0); present (1). The nature of the reserves of the fruit was coded according to the data available in the literature (Michaud 1966; Hegnauer 1966, 1969, 1973, in Sleumer 1984a, 1984b). This character was used by Engler (1897) to distinguish the subfamilies of Olacaceae. In general, starch and/or lipid quantity is not known and, according to Sleumer (1984b), varies in the same genus and even in the same species. Thus some taxa that were recorded as lacking either starch or lipid may contain these, as well as other types of seed reserves. Despite the absence of data for some taxa, the presence/absence of starch and lipid (character 66) was coded.

66. Lipids in fruit: absent (0); present (1).

Pollen

67. Pollen shape: equiaxial (0); longiaxial (1); breviauxial (2). The ratio of the distance between the poles and the equatorial diameter of the pollen grains results from the observations of Lobreau-Callen (1980, 1982). The values used to distinguish the three character states are those recommended by Punt et al. (1994).

68. Pollen symmetry: isopolar (0); heteropolar (1). Work by Feuer (1977), Lobreau-Callen (1980, 1982, in Sleumer 1984b, in Breteler et al. 1996) and Hiepko and Lobreau-Callen (in Maas et al. 1992) showed that the pollen of certain Olacaceae was asymmetrical.

69. Mesocolpium shape: flat or convex (0); concave (1). According to Lobreau-Callen (1980), the pollen of Aptandreae has a concave mesocolpium, a unique feature in Santalales.

70. Apocolpium shape: convex (0); concave (1). Concave apocolpium is a distinctive feature of tribe Aptandreae.

71. Aperture number: three to four, zonoaperturate (0); six, diploporate (1); more than six, periaperturate (2). In Santalales, the number and position of the apertures are linked: pollen grains with three or four apertures are always zonoaperturate, those with six apertures are always diploporous, and those with more than six apertures (*Misodendrum*) are periaperturate. In some genera, the number of apertures varies between three or four for pollen derived from the same anther, but these are zonoaperturate pollens.

72. Ectoaperture shape: elongate (furrow) (0); round (porous)

or elliptic (1). The ectoaperture of Olacaceae can either be lengthened perpendicular to the equator (furrow), or circular or elliptic.

73. Apertural membrane: smooth or scabrous (0); granular or verrucose (1).

74. Endoaperture shape: elliptic (0); circular (1). The endoaperture can be lengthened perpendicular to the equator, or circular. The absence of endoapertures for certain Opiliaceae prevented coding this character for some taxa, and they were scored as inapplicable.

75. Relative size of the endo- and ectoaperture: ecto- and endoaperture of distinct size (0); ecto- and endoaperture of identical size (1).

76. Endoaperture granules: none and endoaperture smooth (0); present and endoaperture smooth (1); none and endoaperture with endosculpture (2). Lobreau-Callen (1980, 1982) showed that the pollen endoapertures of Olacaceae could be ornamented. Presence of granules in the endoaperture was coded but not other modifications of the nexine (such as endosculpted nexine instead of a true endoaperture).

77. Exine in mesocolpium: smooth or microperforate tectum (1); reticulate exine (1); echinulate tectum (2); other (3). In the mesocolpium and apocolpium the exine can correspond to a continuous tectum with rare perforations, with a microperforate or perforated tectum or with a network (Lobreau-Callen 1980, 1982). However, the transition between these various types is almost continuous and combines two elements, the size of the perforations and the density of the perforations. The terminology used here corresponds to extremes but is not easily applicable to certain intermediate forms.

78. Granules in infratectum: absent (0); present (1). According to Lobreau-Callen (1980), the structure of the infratectum makes it possible to distinguish various groups of Olacaceae. In certain genera this layer consists of individualized grains laid out in several layers, in others only one layer of grains exist, which tend to form columellae (*Anacolosia*, *Aptandra*, *Ptychopetalum*), or individualized columellae (*Chaumochiton*). Homology among these features is not clear and two characters were defined, one for the presence of granules whatever the number of layers, and one for the coding presence of columellae-like structures (character 79).

79. Columella in infratectum: absent (0); present (1).

80. Foot layer surface: smooth (0); irregular with masses (1). Lobreau-Callen (1980) use the foot-layer as a distinctive feature to separate two main set of Olacaceae. Despite the relatively low number of taxa for which this information was available, it appears useful for characterizing some groups among Olacaceae. Various other structural characteristics of the plate and the endexine were highlighted by Feuer (1977) and Lobreau-Callen (1980). These characters are available only for the small number of genera that have been studied using transmission electron microscopy.

APPENDIX 2. Data matrix analyzed in this study. Abbreviations: A = 0 or 1; B = 1 or 2; C = 0 or 2.

	123456789	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777
		0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
Viscaceae								
<i>Korthalsella complanata</i>	101??002	00?1000010	?0??000000	10?1000000	??10110000	01000?0002	?014201000	0001?002????
<i>Notothixos leiophyllus</i>	100011002	00?1000010	?0??000000	10?1000000	??10110000	01000?0002	?014201000	0001?002????
<i>Phoradendron californicum</i>	10A011002	00?1000011	?011000000	10?01-0000	??10110000	01000?0002	?014201000	0001?002????
<i>Phoradendron serotinum</i>	10A011002	00?1000011	?011000000	10?01-0000	??10110000	01000?0002	?014201000	0001?002????
<i>Viscum album</i>	10A011002	00?1000010	?011000000	10?1001000	??1011000A	01000?0002	?014201000	0001?002????
<i>Viscum articulatum</i>	10A011002	00?1000010	?011000000	10?1001000	??1011000A	01000?0002	?014201000	0001?002????
Santalaceae								
<i>Acanthosyris aspapote</i>	000111002	00?1000010	?011000000	11001-A101	??00010002	01000?0000	?014201000	0011?100????
<i>Buckleya distichophylla</i>	100011012	00?1000010	?011000000	11101-010?	??10010001	01000?0002	?014201000	0001?005????
<i>Colpoen compressum</i>	100??0002	00?1000010	?0?000010	1?101-110?	??00010001	01000?0002	?014201000	0001?001????
<i>Exocarpos bidwillii</i>	001011102	00?1000010	?0?000010	1?101-1100	??10010002	01000?0002	?014201100	0001?005????
<i>Okoubaka aubrevillei</i>	100011002	00?1000010	?0?000010	1?001-0000	??10010012	01100?0000	?014201000	00001000010?
<i>Osyris lanceolata</i>	000??0002	00?1000010	1011000010	1?101-1100	??1001000A	01000?0002	?014201100	0001?0000????
<i>Pyrrularia pubera</i>	000111012	00?1000010	?0?000000	10001-210?	??10010002	01000?0002	?014201010	00A1?100????
<i>Rhoicarpus capensis</i>	100??0002	00?1000010	?0?000010	1?101-110?	??0001000B	01000?0002	?014201000	0001?0000????
<i>Santalum album</i>	100A11002	00?1000010	?0?000010	1?101-1100	??00010001	01000?0002	2014201000	00110104????
<i>Scleropyrum pentandrum</i>	000??0002	00?1000010	?0?000010	1?001-210?	??00010002	01000?0002	?014201000	00A1?1000????
<i>Thesium humifusum</i>	000?11002	00?1000010	10??000010	1?101-110?	??0011001B	01000?0002	?014201011	0011?101????
Oplilaceae								
<i>Agonandra macrocarpa</i>	010011000	0011000000	0100?00010	1000001100	??101013--01	01000?0000	1014201000	00010?20000
<i>Champercia maritima</i>	000011000	0011000001	0100?00010	1000001110	??0003--02	01000?0000	1014201000	0001--001010
<i>Opilia amentacea</i>	010011000	0011000000	0110?00010	1010001110	??0003--02	01000?0000	1014201000	000110001010
<i>Pentstemonopilia marquetii</i>	000011000	0011000000	0100?00010	1000001100	??0003--02	01000?0000	1014201000	0001--001010
<i>Rhopalopia umbellata</i>	000011010	0011000001	0100?00010	1000001100	??0013--01	01000?0000	1014201200	000100021010
<i>Urobraya siamensis</i>	000011010	0011000001	0100?00000	1000001100	??0013--02	01000?0000	1014201200	000100001010
Loranthaceae								
<i>Dendrophthoe lepidota</i>	100011002	00?1000010	1000000000	10010000100	??01020202	01000?0002	?014201200	0101?002????
<i>Ligaria cuveifolia</i>	100??0002	00?1000010	?0??000000	10010000100	??01020202	01000?0002	?014201201	0001?005????
<i>Tripodanthus flagellaris</i>	100??0002	00?1000010	?0??000000	100?0000100	??0102020?	01000?0002	?014201201	0001?002????
<i>Tupelia antarctica</i>	100011002	00?1000010	1000000000	1??0???????	??1?2020??	01??0?0002	?014201200	0101?000????
Misodendraceae								
<i>Misodendrum brachystachyum</i>	000011010	00?1000001	0110?00000	11010000100	??1013--00	01100?0002	1014201000	0211211200?
Oleaceae								
<i>Anacolsa frutescens</i>	000111010	1001000001	0011000000	101101A000	0000010112	0100111012	20031?1200	01111110110
<i>Aptandra tubicina</i>	000111001	0001000010	0000000000	1010001000	0001110001	0101032101	2003B11211	10111110110
<i>Catheda acuminata</i>	000111010	1111000001	1011000000	101101A000	A000010012	0100101012	2003110200	0111111010?
<i>Chaunochiton kappleri</i>	000111010	0111000010	0011000000	1011001100	1001011112	0100022102	2003B?1200	00000003010

APPENDIX 2. Continued

	111111111	222222222	333333333	444444444	555555555	666666666	777777777
	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
<i>Coula edulis</i>	010000102	001121101	0001012000	1100010003	B00000002	3002011010	0000-000001
<i>Curipira tefensis</i>	000111000	0001110010	1010001100	1100110011	1000013002	0001?01000	0001-000?0
<i>Doucoa zenkeri</i>	000001000	0011?2111	0100012100	1000010002	0100010002	30001?0000	000100001100
<i>Diouraea consimilis</i>	000111000	0001?10010	10101-1000	1100110011	0000010?02	000?101000	000100001100
<i>Dulacia candida</i>	000111010	0000100010	10100001101	1101211100	0110000002	2002B1A200	00111110101
<i>Engomegoma gordonii</i>	000?0000	0111?2111	0?00012000	100011000B	0100110002	30011?0A0	000100001010
<i>Erythrapalum scandens</i>	000001000	0011?22001	A0A112000	1000000A12	0100010002	1002101000	00010000010
<i>Harmantia mekongensis</i>	000111001	0000000010	1011003100	1101110201	0101032101	2004B01211	10111110110
<i>Heisteria concinna</i>	000001000	1011122211	0B00112000	0000001A22	1000000002	3002011???	00????????
<i>Heisteria parvifolia</i>	000AA1000	0111122211	0B00112000	0000001A22	1000000002	3002011010	000100000100
<i>Mabourea trinervis</i>	010001000	0011?2111	0000012000	1100000112	1000000002	10020?010	000100001???
<i>Malania oleifera</i>	000111000	0001?10010	1010003100	1100100001	1000000002	000??1210	000000000???
<i>Minquartia guianensis</i>	010001102	0011122201	0001012000	0100010112	1000000002	3001010000	000000000000
<i>Ochanostachys ameritacea</i>	000000102	0011121101	0001012000	1100110001	B000000000	3002010010	0001-000001
<i>Octoknema dinklagei</i>	020001000	0011222201	0101112000	?110020002	0100000000	3002A?000	0001-110110
<i>Olax subscorpioides</i>	000111010	0000000001	1010001101	1101211120	10100010000	2002B01200	00111110101
<i>Ongokea gore</i>	000111000	0000000010	1010003100	1?01110002	0111032101	2004B?1211	10111110111
<i>Platanodiscus perrieri</i>	000111000	0000?00000	1001000000	1100C00012	0100011102	2003??1201	01111110110
<i>Psychotepalum petiolatum</i>	000111010	0000100000	1011003101	1001010012	100001000?	2004201200	01111110101
<i>Schoepfia schreberi</i>	000001000	0000000001	0001000000	?000020222	01000?0000	1012101010	000110000100
<i>Scorodocarpus bornuensis</i>	000001000	0011222201	0001012000	1101010012	1100010000	2002A10010	000100000100
<i>Strombosia jamaica</i>	000001000	1011122201	0101012000	1101010012	0100000002	2024110000	000100001010
<i>Strombosiaopsis tetrandra</i>	000001A00	1011122101	0101012000	1001110010	0100010000	30211?000	000100001100
<i>Tetrastylidium peruvianum</i>	000001000	1011121101	0101012000	0000110101	0100100002	1001101000	000100000100
<i>Ximenea americana</i>	000111000	0001110010	100001-1100	1001110011	1000010002	00040010A0	000100000111
outgroups							
<i>Daphniphyllum pentandrum</i>	000??0100	10??2?011	02001-1000	??0??00???	?00?0?00?	?10000????	00????????
<i>Rhabdodendron amazonicum</i>	020??0101	1011222210	0210002000	0000010003	2000110002	11140?0000	0001????1???