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TAXONOMY

A revised classification of Santalales

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Abstract We present here a revised classification of Santalales, an angiosperm order that contains 18 families, 160 genera, and over 2200 species. Both nonparasitic and parasitic flowering plants occur in the traditionally circumscribed family Olacaceae whereas all other families are composed entirely of parasites. The five evolutionary radiations of aerial parasitism produced mistletoes that constitute most of the generic and specific diversity seen in the order. This classification, although based primarily upon results from molecular phylogenetic investigations, brings together all currently available information that contributes to our understanding of relationships among these plants. Monophyletic groups (clades) obtained from molecular analyses were named using a Linnaean ranked system. Four new families are named that formerly resided in Santalaceae s.l.: Amphorogynaceae, Cervantesiaceae, Comandraceae, and Nanodeaceae. A new tribal and subtribal classification for Loranthaceae is presented where nine new subtribe names are proposed.

Keywords classification; mistletoe; monophyletic; parasitic plant; sandalwood order

INTRODUCTION

It has been over one decade since the emergence of the first classification of flowering plants based entirely on phylogenetic principles (APG, 1998). That work was made possible by the availabilty of hundreds of DNA sequences whose analyses provided new insight into higher-level relationships among angiosperms. Indeed the continued rapid assembly of data prompted a revision of the original classification system (APG, 2003) such that now nearly all angiosperm orders and families have been placed in the phylogenetic scheme. It was acknowledged that the monophyly of many families remained in question, thus calling for additional molecular phylogenetic investigations. This paper represents a response to that challenge, i.e., the application of a molecular phylogenetic approach to one of the major angiosperm clades: Santalales. This study utilizes existing molecular and morphological data and generally follows the APG system philosophy in recognizing only monophyletic groups. Moreover, the arrangement of these clades is translated into a hierarchical classification system that uses Linnaean ranks. Because of the tremendous predictive value inherent in the resulting classification, we envision it will be useful not only for plant systematists but also for those working in other biological science subdisciplines.

TRADITIONAL TAXONOMIC TREATMENTS OF SANTALALES

Although various works were in existence in the early and mid 1800s, we will begin our taxonomic discussion with works from the end of that century. A number of descriptive treatments of various families and genera of Santalales were published in the late 1890s by Tieghem (e.g., 1895a, 1896, 1897, 1899a). This information, plus the contributions of German scientists such as Engler (1897a,b,c) and Hieronymus (1889a,b), resulted in the first comprehensive taxonomic treatment of Santalales in *Die natürlichen Pflanzenfamilien*. A later iteration of this series included treatments of Olacaceae (Sleumer, 1935a) and Opiliaceae (Sleumer, 1935b), Octoknemaceae (Mildbread, 1935), Misodendraceae (Skottsberg, 1935), Loranthaceae (Engler & Krause, 1935), and Santalaceae (Pilger, 1935). The holoparasite families Rafflesiaceae and Hydnoraceae were placed in Aristolochiales and Balanophoraceae in Balanophorales, orders that followed Santalales (Harms, 1935).

Prior to the use of DNA sequence data, numerous phylogenetic hypotheses have been proposed for relationships within Santalales as well as between this order and other flowering plants. The classification in Schultze-Motel (1964) essentially followed the treatment in *Die natürlichen Pflanzenfamilien* listing Olacaceae (including Octoknemaceae), Opiliaceae, Santalaceae, Misodendraceae, and Loranthaceae, as well as the nonparasitic families Dipentodontaceae and Grubbiaceae. Dipentodontaceae is now placed in Huerteales (Worberg & al., 2009) and Grubbiaceae in Cornales (APG, 2003). In the Schultze-Motel system, Santalales were followed by Balanophorales (with one family of holoparasites, Balanophoraceae). Although the concept of an affinity dates to the 19th century, Cronquist (1981) was apparently influenced by the work of Fagerlind (1948) in that both workers derived Balanophoraceae from within Santalales. Other authors, such as Thorne (1983), Dahlgren (1983), and Takhtajan (1980) placed Balanophorales immediately following Santalales. Further variation is apparent in the classification of the holoparasitic order Rafflesiales (Rafflesiaceae plus Hydnoraceae). Cronquist (1981) placed this order in subclass Rosidae (allied with Santalales) whereas most other authors placed it with magnoliid angiosperms. Also included in Santalales by Cronquist (1981) were Dipentodontaceae and Medusandraceae. The latter is now placed in Peridiscaceae of Saxifragales (Soltis & al., 2007).

In addition to the holoparasites, various relationships within and among the remaining families of Santalales have also been suggested. Most authors (e.g., Kuijt, 1968, 1969) considered Olacaceae as the most plesiomorphic family in the order because some of its members have bisexual, dichlamydous, hypogynous flowers and because of the presence of both nonparasites as well as hemiparasites. But as reviewed in Malécot & al. (2004), the exact composition of Olacaceae has been extremely variable historically. A number of families, such as Aptandraceae, Erythropalaceae, Octoknemaceae, Opiliaceae, and Schoepfiaceae, have either been considered a component of, or distinct from, Olacaceae.

The mistletoe habit has also overly influenced workers in classifying together those plants sharing this habit. The most frequent case of this is Loranthaceae that sometimes also includes Viscaceae. The New World mistletoe family Eremolepidaceae (Kuijt, 1988) has had a varied taxonomic history with its component three genera at some time residing in either Loranthaceae, Viscaceae or Santalaceae. The underlying cause for such discrepancies in classification is that various workers have focused upon different characters that they considered "key." For example, Fagerlind (1948) associated Opiliaceae with Misodendraceae owing to their shared "amentiferous" inflorescence. Kuijt (1968) derived Eremolepidaceae from Olacaceae via *Opilia* (Opiliaceae) following this same line of reasoning. Another example is the rationale for drawing a relationship between Rafflesiales and Santalales. Although Cronquist (1981) could cite few characters in common, he focused upon the tendency toward simplification of the ovules, despite the admission that this reflected parallel adaptations to parasitism. He then stated (p. 698) that "parallelism in a number of features is in itself some indication of relationship, to be considered along with other evidence." Without robust phylogenetic analyses, it is extremely difficult to determine which morphological characters are "key" and when attempting to delimit taxa using such characters, polyphyletic groups inevitably result (Chase & al., 2000). An aim of the molecular phylogenetic approach is to bypass this process and obtain empirical data that allow one to address common ancestry and the actual level of genetic divergence among the taxa.

■ MOLECULAR PHYLOGENETIC STUDIES OF SANTALALES

The most recent broad-scale molecular phylogenetic studies of angiosperms resolve Santalales as monophyletic with high support, but the placement of this clade among other angiosperm clades was uncertain (Hilu & al., 2003; Soltis & al., 2000, 2003). In these early studies, Santalales emerged from a polytomy with Berberidopsidales, caryophyllids, Saxifragales, rosids and asterids (Judd & Olmstead, 2004). More recently, a molecular phylogenetic study was conducted that utilized over 66 kb of chloroplast sequence data (all protein-coding and four rRNA genes) for 86 angiosperms (Moore & al., 2008). That study gave strong support to the successive sister relationships of Santalales and Berberidopsidales to the Caryophyllales + asterid clade. The four-gene analysis of Soltis & al. (2003) obtained similar relationships but without support, thus this is at present the best hypothesis for the position of Santalales among eudicots.

The first molecular phylogeny of Santalales sampled only four members of this order but documented the utility of nuclear small-subunit (SSU) ribosomal DNA sequences (Nickrent & Franchina, 1990). In a study that compared molecular evolutionary features of SSU rDNA and chloroplast *rbcL* among 62 angiosperms, 15 were from Santalales (Nickrent & Soltis, 1995). That study documented increased substitution rates in SSU rDNA in these parasitic plants, a feature that allowed the resolution of relationships at approximately the same level as *rbcL*. Although taxon sampling was still modest, that study showed a sister relationship between Viscaceae and Santalaceae, the association of Eremolepidaceae with Santalaceae, and the presence of a clade composed of *Schoepfia*, Loranthaceae and Misodendraceae. The following year witnessed the steady accumulation of DNA sequences for additional taxa. An SSU rDNA phylogeny that included 62 members of Santalales was presented by Nickrent & Duff (1996). The first analysis that concatenated SSU and *rbcL* sequences was by Nickrent & al. (1998) wherein a maximum parsimony tree with 37 taxa of Santalales was shown. Strong support was obtained for the monophyly of Loranthaceae, Opiliaceae, and Viscaceae, but Olacaceae and Santalaceae were paraphyletic. Nickrent & Malécot (2001) analyzed SSU and *rbcL* sequences from 54 of the 160 total genera in the order. This increased sampling, focused mainly upon Olacaceae and Santalaceae, allowed additional resolution of clades within these groups, although relationships among the clades along the "spine" of this tree remained poorly resolved. It became apparent that DNA sequences from more rapidly evolving genes would be required to break these polytomies.

Since 2001, phylogenetic studies have been conducted that focused upon relationships within the three largest families: Olacaceae, Santalaceae, and Loranthaceae. In addition to DNA sequences from SSU rDNA and *rbcL*, additional genes have been sampled for these families including chloroplast *matK*, the *trnL-F* region, and *accD* as well as nuclear large-subunit (LSU) rDNA. A molecular phylogeny is now available for Olacaceae that includes all but two genera (Malécot & Nickrent, 2008). Complete generic-level sampling was achieved for Santalaceae and a three-gene concatenated dataset yielded strong support for eight clades (Der & Nickrent, 2008). A molecular phylogeny of all eight species of *Misodendrum* has also been published (Vidal-Russell & Nickrent, 2007). Past molecular phylogenetic work showed that aerial parasites evolved five times independently in Santalales (Nickrent, 2002), but the relative timing of these diversifications was not addressed. Vidal-Russell

& Nickrent (2008b) showed that *Misodendrum* was the first santalalean lineage to evolve the mistletoe habit (ca. 80 Ma) followed by Viscaceae (72 Ma), eremolepidaceous mistletoes in Santalaceae (53 Ma), tribe Amphorogyneae in Santalaceae (46 Ma), and lastly Loranthaceae (28 Ma). The topology of the five-gene tree that included 39 santalalean taxa was essentially fully resolved. A molecular phylogeny of the largest mistletoe family, Loranthaceae, has been generated using multiple gene sequences from 60 of the 73 genera (Vidal-Russell & Nickrent, 2008a). Major findings were that *Nuytsia* was sister to the remaining genera in the family, that aerial parasitism arose once, and that base chromosome numbers correlate well with clades on the tree. One of the most surprising results of molecular phylogenetic work on the holoparasite families Cynomoriaceae and Balanophoraceae was the discovery that the latter family is apparently related to "core" Santalales (Nickrent & al., 2005). This relationship was seen with both nuclear and mitochondrial genes, however, sampling was insufficient to pinpoint the exact phylogenetic placement. The result has been independently corroborated (Barkman & al., 2007; Su & Hu, 2008).

DNA sequence data have been analyzed for most genera in Santalales. Although some relationships remain to be resolved (such as with Balanophoraceae), support is high for a number of major clades. It is therefore timely to draw together the molecular and morphological data on these santalalean clades and propose a revised classification for the entire order.

■ FEATURES CHARACTERIZING SANTALALES

The presence of unusual fatty acids may be a synapomorphy for Santalales. Long chain polyunsaturated fatty acids, such as minquartynoic, ximeninic or santalbic acids, that are otherwise rare or nonexistent in other angiosperms are found here (Hopkins & Chisholm, 1969; Spitzer & al., 1994, 1997; Orhan & Orhan, 2006; Butaud & al., 2008).

One of the few morphological features that appears to be a synapomorphy for the order is free central placentation with the ovules arranged in a pendulous fashion from the apex of the central column. This type is best developed in Olacaceae and Santalaceae (both s.l.), but it has various modifications such as reduction of the placental column. These reductions are most obvious in viscaceous mistletoes where there is no placenta *per se* but a mound of tissue traditionally called the mamelon (= placental nucellar complex) in which the one functional megaspore mother cell is embedded. A similar reductional trend can be seen in the placenta of various Loranthaceae. In some taxa, such as *Helixanthera*, the placenta is completely absent and the archesporial cells differentiate at the base of the ovarian cavity (Maheshwari & al., 1957; Bhatnagar & Johri, 1983). Apparently not acknowledging the potentiality of convergence or parallelism, Fagerlind (1948) used such data to propose a phylogenetic tree where Balanophorales were derived from within Loranthaceae.

Another rather peculiar feature that occurs throughout various members of the order is the growth of embryo sac cells outside the ovule and in some cases for considerable distances within the style. This "aggressive" embryo sac behavior is seen in *Olax* (Agarwal, 1963), various Loranthaceae (Bhatnagar & Johri, 1983) and Santalaceae (Rao, 1942).

The flowers in Santalales can be dichlamydous or monochlamydous with either superior or inferior ovaries. When these two features are examined in the context of a molecular phylogenetic tree, the general trend is toward monochlamydous flowers with inferior ovaries as one progresses to more derived taxa (e.g., Viscaceae). That the dichlamydous perianth in many members of Olacaceae s.l. represent sepals and petals has not been questioned, but interpretations begin to diverge when only one perianth whorl exists. In such monochlamydous flowers, the perianth is then either referred to as sepals, petals, or noncommittal terms such as perigone and tepal (Dawson, 1944; Hiepko, 2000). In several santalalean groups, particularly Olacaceae s.l., Schoepfiaceae, Opiliaceae, and Santalaceae s.l., protruberances that alternate with the perianth lobes may occur at the top of the inferior ovary. This structure has been called the calyculus, but whether it is homologous with the calyx (in santalalean taxa where that floral whorl is fully developed) has been contentious. The floral anatomical work of Patil & Pai (1984) demonstrated that the calyculus receives vascular traces, hence they designated this whorl a true calyx, in agreement with Agarwal (1963) and Smith & Smith (1943). Others such as Baillon (1862), Eichler (1878), Engler & Krause (1935) and Schaeppi (1942) consider it as an outgrowth of the floral axis, dilation of the peduncle or even an organ *sui generis* (Maheshwari & Singh, 1952). Bentham & Hooker (1883) as well as most modern workers (Stauffer, 1961a; Patil & Pai, 1984; Endress, 1994; Kuijt, 2003; Der & Nickrent, 2008) regard the calyculus as a remnant of a reduced calyx. An alternative view, that the calyculus is actually of bracteolar (prophyllar) origin, was put forth by Venkata Rao (1964) and this idea is also being advanced by Ronse De Craene (2007) and collaborators. Until detailed evolutionary developmental data have been collected, we will here consider the calyculus homologous with the calyx. When only a single floral whorl is present, we interpret this as the corolla. In most santalalean taxa, the petals are valvate, often with an uncinate thickening at the tip. Stamens are frequently epipetalous and this adnation may occur only very slightly at the base of the corolla or the staminal filament may fuse with nearly the entire length of the corolla tube.

Stauffer (1961a) interpreted the three staminal whorls seen by Valeton in Olacaceae such as *Coula* as two-whorled, with the numbers increased by fission of initials in the inner whorl. Thus, he argued that the basic Bauplan for Santalales was the diplostemonous condition (i.e., the outer staminal whorl opposite the sepals, inner opposite the petals). This basic plan is seen in *Heisteria* and *Ximenia*, but more advanced genera such as *Schoepfia* have lost the outer, antesepalous whorl leaving only the antepetalous whorl. These haplostemonous flowers are then found throughout all remaining families of Santalales. The genus *Olax* and its relatives present floral variants that may represent natural genetic mutants useful in tracing evolutionary and developmental changes. In *Ptychopetalum*, only three of the five outer whorl (antesepalous) stamens are staminodes, the other two remain fertile. In species of *Olax*, the outer whorl is usually converted to staminodes and some of these may be lost. For example, in *O. tessmannii* Engl. (a 6-merous species), three of the six staminodes remain whereas in 5-merous species such as *O. subscorpioides* Oliv. and *O. laurentii* (de Wild.) Engl., two have been lost leaving three staminodes. In the 5-merous *O. scandens* Roxb. three stamens are fertile and five are staminodes. Moreover, two of the three fertile stamens are antesepalous and one occurs on the opposite flank of a petal along with a staminode. This petal also has two vascular traces instead of one. These observations, plus the fact that some *Olax* are hexamerous, compels one to consider that the floral plan of pentamerous species is pseudodiplostemonous, i.e., derived from a trimerous protype. This plan is likely the one followed by Caryophyllales (Ronse De Craene & al., 1998), which from recent molecular phylogenetic evidence (Moore & al., 2008; Soltis & al., 2003) is the next clade to evolve among the asterids after Santalales.

Published chromosome numbers have been compiled for all Santalales genera examined (Electronic Supplement to this article).

■ CLASSIFICATION PHILOSOPHY

In this paper we present a revised classification system for Santalales that incorporates molecular and morphological data. This classification is needed because relationships among all members of the order have not been addressed for many decades and none have used explicit phylogenetic principles. The major features of our classification system are based upon molecular phylogenetic trees, mainly because cladistic analyses of morphological characters are lacking for most groups (the exception being Olacaceae by Malécot & al., 2004). In addition to recognizing monophyletic groups, we have chosen to assign Linnaean ranks to various clades within the order (Freudenstein, 2005). Because of its size, we have also proposed infrafamilial ranks for the large family Loranthaceae. For families, we have followed Recommendation 16B.1 of the *ICBN* (McNeill & al., 2005) that advises authors to use the oldest name. These names were obtained primarily from Reveal (1997–) and from Hoogland & Reveal (2005).

Although we consider the assignment of ranks to be a somewhat subjective process, we also do not feel that a rank-free system (such as *PhyloCode*) will be fully accepted nor widely adopted in academic and nonacademic circles. We acknowledge that the Linnaean hierarchy has a number of inherent problems such as (1) insufficient ranks to encompass all clades on complex phylogenetic trees; (2) ranks being incomparable across different taxonomic groups; and (3) mandated name changes that cascade into other parts of the classification when taxa are reassigned (Pennisi, 2001; Withgott, 2000). The first problem is not an issue if one accepts that not all clades need to be named (APG, 1998). The second problem would remain even if ranks did not exist; e.g., informal names used for clades could still be used inappropriately, for example when comparing the extent of biodiversity across distantly related taxa. Although we can seldom be certain that a particular phylogenetic relationship is known, the third problem becomes less of an issue as clade membership is stabilized with increasing amounts of data. Our classification follows the nomenclatural philosophy described as "the monophyletic Linnaean position" (Stevens, 2006).

Classifications become most useful when they simultaneously serve many functions. This is true from a scientific perspective if they are maximally predictive for all biological disciplines and true from a practical perspective if they serve as a means to organize and retrieve information (e.g., herbaria, floras, GenBank, etc.). But as pointed out by Smith & al. (2006), traditional and molecular phylogenetic-based classifications are often incompatible if the principle of monophyly is adopted. They list three directions that can be taken when a traditionally recognized family resides within another (i.e., paraphyly): (1) recognition of paraphyletic families, (2) splitting to maintain monophyletic families, and (3) lumping one family into another. We agree that choice 1 is undesirable and acknowledge that picking between 2 and 3 depends partly upon taste. Although the lumping approach provides the "quick fix," diversity within the resulting family would likely result in the naming of additional, well-marked clades.

Criteria used to decide how to circumscribe families fall into several categories, but a beginning point for discussion can be taken from Backlund & Bremer (1998). Aside from the primary principle of monophyly, they list four secondary principles that involve maximizing (1) stability (= minimizing nomenclatural changes), (2) phylogenetic information (= minimizing redundancy), (3) support for monophyly, and (4) ease of identification (= recognizability). Stevens (pers. comm.) adds two more principles: (5) preservation of groups that are well-established in the literature and (6) family size optimization. Attempts to adhere to these principles were made in this work and specifics relating to particular decisions will be discussed below under "Perspectives on the New Santalales Classification".

■ CLASSIFICATION OF SANTALALES

The following reclassification of the monophyletic order Santalales contains 18 families, 160 genera, and over 2200 species. Balanophoraceae are not included at this time. This classification is summarized in the consensus phylogeny shown in Fig. 1. Because of its size, Loranthaceae are further classified into tribes and subtribes (Fig. 2 on p. 545).

1. Family Erythropalaceae Planch. ex Miq. (1856). — Three genera: *Erythropalum* Blume with one species, *E. scandens* Blume, of Indomalaysia; *Heisteria* Jacq. with ca. 33 species of tropical America and three African species; and *Maburea* Maas with one species, *M. trinervis* Maas, of Guyana.

Erythropalum is a woody climber with axillary tendrils whereas the other two genera are shrubs or trees. Because of its divergent habit, the affinities of *Erythropalum* have never been clear and have led many workers to isolate *Erythropalum* in its own family, Erythropalaceae. Plesiomorphic features shared by all three genera are alternate, simple, petiolate, exstipulate leaves, bisexual flowers, lack of a glandular disk, and

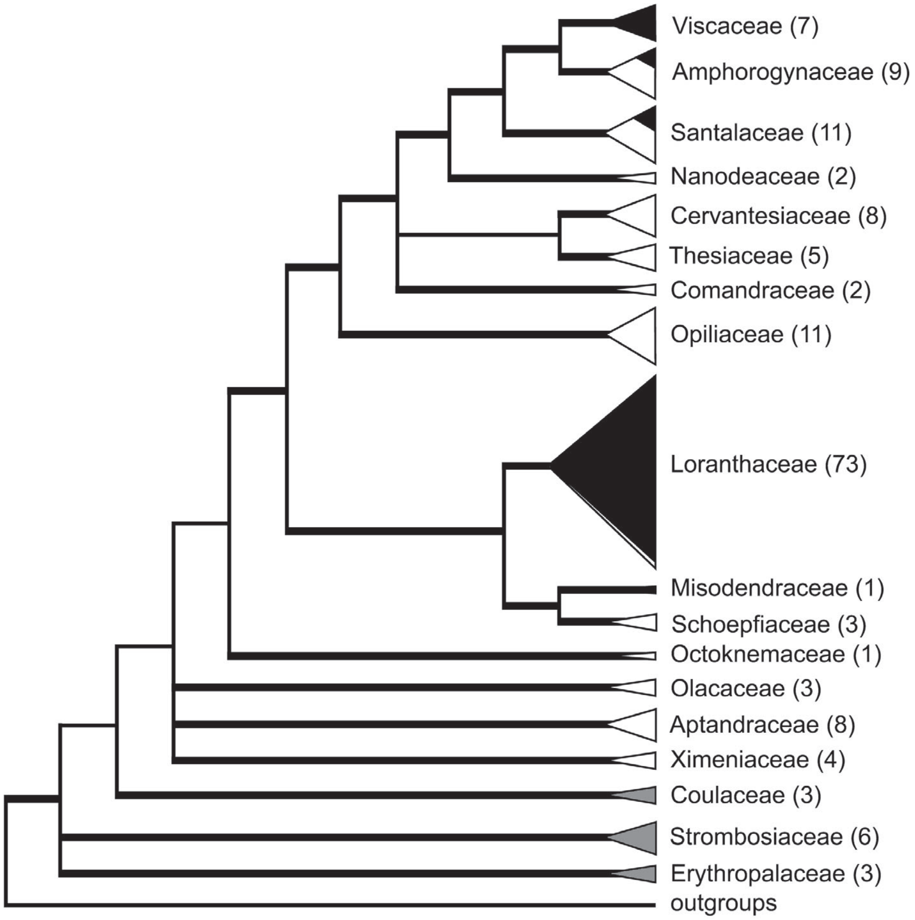

Fig. 1. Consensus phylogeny showing relationships among all families in Santalales. This tree summarizes results from several molecular phylogenetic investigations (Malécot & Nickrent, 2008; Der & Nickrent, 2008; Vidal-Russell & Nickrent, 2008a,b). Nodes resolved with 90%–100% bootstrap support and Bayesian posterior probabilties of 1.0 are shown with bold lines. The size of the triangle represents number of genera per family and the actual number is given in parentheses. Aerial parasitism is shown by dark fill within the triangles. Root parasites are depicted with white fill whereas nonparasites are shown in grey. The trophic natures of Octoknemaceae and Aptandraceae are currently unknown but are shown as parasitic assuming a single origin of parasitism and their positions on the tree.

hypogynous ovaries composed of three carpels. The pentamerous flowers may be diplostemonous or isostemonous with intercalary staminodes or scales (*Erythropalum* and *Heisteria asplundii* Sleumer) and the fruits have thin crustaceous endocarps. The accrescent calyx so characteristic of *Heisteria* is not present in the other two genera. In the mature fruit of *Erythropalum*, the bright red mesocarp splits into five reflexed valves that resemble the accrescent calyx of *Heisteria* and may serve a similar function in attracting fruit-dispersing birds.

The various anatomy- or morphology-based studies of Olacaceae have never clearly identify a group consisting of genera in this clade whereas it received strong support with Bayesian analyses of molecular data (Malécot & Nickrent, 2008). Maas & al. (1992) stated that wood anatomy links *Maburea* to *Heisteria* whereas palynology (Lobreau-Callen, 1980, 1982) and leaf anatomy (Baas, 1982) link it to tribe Couleae (here family Coulaceae).

2. Family Strombosiaceae Tiegh. (1899). — Six genera: *Diogoa* Exell & Mendonça with two species of tropical Africa; *Engomegoma* Breteler with one species, *E. gordonii* Breteler, of tropical Africa; *Scorodocarpus* Becc. with one species, *S. borneensis* Becc., of Malaysia; *Strombosia* Blume with three species of tropical Asia and six species of tropical Africa; *Strombosiopsis* Engl. with three species of tropical Africa; and *Tetrastylidium* Engl. with two species of South America.

Members of this family are shrubs or small to large trees with alternate, simple, petiolate, exstipulate leaves. Inflorescences occur in axillary or extra-axillary fascicles or short racemes. The flowers are bisexual, isostemonous (except *Scorodocarpus* where they are diplostemonous), pentamerous or tetramerous with valvate petals. The cup-shaped calyx may be accrescent (*Tetrastylidium*) or not (*Engomegoma*, *Scorodocarpus*), or with an accrescent conceptacle from the transformation of the pedicel/receptacle (*Diogoa*, *Strombosia*, *Strombosiopsis*). Petals, in some genera have an apiculate connective that exceeds the anther locules (*Diogoa*, *Engomegoma*, *Strombosiopsis*, *Tetrastylidium*). A glandular (but not accrescent) disk is present. Ovary position varies from superior to half-inferior or it may become inferior during fruit development (*Strombosia*, *Strombosiopsis*). The fruit is a drupe whose endocarp is woody and thick.

The Bayesian analysis of the three-gene dataset of Malécot & Nickrent (2008) gave only weak support for a sister relationship between Erythropalaceae and Strombosiaceae. Additional sequence data (nuclear 26S rDNA and chloroplast *accD*) was generated but for a subset of the taxa used in the above study. When combined with the three-gene data, analysis of the five-gene matrix yielded higher BS support for that clade. Moreover, this clade was also recovered in the cladistic analysis of Olacaceae using anatomical and morphological characters (Malécot

& al., 2004). A potential synapomorphy for the clade is anisocytic, cyclocytic stomata. If additional work further supports this relationship, recognition of one family, Erythropalaceae (with two subfamilies), may be justified.

3. Family Coulaceae Tiegh. (1897). — Three Old World genera: *Coula* Baill. with one species, *C. edulis* Baill. of tropical W. Africa; *Minquartia* Aubl. with one species, *M. guianensis* Aubl., of tropical America; and *Ochanostachys* Mast., with one species, *O. amentacea* Mast., in western Malaysia.

Members of this family are medium to large trees with alternate, simple, petiolate, exstipulate leaves. The family is marked by several anatomical synapomorphies such as leaf dendritic hairs, lignified secondary walls of the epidermis, leaf laticifers, and epidermal druses. Inflorescences occur as spike-like thyrses. The bisexual flowers are diplostemonous to polystemonous and tetra- or pentamerous. The sepals are developed and connate but do not form an accrescent calyx upon fruiting. The glabrous or pubescent petals may be apopetalous or sympetalous only at the base. Stamens occur in two and three whorls, the number equaling the number of petals or higher (staminodes sometimes present). A glandular disk is absent. The ovary is hypogynous with three and four locules. Fruits are medium to large drupes; those of *Coula* eaten by humans.

This very homogeneous group of three genera was recognized as early as 1899 (Tieghem, 1899a,b) and by subsequent workers (Sleumer, 1935a; Stauffer, 1961b) and was classified in tribe Couleae. Both morphological and molecular analyses (Malécot & al., 2004; Malécot & Nickrent, 2008) had high bootstrap support for the clade representing this family. Although the clade is clearly monophyletic, it emerges as part of a polytomy with the next three families.

4. Family Ximeniaceae Horan. (1834). — Four genera: *Curupira* G.A. Black with one species, *C. tefeenis* G.A. Black of Amazonian Brazil; *Douradoa* Sleumer with one species, *D. consimilis* Sleumer, of Brazil (Amapa, Para); *Malania* Chun & S.K. Lee, with one species, *M. oleifera* Chun & S.K. Lee, of W. Guangxi and eastern Yunnan provinces of China; and *Ximenia* L. with ten species in the Old and New World tropics.

Members of this family are shrubs or small to large trees with alternate, simple, petiolate, exstipulate leaves. *Ximenia* possess axillary spines and/or ramal thorns. Inflorescences are fundamentally umbellate (reduced to solitary flowers in some species of *Ximenia*). The bisexual, tetramerous flowers have sepals that are are partially or completely connate but do not become accrescent upon fruiting. Stamens occur in one or two whorls and staminodes are absent. The ovary is superior with a long conical style. Fruits are drupes with a thin pulpy pericarp and a crustaceous to woody endocarp.

No molecular data were available for the rare *Douradoa*, however, the cladistic analysis by Malécot & al. (2004) placed it in this clade. The fruits from *Malania* produce an edible oil, although it is more commonly used as a lubricant for machinery (Lee, 1980). Similarly, the fatty fruits of *Curupira* are used to make soap (Sleumer, 1984).

5. Family Aptandraceae Miers (1853). — Eight genera: *Anacolosa* (Blume) Blume with 16 species in the Old World tropics; *Aptandra* Miers with three species in tropical America and one in Africa; *Cathedra* Miers with five species in South America; *Chaunochiton* Benth. with three species in tropical America; *Harmandia* Pierre ex Baill. with one species, *H. mekongensis* Pierre ex Baill. in SE Asia and Malaysia; *Ongokea* Pierre with one species, *O. gore* Pierre in tropical West Africa; and *Phanerodiscus* Cavaco with three species endemic to Madagascar. Also, a monotypic genus from Honduras, *Hondurodendron urceolatum* C. Ulloa, Nickrent, Whitefoord & D. Kelly, has recently been described (Ulloa & al., in press).

All members are shrubs and trees with alternate, simple, petiolate, exstipulate leaves. DNA sequence data reported are available for all genera in the family and relationships are fully resolved (Ulloa & al., in press). Molecular analyses gave two clades within the family, the first composed of *Anacolosa*, *Cathedra*, and *Phanerodiscus.* Synapomorphies for these genera include lignified guard cells, petals with apical thickenings, porose anther dehiscence, prolonged anther connectives, and diploporate pollen. Both *Anacolosa* and *Cathedra* have an accrescent disk that surrounds the mature drupe. Although one would assume that *Phanerodiscus*, given its name, also has an accrescent disk, the situation in this genus is more complex. The disk tissue that is homologous with *Anacolosa* and *Cathedra* is not accrescent. Instead, tissues that are not present at flowering but develop upon fruiting between the disk and the calyx (the extradiscal and induvial cupules) expand greatly eventually forming inflated festoons that surround the drupe. Members of the second clade, with *Aptandra*, *Chaunochiton*, *Harmandia*, *Hondurodendron* and *Ongokea*, all have valvate anther dehiscence and an accrescent calyx. The genera *Aptandra*, *Harmandia* and *Ongokea* also share the character of fused staminal filaments, a glandular disk between the stamens and petals, and a concave apocolpium on the pollen. All members of the family have a basally bilocular ovary, alternate intervascular pits, and breviaxial pollen grains. It is of interest that the tendency towards accrescence in Aptandraceae occurs in all members but the affected tissues vary. The variation among taxa in the morphogenetic effect, from the inner (disk), to the middle (induvial cupule) to the outer (calyx) portions of the receptacle may represent a gradient response to a transcription factor. Unlike typical floral homeotic mutants, however, this process does not result in the loss of floral organs (or their transformation into another) but in the expansion of existing or novel organs.

6. Family Olacaceae R. Br. (1818), emend. — Three genera: *Dulacia* Sleumer with 13 species of South America; *Olax* L. with ca. 40 species in Old World tropics and Africa; and *Ptychopetalum* Benth. with two species in tropical South America and two in tropical western and central Africa.

Members of Olacaceae s.str. are trees, shrubs or rarely lianas with alternate, simple, petiolate, glabrous, exstipulate leaves. The elongate flowers (oval in bud) are pentamerous or sometimes tetra- or hexamerous. A calyx or calyculus is present (in *Olax* and *Dulacia*) which becomes accrescent, tightly surrounding the fruit. The androecium comprises two whorls that often include staminodes. A glandular disk is absent. The ovary is superior or half-inferior, composed of three carpels but with one locule. Fruits are drupes or pseudo-drupes, the latter term used by Sleumer (1984) to account for taxa with concrescent tissues.

This family, first recognized by Tieghem (1896), shares several anatomical (e.g., silica bodies in wood rays cells), morphological, and palynological synapomorphies (Malécot & al., 2004). Molecular data link the genus *Dulacia* to African members of *Olax* sect. *Triandrae* Engl. (Malécot & Nickrent, 2008). Indeed, a molecular phylogenetic investigation that includes robust sampling of both *Olax* and *Dulacia* is required to determine whether these two genera are distinct or not.

7. Family Octoknemaceae Soler (1908). — Monogeneric, with *Octoknema* Pierre having ca. seven species of tropical Africa.

Octoknema includes dioecious trees and shrubs with alternate, simple, petiolate, exstipulate leaves with stellate pubescence. The inflorescences are fasciculate and emerge from endogenous buds below the bark. Male flowers are pentamerous with small calyx teeth alternating between the valvate petals. A lobed glandular disk surrounds the pistillode. The pentamerous female flowers bear a staminode opposite each petal and have a multilobed stigma atop the style. The inferior ovary is 3-locular below but becomes unilocular above. The fruit is a drupe crowned by the persistent perianth. The exterior of the seed is deeply ruminate-lobed.

This enigmatic taxon has challenged classification for over 100 years. The genus was placed in its own family by Tieghem (1905) and has since been allied with Olacaceae by most workers. Louis & Léonard (1948) recognized Octoknemaceae as a family, but included within it *Okoubaka* (here in Cervantesiaceae). Morphological features are either unusual for Santalales, such as expanded stigmatic excrescences in the female flowers, or provide conflicting links to various groups. For example, the floral stellate trichomes and wood anatomy link to Coulaceae (Mildbread, 1935; Reed, 1955). Leaf and wood anatomy (Baas, 1982; van den Oever, 1984) indicate this taxon is isolated from other Olacaceae. Pollen ultrastructure suggested a relationship with Opiliaceae (Lobreau-Callen, 1982), a more derived position within the order that follows Schultze-Motel (1964) who made it a tribe in subfamily Schoepfioideae. The reduction or loss of sepals in some *Oktoknema* species is in accord with trends seen in more derived members of Santalales. The position of *Octoknema* on the molecular tree (Malécot & Nickrent, 2008) as sister (but with low support) to a clade composed of Schoepfiaceae, Misodendraceae, Loranthaceae and Opiliaceae also supports this concept. Parasitism has not been documented for *Octoknema*, but its phylogenetic position points towards this trophic condition.

8. Family Schoepfiaceae Blume (1850). — Three genera: *Arjona* Comm. ex Cav. with ten species of tropical and temperate South America; *Quinchamalium* Molina with ca. 20 species of Andean South America; and *Schoepfia* Schreb. with ca. 25 species in tropical America, Africa, and Asia.

Schoepfiaceae include plants with diverse habits: root-parasitic trees, subshrubs with xylopodia (*Arjona* sect. *Xylarjona* Skottsberg) and herbaceous perennials with alternate, simple, exstipulate leaves. The bisexual flowers are borne in axillary and terminal inflorescences of various types. The floral bracts and bracteoles are persistent, separate or fused into a cup in *Quinchamalium* and *Schoepfia*. The calyx is represented by a calyculus in *Schoepfia*. Hairs occur opposite the stamens on the 4 or 5 petals of *Arjona* and *Schoepfia*. The ovary is inferior with 2 or 3 locules at the base and unilocular above. The mature fruit in *Schoepfia* is a drupe whereas in *Arjona* and *Quinchamalium* it is a nutlet, crowned by persistent perianth parts. The bracts that enclose the fruit are accrescent with a sclerotic layer in *Arjona* and *Quinchamalium*.

The association of *Arjona* and *Quinchamalium* has never been disputed, however, their affinity with *Schoepfia*, as originally noted by Tieghem (1896), was only recently confirmed using molecular phylogenetic methods (Der & Nickrent, 2008). This relationship is supported by the above morphological features.

9. Family Misodendraceae J. Agardh (1858). — Monogeneric, with *Misodendrum* Banks ex DC. having eight species of aerial hemiparasitic shrubs endemic to temperate forests of South America, mainly south of 33 degrees.

Branching in *Misodendrum* is sympodial and the leaves are alternate. Plants are dioecious (rarely monoecious or with bisexual flowers). The inflorescences are of spikes or racemes that bear reduced flowers subtended by bracts. The staminate flowers lack a perianth and have a central nectariferous disk surrounded by two or three stamens. The carpellate flowers are epigynous (not hypogynous, see Vidal-Russell & Nickrent, 2007) and the staminodes (or stamens in bisexual flowers) are fused to the ovary only at the base (epihypogynous). The staminodes emerge from grooves between the perianth members. Perianth lobes (petals) are recognizable at the apex of the ovary in some species. A nectariferous disk occurs between the petals and the style with three stigmas. The mature achene bears three accrescent feathery staminodes that keep the fruit aloft and also aid in attachment to the host branch.

All recent multigene molecular analyses (Der & Nickrent, 2008; Malécot & Nickrent, 2008; Vidal-Russell & Nickrent, 2008b) place Misodendraceae as sister to Schoepfiaceae and that clade sister to Loranthaceae. Among the five independent evolutions of aerial parasitism, molecular dating indicate *Misodendrum* first achieved this habit ca. 80 Ma (Vidal-Russell & Nickrent, 2008b).

10. Family Loranthaceae Juss. (1808). — Seventy-three genera mainly of the Old and New World tropics with some genera occurring in temperate regions. The subfamilial name Loranthoideae Eaton (1836) was used by Engler & Krause (1935) for the taxon equivalent to what is here considered family Loranthaceae. The other subfamily, Viscoideae, is here recognized as a distinct family (see discussion under Viscaceae below).

Hemiparasitic on the roots and/or branches of host plants by means of primary or secondary haustoria and with or without epicortical runners. The leaves are mostly opposite (more rarely alternate or whorled), simple, curvinerved or penninerved. Inflorescences are terminal and lateral, in various forms including spikes, racemes, umbels, and capitula, but the basic unit is often a dichasium. Flowers are bisexual or unisexual, radially or bilaterally symmetrical, 4–6(–8)-merous, with a calyculus (calyx reduced to a rim, a tube, or short teeth), and a gamopetalous or choripetalous corolla, with valvate petals. The stamens are as many as the petals and epipetalous, the anthers are 2- or 4-locular, basifixed or dorsifixed. The ovary is inferior, unilocular (or its locules sometimes have obscure lobes at the base), and lacks differentiated ovules (the embryo sacs form within a mamelon). The fruit is a berry (except in *Nuytsia*) with a single viscid seed.

Three genera, *Nuytsia*, *Atkinsonia* and *Gaiadendron* are solely or primarily root parasites whereas the majority of the remaining genera are stem parasites (mistletoes). Root and stem parasitism (the amphiphagous condition, see Vidal-Russell & Nickrent, 2008a,b) can be found in various species of *Tripodanthus* and *Helixanthera*. The family is strongly supported as monophyletic as is the sister relationship between *Nuytsia* and the remaining genera.

Loranthaceae are here divided into tribes, and in some cases subtribes (Fig. 2). Although the molecular tree (Vidal-Russell & Nickrent, 2008a) has hierarchical structure that could be used to propose additional ranks (i.e., grouping of Tribes), in some cases relationships among the clades are not well supported, hence these will not be proposed here. Thus, the following infrafamilial classification takes into account the molecular tree topology, clade support, morphology, and base chromosome number. Given the topology of the molecular tree (Fig. 2), it appears that four major aneuploid reductions from $n = 12$ occurred throughout the evolutionary history of the family: first in *Ligaria* to $n = 10$, second in subtribe Psittacanthinae to $n = 8$, third in subtribe Ileostylinae to $n = 11$, and fourth in the clade comprising subtribes Loranthinae, Amyeminae, Scurrulinae, Dendrophthoinae, Emelianthinae, and Tapinanthinae, all $n = 9$.

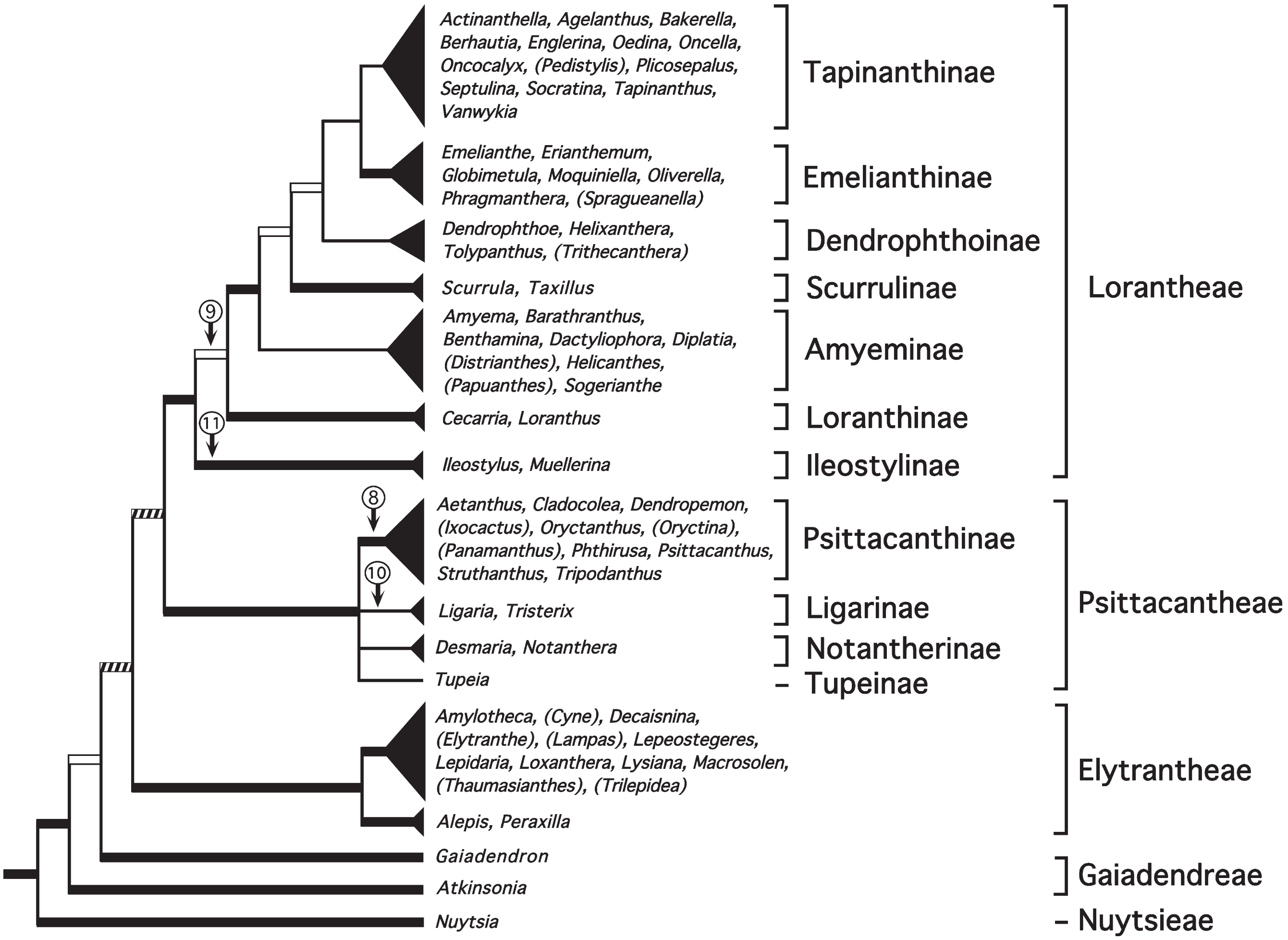

Fig. 2. Diagramatic phylogenetic tree showing relationships among the tribes and subtribes of Loranthaceae. This tree is based primarily upon the molecular phylogenetic investigation by Vidal-Russell & Nickrent (2008a). Nodes resolved with 100% bootstrap support and/or Bayesian posterior probabilties of 1.0 are shown with bold lines, 80%–99% with dashed lines, 70%–79% open lines, and <70% with thin lines. Additional well-supported topologies may exist within the larger clades but are not shown (see Vidal-Russell & Nickrent, 2008a). Genera not sampled in the molecular studies (enclosed within parentheses) are placed in clades based upon morphological evidence. The four aneuploid reductions from $n = 12$ are indicated with arrows (in subtribe Ligarinae $n = 10$ applies only to *Ligaria*; *Tristerix* remains $n = 12$).

10.1. Tribe Nuytsieae Tiegh. — This tribe, recognized by Danser (1933), includes only *Nuytsia* R. Br. with one species, *N. floribunda* (Labill.) R. Br., of western Australia.

Within Loranthaceae, *Nuytsia* has numerous unique features such as its fruit (a dry three-winged, wind-dispersed samara), and unique haustorial behavior and anatomy (Beyer & al., 1989; Calladine & Pate, 2000). Plants are monoecious with a bisexual flower central in the dichasium and male lateral flowers. Flowers bear a calyculus (with vascular strands) and six gamopetalous petals each with a stamen. At the base of the inferior ovary are three semilocules but the ovary is unilocular above.

10.2. Tribe Gaiadendreae Tiegh. — This tribe includes *Atkinsonia* F. Muell. with one species, *A. ligustrina* (Lindl.) F. Muell., endemic to the Blue Mts. of New South Wales, Australia, and *Gaiadendron* G. Don with one species, *G. punctatum* (Ruiz & Pavon) G. Don, of Central and South America.

Atkinsonia is a 1 m tall shrub with opposite, glabrous, lanceolate leaves. It bears an axillary raceme of 6-merous gamopetalous flowers that turn from yellow to orange as they mature. *Gaiadendron* is a shrub or tree up to 14 m tall, existing either as a terrestrial root parasite or as an epiphyte (Kuijt, 1963). It has opposite to subopposite leaves and bears racemose or paniculate inflorescences containing dichasia, with each triad subtended by two smaller and one larger bract. Both genera have vascular strands in the calyculus, drupaceous fruits, furrowed endosperm, and versatile, dorsifixed anthers. The inflorescence of *Atkinsonia* is composed of monads whereas *Gaiadendron* has triads, but otherwise the floral morphology in these genera is very similar and matches well the hypothetical ancestral type that may have had an open, yellow, choripetalous, entomophilous flower (Vidal-Russell & Nickrent, 2008a).

Engler (1897a) and Danser (1933) called this group subtribe Gaiadendrinae whereas Tieghem (1895a) recognized it as a tribe. Molecular data do not consistently resolve these two genera as a clade but as a successive grade. Additional molecular work is needed to confirm their monophyly. They are placed in the same tribe here owing to the high degree of morphological similarity. The parasitic nature of *Gaiadendron* requires further investigation. In addition to being a root parasite, individuals have been observed growing in the canopy of large forest trees. This species is not adapted to branch parasitism as its seedlings lack a primary haustorium. It has been suggested (Kuijt, 1963, 1964, 1982) that *Gaiadendron* is a root parasite on the epiphytes that grow with it on the canopy branches.

10.3. Tribe Elytrantheae Engl. — This tribe, recognized by Danser (1933) and treated as a subtribe by Engler (1897a), contains 14 genera: *Alepis* Tiegh. with one species, *A. flavida* (Hook. f.) Tiegh., of New Zealand; *Amylotheca* Tiegh. with four species of Australia, New Guinea, and Melanesia; *Cyne* Danser [including *Tetradyas* Danser of New Guinea] with six species of the Philippines, Moluccas and New Guinea; *Decaisnina* Tiegh. with 25 species of Malesia to tropical Australia and Tahiti; *Elytranthe* Blume with ten species from southeast Asia and Malaysia; *Lampas* Danser with one species, *L. elmeri* Danser, of northern Borneo; *Lepeostegeres* Blume with nine species of Malesia; *Lepidaria* Tiegh. with twelve species of Malaysia; *Loxanthera* Blume with one species, *L. speciosa* Blume, of Malaysia and Indonesia; *Lysiana* Tiegh. with six species of Australia; *Macrosolen* (Blume) Rchb. with 25 species from India to Southeast Asia and New Guinea; *Peraxilla* Tiegh. with two species of New Zealand; *Thaumasianthes* Danser with two species of the Philippines; and *Trilepidea* Tiegh. with one species, *T. adamsii* (Cheesm.) Tiegh., that previously existed in New Zealand but is now extinct (Norton, 1991).

With the exception of *Lysiana*, mistletoes in this Tribe form epicortical roots. Inflorescence development is endogenous in *Peraxilla* and *Cyne* where the young floral buds break through a corky layer on the twig (Kuijt, 1981). A parallel condition exists in *Cladocolea* (subtribe Psittacanthinae). All have bisexual, actinomorphic flowers that are mostly 6-merous (*Alepis* and *Peraxilla* are 4-merous). The corolla can be either choripetalous or gamopetalous and the lobes are reflexed. The anthers are basifixed except in *Alepis* and *Loxanthera* where they are dorsifixed. Danser (1933) states, however, that these anthers have "nothing in common with the really dorsifixed anthers of other Loranthaceous genera." Some members of this tribe have ovaries (at least when young) that have locular divisions at the base, as in *Lysiana* with a four-lobed central placenta that fuses with the upper portion of the ovarian locule (Bhatnagar & Johri, 1983). Danser (1933) stated that members of this tribe had embryo sacs that only penetrated to the base of the style, this is apparently only true for some genera (e.g., *Elytranthe*, *Macrosolen*, *Peraxilla*) but not others such as *Lepeostegeres* and *Lysiana* that extend farther (Bhatnagar & Johri, 1983).

A clade containing 8 of the 14 genera of tribe Elytrantheae received high support in molecular analyses (Vidal-Russell & Nickrent, 2008a). *Alepis* and *Peraxilla* form a well-supported clade based on molecular and morphological data, thus they may warrant later segregation as a subtribe.

10.4. Tribe Psittacantheae Horan. — Classified as a subtribe by Engler (including only *Aetanthus*, *Psittacanthus*, and *Ligaria*), it is here circumscribed as a tribe with four subtribes totaling 16 genera. This tribe has the greatest diversity of base chromosome numbers in the family and subtribe circumscription generally reflects these numbers. With the exception of *Tupeia* (New Zealand), all the genera are native to the New World.

Stem parasites with alternate or opposite leaves, with or without epicortical roots. The basic inflorescence units are monads, diads, and triads formed into various determinate or indeterminate inflorescences (spikes, racemes, umbels, capitula). The actinomorphic flowers are bisexual but unisexuality has evolved, apparently independently, in *Tupeia* and small-flowered $n = 8$ members such as *Cladocolea*, *Ixocactus*, *Oryctina*, and *Phthirusa*. The (4 to 5-) 6-merous flowers can be choripetalous or gamopetalous. The anthers are either basifixed or dorsifixed and are frequently dimorphic and with an apiculate extension from the connective in the $n = 8$ clade. *Aetanthus* and *Psittacanthus* are unique among all Loranthaceae in lacking endosperm.

10.4.1. Subtribe Tupeinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Tupeia* Cham. & Schltdl. One genus: *Tupeia* Cham. & Schltdl. with one species, *T. antarctica* Chamb. & Schltdl., of New Zealand.

Frutices pubescentes in caulibus parasitici radicibus epicorticalibus carentes; ramis oppositis suboppositisve. Folia alterna. Inflorescentia terminalis involucro basali ex squamarum paribus decussatis pluribus constante subtenta, floribus in racemos monadorum ebracteolatorum dispositis. Flores unisexuales (raro bisexuales) luteovirides actinomorphi choripetali 4-meri; perianthii lobulis patentibus; staminibus epipetalis, antheris basifixis.

Pubescent stem parasites without epicortical roots. The inflorescence is a condensed raceme of monads containing unisexual flowers (Smart, 1952). Engler & Krause (1935) describe *Tupeia* as having bisexual or unisexual flowers, thus being trioecious. The report of "abnormal hermaphroditism" by Thompson (1949) was attributed to hybridization between *Ileostylus micranthus* and *Tupeia*. This report is suspect given the phylogenetic distance of these two genera, and because the author failed to cite earlier observations of bisexual flowers. The flowers are 4-merous with spreading lobes and the anther is basifixed. *Tupeia* pollen is unusual in the family in that it is spheroidal, either tetra- or tricolpate and has echinate sculpturing (Feuer & Kuijt, 1978).

Tupeia has been considered a relictual genus based upon its *n* = 12 chromosome number and its presence on Gondwanan landmasses (Barlow, 1983).

10.4.2. Subtribe Notantherinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Notanthera* (DC.) G. Don. Two genera: *Desmaria* Tiegh. with one species, *D. mutabilis* (Poepp. & Endl.) Tiegh. ex Jacks, of southern Chile; *Notanthera* (DC.) G. Don. with one species, *N. heterophylla* (Ruiz. & Pav.) G. Don, of temperate South America.

Frutices glabri in caulibus parasitici radicibus epicorticalibus praediti. Folia alterna. Inflorescentia ex racemo triadorum constans. Flores bisexuales actinomorphi choripetali 5-meri; perianthii lobulis reflexis; antheris dorsifixis.

Glabrous stem parasites with epicortical roots. The inflorescence is a raceme of bisexual flowers arranged in triads. In *Notanthera* the central flower of the triad is sessile, the lateral flowers pedicellate. The choripetalous flowers are 5-merous with reflexed corolla lobes and the anthers are dorsifixed.

Notanthera has been considered a relictual genus based upon its *n* = 12 chromosome number and its presence on Gondwanan landmasses (Barlow, 1983). Kuijt (1985) allied *Desmaria* with *Notanthera* (as well as *Gaiadendron* and *Tripodanthus*) based mainly on inflorescence type.

10.4.3. Subtribe Ligarinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Ligaria* Tiegh. Two genera, *Ligaria* Tiegh. with two species of arid and subtemperate South America and *Tristerix* Mart. with eleven species of temperate and high Andean South America.

Frutices glabri in caulibus parasitici radicibus epicorticalibus carentes. Folia alterna. Inflorescentia ex racemo vel fasciculo axillari 2- vel 3-floro constans. Flores bisexuales rubri actinomorphi gamopetali 4- ad 6-meri; perianthii lobulis reflexis; staminibus exsertis, antheribus dorsifixis.

Glabrous mistletoes without epicortical roots. The red tubular flowers are 4- or 5-merous in *Tristerix* and 6-merous in *Ligaria*, both with exserted stamens and dorsifixed anthers. The *Ligaria* flower is subtended by a cupule that is derived from the fusion of 3 or 4 bracts (and/or bracteoles). This cupule, originally thought to be a link between *Ligaria* and *Psittacanthus*, is now considered an independently evolved structure (Barlow & Wiens, 1973; Kuijt, 1981). The inflorescence in *Tristerix* is an indeterminate raceme whereas interpretations of the single flower (a monad, occasionally with one lateral) in *Ligaria* vary. Tieghem (1895b) viewed this as a reduced raceme, but Kuijt (1981) preferred an interpretation involving a reduction from a multi-flowered determinate system where the cupule represents bracts derived from the lost flowers. The articulated system in *L. teretiflora* (Rizzini) Kuijt (Kuijt, 1990) could be interpreted as a pedicel and peduncle, thus supporting the reduced raceme concept (as does molecular data where *Ligaria* and *Tristerix* are sister).

10.4.4. Subtribe Psittacanthinae Engl. — Eleven genera: *Aetanthus* (Eichl.) Engl. with ca. ten species of the northern Andes; *Cladocolea* Tiegh. with 25 species from Mexico to South America; *Dendropemon* (Blume) Rchb. with ca. 25 species of the New World tropics and Caribbean; *Ixocactus* Rizzini with three species of South America; *Oryctanthus* Eichl. with ten species of tropical America; *Oryctina* Tiegh. [including *Maracanthus* Kuijt] with six species of Western Venezuela, Guianas, and Brazil; *Panamanthus* Kuijt with one species, *P. panamensis* (Rizz.) Kuijt, of Panama; *Phthirusa* Mart. with ca. 60 species of tropical America and the Caribbean; *Psittacanthus* Mart. with 120 species of Mexico, Honduras, and South America; *Struthanthus* Mart. with ca. 50 species of tropical America; and *Tripodanthus* (Eichl.) Tiegh. with three species of subtemperate and high Andean South America.

Stem-parasitic mistletoes with or without epicortical roots. *Ixocactus hutchisonii* Kujit shows several autapomorphies, including its squamate habit with flattened stems, a conical style that is persistent on the fruit, and spherical (not triangular) pollen (Feuer & Kuijt, 1985). *Tripodanthus acutifolius* Tiegh. is remarkable in that it begins life as an epiphyte but later its epicortical roots grow downward into the soil and there attach to host roots. The basic inflorescence units are monads and triads, (also diads in *Aetanthus* and *Psittacanthus*) and these can be arranged in spikes, condensed spikes (glomerules), racemes, and capitula. Floral bracts are present and are often fused into a cupule (*Phthirusa*, *Psittacanthus*, etc.). The actinomorphic flowers are bisexual or unisexual, and in the latter both staminodes and pistillodes may be present. In small-flowered genera the petals are free or only slightly fused at the base whereas in the two large-flowered genera (*Aetanthus* and *Psittacanthus*), a long corolla tube is seen. Stamens are usually dimorphic, occurring at different heights within the flower bud. In *Phthirusa*, pressure from short stamen anthers causes indentations in the filaments of the longer stamens. Anthers can be either basifixed or dorsifixed and in some genera the connective is apiculate. The style is contorted in *Cladocolea* and *Struthanthus*.

Molecular phylogenies and palynological evidence (Feuer & Kuijt, 1985) reveal the close relationships among the seven small-flowered genera (*Cladocolea*, *Dendropemon*, *Ixocactus*, *Oryctanthus*, *Oryctina*, *Panamanthus*, *Phthirusa*, *Struthanthus*), thus future work is needed to more clearly define generic boundaries.

10.5. Tribe Lorantheae Rchb. — This tribal name was also used by Engler & Krause (1935). This is the largest tribe in Loranthaceae and contains seven subtribes and 40 genera. Engler's subtribe Loranthinae included seven genera, but one of these was *Loranthus* that, according to modern concepts, encompasses 37 genera. Subtribe Ileostylinae has a base chromosome number of $x = 11$ and this clade is sister to a clade containing the remaining six subtribes (38 genera) that all have $x = 9$. This represents the fourth aneuploid reduction in Loranthaceae, and one that affected the largest number of genera and species.

10.5.1. Subtribe Ileostylinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Ileostylus* Tiegh. Two genera: *Ileostylus* Tiegh. with one species, *I. micranthus* (Hook. f.) Tiegh., of New Zealand and *Muellerina* Tiegh. with four species endemic to eastern Australia.

Frutices glabri in caulibus parasitici radicibus epicorticalibus praediti. Folia opposita. Inflorescentia ex racemis simplicibus vel umbellis monadorum triadorumve constans, floribus bracteis solitariis subtentibus. Flores bisexuales actinomorphi, aut parvi choripetali 4-meri antheris basifixis (*Ileostylus*) aut grandes gamopetali 5-meri antheris dorsifixis (*Muellerina*).

Glabrous mistletoes with opposite leaves and epicortical roots. The basic inflorescence units are monads or triads arranged in simple racemes or umbels. In *Muellerina* the central flower of the triad is sessile. No bracts are associated with the inflorescence, but each bisexual, actinomorphic flower is subtended by one bract. The overall floral morphology of the two genera is different. *Ileostylus* has small (2.5 mm), choripetalous flowers with four petals whereas *Muellerina* has larger (2.5 cm), gamopetalous flowers with five petals. In the former genus the anthers are basifixed and in the latter dorsifixed. Indeed, the flowers of *Ileostylus* resemble *Tupeia*, but this must have evolved in parallel given their phylogenetic distance.

10.5.2. Subtribe Loranthinae Engl. — Two genera: *Cecarria* Barlow with one species, *C. obtusifolia* (Merr.) Barlow, of the Philippines, New Guinea, New Britain, and the Solomon Islands and *Loranthus* Jacq. with ca. ten species of Europe to southern China, and Sumatra.

These glabrous, alternate leaved mistletoes either have (*Loranthus*) or lack (*Cecarria*) epicortical roots. The inflorescence has been described as a spike for both genera, but for *Cecarria*, additional descriptions exist, such as a 2-flowered cyme (Danser, 1931), a 2-flowered umbel (Barlow & Wiens, 1973), or a 4-flowered raceme (Barlow, 1984). These descriptive differences highlight the difficulties associated with inflorescence terminology that are especially acute in Loranthaceae (Kuijt, 1981). The 5- or 6-merous, choripetalous flowers are bisexual in *Cecarria* but both bisexual and unisexual flowers occur in *Loranthus* (plants then dioecious). Anthers are basifixed in *Loranthus* but dorsifixed in *Cecarria*.

The dorsifixed anthers caused Merrill to place the taxon now known as *Cecarria* in *Phrygilanthus*. The generic name *Phrygilanthus* Eichler, that included a heterogeneous assemblage of Old and New World mistletoes, was rendered illegitimate and its species allocated to ten different genera, including the new genus *Cecarria* (Barlow & Wiens, 1973). These authors stated: "*Cecarria* may be an unspecialized, relic genus near the stem of this Old World line. The only other Old World members of the *Phrygilanthus* group are the four temperate Australian species now referred to *Muellerina*." These concepts are not in conflict with the actual phylogenetic relationships where *Ileostylus*/*Muellerina*, *Cecarria*/*Loranthus*, and the remaining $x = 9$ taxa all form successive clades. The nomenclatural history of the genus *Loranthus* has been mercurial. The name encompassed nearly all mistletoes at the time of Linnaeus, was split into a plethora of genera by Tieghem (publications between 1894 and 1911), and recircumscribed by Danser (publications between 1929 and 1941). Barlow (1995) concluded that the nine species assigned to *Hyphear* by Danser were all conspecific with *L. odoratus*. With *L. europaeus*, the genus was then thought to include just two species. The *Flora of China* treatment (Qiu & Gilbert, 2003) lists six species from China and ten total for the genus. Molecular evidence (Jer-Ming Hu, pers. comm.) supports the monophyly of the Chinese and European species.

10.5.3. Subtribe Amyeminae Nickrent & Vidal-Russell, subtr. nov. — Type *Amyema* Tiegh. Nine genera: *Amyema* Tiegh. with ca. 100 species from Malesia, Australia, Philippines, and western Pacific; *Barathranthus* (Korth.) Miq. with three species of Sri Lanka and Malaysia; *Benthamina* Tiegh. with one species, *B. alyxifolia* (F. Muell. ex Benth.) Tiegh., of Australia; *Dactyliophora* Tiegh. with three species of Papuasia and northern Queensland Australia; *Diplatia* Tiegh. with three species of tropical Australia; *Distrianthes* Danser with one species, *D. moliflora* (Krause) Danser, of New Guinea; *Helicanthes* Danser with one species, *H. elastica* (Desr.) Danser of India; *Papuanthes* Danser with one species, *P. albertisii* Danser of New Guinea; and *Sogerianthe* Danser with four species from eastern New Guinea to the Solomon Islands.

Frutices glabri pubescentesve in caulibus parasitici radicibus epicorticalibus (praeter *Diplatiam*) praediti. Folia alterna opposita verticillatave. Inflorescentia ex racemo umbella capitulove constans, floribus in triada simplicia aggregatave dispositis, vel ad florem solitarium reducta; bracteis floralibus interdum accrescentibus vel cupulam formantibus. Flores bisexuales unisexualesve, 5- vel 6-meri, choripetali gamopetalive.

Glabrous or pubescent mistletoes, all but *Diplatia* with epicortical roots and most with opposite leaves (also alternate and verticillate in *Amyema*). The basic inflorescence unit appears to be a triad which may then be aggregated into conflorescences of racemes, umbels and capitula, or sometimes reduced to single flowers or a simple umbel of dyads in some *Amyema* (see fig. 5 in Barlow, 1966). In *Diplatia* and *Papuanthes* the floral bracts are enlarged, foliaceus, and connate thus covering the inflorescence during development. This bract fusion is more weakly developed in some species of *Sogerianthe* where the bracts form a cupule at the base of the peduncle. The flowers are bisexual (except in *Barathranthus*), generally 5- or 6-merous, choripetalous (e.g., *Barathranthus*, *Dactyliophora*, *Diplatia*) or gamopetalous, and with or without reflexed lobes. An articulated style is seen in *Dactyliophora*, a feature rarely seen outside Tribe Elytrantheae.

Six genera representing the "*Amyema* complex" were strongly supported as a clade from molecular analyses (Vidal-Russell & Nickrent, 2008a). *Barathranthus*, weakly supported as sister to this clade, has a very different morphology: the plants are dioecious with tiny, 4-merous, unisexual flowers that emerge from hollows in the stem. Various generic names coined by Tieghem and Danser for taxa within the *Amyema* complex (e.g., *Dicymanthes*) have been placed in synonymy with *Amyema*. The two species of *Amyema* sampled in Vidal-Russell & Nickrent (2008a) were not monophyletic. These facts, plus the high degree of morphological variation among the large number of species, highlight the need for additional molecular work to better establish generic limits in Amyeminae.

10.5.4. Subtribe Scurrulinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Scurrula* L. Two genera: *Scurrula* L. with ca. 50 species of China, Southeast Asia and Malaysia; and *Taxillus* Tiegh. with ca. 35 species of tropical Asia (India and Sri Lanka to China, Japan, Philippines, Borneo) and Africa (Kenya coast).

Frutices pubescentes in caulibus parasitici radicibus epicorticalibus praediti, trichomatibus stellatis dendriticisve induti. Folia opposita. Inflorescentia ex racemo umbellave monadorum constans. Flores bisexuales zygomorphi gamopetali, 4- vel 5-meri, corolla aperta rimam V-formem faciente.

Mistletoes with epicortical roots and opposite (decussate) leaves. In many species nearly all parts of the plant are covered with an indumentum of stellate or dendritic trichomes. Floral monads are arranged in racemes or umbels. The flowers are bisexual, zygomorphic, 4- (rarely 5-) merous, and gamopetalous and form a V-shaped slit along the corolla tube when open. Flowers in the sole African species *T. wiensii* Polhill open explosively when probed by pollinating birds (Polhill & Wiens, 1998). *Scurrula* and *Taxillus* have long been considered closely related and indeed Danser (1931) moved seven species from the former into the latter genus. *Scurrula* has club-shaped, stipitate fruits whereas *Taxillus* has ellipsoid, nonstipitate, warty fruits (Barlow, 1991). *Taxillus* has a wide geographic distribution, from coastal Kenya through India to China, Japan, Southeast Asia, the Philippines, and Borneo. This can be attributed to the generally low host specificity. The one Malesian species, *T. chinensis* (DC.) Danser, is widespread west of Charles' Line but may be a recent introduction into that flora (Barlow, 1991).

10.5.5. Subtribe Dendrophthoinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Dendrophthoe* Mart. Four genera: *Dendrophthoe* Mart. with 30 species from tropical Africa to Malesia and Australia; *Helixanthera* Lour. with ca. 50 species of tropical Africa to Sulawesi; *Tolypanthus* Blume with four species from India to southeastern China; and *Trithecanthera* Tiegh. [including *Kingella* Tiegh.] with four species of western Malaysia.

Frutices glabri pubescentesve in caulibus parasitici radicibus epicorticalibus praediti carentesve. Folia alterna opposita verticillatave. Inflorescentia ex spica racemo umbella vel capitulo monadorum constans, bracteis floralibus interdum involucrum formantibus (*Tolypanthus*). Flores bisexuales gamopetali vel choripetali (*Helixanthera*) 4- ad 6-meri, perianthii lobulis reflexis, antheris basifixis.

Vegetatively these mistletoes are variable: pubescent or not, with or without epicortical roots, and alternate, opposite, or whorled leaves. The basic inflorescence unit is a monad, but this is arranged in spikes, racemes, umbels, or capitula. In *Tolypanthus* the floral bracts are greatly expanded and either free (e.g., *T. gardneri* Tiegh.) or connate into a bell-shaped involucre (*T. lageniferus* Tiegh.). The gamopetalous corolla generally has five reflexed lobes, but variation is seen in *Helixanthera* whose typically four choripetalous lobes are only weakly reflexed. The anthers are basifixed with longitudinal (and in *Helixanthera* transverse) septae. The ovarian placenta is unlobed or absent entirely.

The molecular analysis (Vidal-Russell & Nickrent, 2008a) showed *Helixanthera* to be polyphyletic, with *H. cylindrica* occurring between Scurrulinae and Amyeminae. With a dozen species occurring in Africa, Polhill & Wiens (1998) state that *Helixanthera* "is the most primitive genus in the family in Africa," Barlow (1995) regarded *Loranthus* as very closely related to *Helixanthera*, but this is not borne out by molecular data, at least when considering the sampled Malesian species. Further sampling among the African and Asian species is required to further understand relationships in this genus. *Helixanthera terrestris* Danser and *H. scoriarum* Danser are reported to be root parasites in China (Qiu & Gilbert, 2003), thus these require additional investigation to determine whether they are solely such or amphitrophic (as in *Tripodanthus*, tribe Psittacantheae above).

10.5.6. Subtribe Emelianthinae Nickrent & Vidal-Russell, subtr. nov. — Type *Emelianthe* Danser. Seven genera: *Emelianthe* Danser with one species, *E. panganensis* (Engl.) Danser, of eastern and northeastern Africa; *Erianthemum* Tiegh. with 16 species of eastern and southern Africa; *Globimetula* Tiegh. with 13 species of tropical Africa; *Moquiniella* Balle with one species, *M. rubra* (Spreng. f.) Balle, of Namibia and the Cape Province of South Africa; *Oliverella* Tiegh. with three species of eastern and southern Africa; *Phragmanthera* Tiegh. with 34 species of tropical Africa and Arabia; and *Spragueanella* Balle with two species of eastern and southern Africa.

Frutices glabri pubescentesve in caulibus parasitici radicibus epicorticalibus carentes. Folia alterna oppositave. Inflorescentia ex umbella vel capitulo monadorum (*Erianthemum*) constans. Flores bisexuales actinomorphi zygomorphive gamopetali plerumque 5-meri, in alabastro fenestrati, filamentis plerumque in spiram contortis.

Glabrous or pubescent mistletoes without epicortical roots and with opposite or alternate leaves. The inflorescences are monads composed into umbels or, in *Erianthemum*, contracted to a capitulum. Among the seven genera, only in *Erianthemum* is the calyculus expanded into an urceolate cup that is persistent on the fruit. This feature is more developed in subtribe Tapinanthinae. Flowers are bisexual, zygomorphic (or actinomorphic in *Emelianthe* and *Erianthemum*), and composed of five gamopetalous lobes (four in *Emelianthe*). All genera except *Globimetula* have vents (fenestrae) on the corolla tube when in bud. How the corolla lobes reflex upon anthesis varies. In *Moquiniella* and *Globimetula* the lobes form spiral coils whereas in *Oliverella* the lobes are involute, rolling up like a window shade. A distinctive tooth on the staminal filament is seen in *Phragmanthera* and *Spragueanella*. Aside from *Emelianthe*, all genera have filaments that coil and in two genera (*Erianthemum*, *Moquiniella*) the anther actually breaks away during pollination by birds (Polhill & Wiens, 1998).

As noted by Kuijt (1981), all African and Malagasy Loranthaceae have indeterminate inflorescences composed of monads, thus this may be a synapomorphy for subtribes Emelianthinae and Tapinanthinae. Molecular analyses gave strong support for subtribe Emelianthinae, however, no morphological character has been identified as a synapomorphy for the clade. The African loranth genera have undergone the most recent adaptive radiation in the family (Vidal-Russell & Nickrent, 2008b), thus many of the floral characters associated with bird pollination appear homoplastic (or atavistic).

10.5.7. Subtribe Tapinanthinae Nickrent & Vidal-Russell, subtr. nov. — Type: *Tapinanthus* (Blume) Rchb. Fourteen genera: *Actinanthella* Balle with two species of southern and southeastern Africa; *Agelanthus* Tiegh. with 59 species of Africa and the Arabian peninsula; *Bakerella* Tiegh. with ca. 16 species of Madagascar; *Berhautia* Balle with one species, *B. senegalensis* Balle, of Senegal and Gambia; *Englerina* Tiegh. with 25 species in tropical Africa; *Oedina* Tiegh. with four species of eastern Africa; *Oncella* Tiegh. with four species of eastern Africa; *Oncocalyx* Tiegh. [including *Tieghemia* Balle] with 13 species of eastern and southern Africa to Arabia; *Pedistylis* Wiens with one species, *P. galpinii* (Schinz ex Sprague) Wiens, of South Africa; *Plicosepalus* Tiegh. with twelve species of the Middle East and Arabia, to eastern Africa, Angola and South Africa; *Septulina* Tiegh. with two species of South Africa; *Socratina* Balle with two species of Madagascar; *Tapinanthus* (Blume) Rchb. with 30 species of tropical and southern Africa; and *Vanwykia* Wiens with two species of eastern and southeastern Africa.

Frutices glabri pubescentesve in caulibus parasitici radicibus epicorticalibus praediti carentesve. Folia opposita alternave. Inflorescentia ex umbella constans vel ad fasciculum axillarem 1- ad 3-florum reducta. Flores bisexuales actinomorphi zygomorphive gamopetali 4- vel 5-meri, interdum in alabastro fenestrati, filamentis plerumque in spiram contortis. Fructus interdum calyculo accrescente persistente subtentus.

Glabrous or pubescent mistletoes with epicortical roots (*Bakerella*, *Plicosepalus*, *Vanwykia*) or more commonly without. Phyllotaxy can be opposite or alternate, sometimes even among species of one genus. Inflorescences are commonly umbels, although several genera also show single flowers (or groups of 2–3) in the axils. Six genera have fruits with a persistent expanded calyculus. Four of the 14 genera have actinomorphic flowers. The gamopetalous corolla is composed of four or five lobes that are generally vented (exceptions being *Tapinanthus*, *Vanwykia* and some species of *Septulina*). The corolla lobes may or may not be reflexed upon anthesis. Nine of the 14 genera show coiled filaments, two of which (*Oedina*, *Oncella*) have anthers that break away upon pollination.

Only three genera of African Loranthaceae form epicortical roots and two of these occur in subtribe Tapinanthinae: *Plicosepalus* and *Vanwykia*. The molecular analysis of Vidal-Russell & Nickrent (2008a) included 13 of the 14 genera. Eight of these occurred in a moderately supported clade whereas the remaining four (*Socratina*, *Vanwykia*, *Bakerella*, *Plicosepalus*) occurred in a polytomy. These four genera are tentatively classified in this subtribe, thus additional work will be required to determine whether these mistletoes belong here or in subtribe Emelianthinae.

11. Family Opiliaceae Valeton (1886). — Eleven genera: *Agonandra* Miers ex Benth. with ten species of Mexico, Central and tropical South America; *Anthobolus* R. Br. with three species of Australia; *Cansjera* Juss. with three species of India and Ceylon to southern China, New Guinea and northern Australia; *Champereia* Griff. with one variable species, *C. manillana* (Blume) Merr., from Southeast Asia to Sumatra and western New Guinea; *Gjellerupia* Lauterb. with one species, *G. papuana* Lauterb., of New Guinea; *Lepionurus* Blume with one species, *L. sylvestris* Blume, from Nepal and Assam to western Malesia; *Melientha* Pierre with one species, *M. suavis* Pierre, of southeast Asia to the Philippines; *Opilia* Roxb. with three species of Africa, Asia, Indonesia, and Australia; *Pentarhopalopilia* Hiepko with four species of Africa and Madagascar; *Rhopalopilia* Pierre with three species of tropical Africa; and *Urobotrya* Stapf. with ca. five species of Africa and southeast Asia.

The family contains root-parasitic trees, shrubs and lianas. *Cansjera rheedii* is a shrub or climbing liana that has thorns derived from short shoots. Cystoliths are present in the leaves of all genera but appear to be absent in *Anthobolus*. Flowers are bisexual or unisexual (the plants then dioecious). Inflorescences axillary, of various types. Inflorescence bracts are peltate in *Agonandra* and *Opilia*. Floral bracts are often caducous (persistent in *Cansjera* and *Melientha*). A calyculus is present in all taxa except *Lepionurus*. Petals number 3–6 and lack hairs opposite the petals. The ovary is superior with a single locule that bears one ovule. The fruit is a drupe whose pedicel may be thickened or fleshy in *Anthobolus*, *Agonandra*, and *Opilia*.

Anthobolus was formerly classified in Santalaceae but molecular data strongly support its placement in Opiliaceae (Der & Nickrent, 2008). Its floral morphology is not out of place in the family and the only discrepancy appears to be the lack of cystoliths. Molecular data are lacking for three genera (*Gjellerupia*, *Melientha*, *Rhopalopilia*).

12. Family Comandraceae Nickrent & Der, fam. nov. — Type: *Comandra* Nutt. Two genera: *Comandra* Nutt. with one species, *C. umbellata* (L.) Nutt., of North America, Europe and the Mediterranean; and *Geocaulon* Fern. with one species, *G. lividum* Fern., of Alaska and Canada and extending southward to the northeast, north central and northwest U.S.

Herbae perennes rhizomatosae in radicibus parasiticae. Folia alterna. Inflorescentiae ex cymis axillaribus terminalibusque constantes. Flores bisexuales unisexualesve monochlamydei 4- ad 6-meri, disci lobulis glandularibus inter tepala alternantibus, antherarum connectivis ad tepala trichomatibus affixis. Fructus drupaceus, epicarpio sicco (*Comandra*) vel carnoso (*Geocaulon*).

Comandra and *Geocaulon* are closely related and were once considered congeneric. Both are root hemiparasitic herbaceous perennials with alternate, simple leaves. Inflorescences occur as axillary and terminal cymes. Flowers in *Comandra* are bisexual whereas in *Geocaulon* they are unisexual (plants monoecious or andromonoecious). The flowers are monochlamydous with no trace of a calyx or calyculus. There are 4–6 petals with an equal number of opposite stamens. Hairs arising from the petals attach to the stamen connective after anthesis. Carpellate flower staminodes and staminate flower pistillodes are present in *Geocaulon*. A lobed glandular disk occurs on the top of the inferior ovary that is unilocular throughout. The fruit is a drupe (pseudodrupe) whose epicarp dries following dehiscence in *Comandra* (Piehl, 1965) but becomes more fleshy in *Geocaulon*.

The traditional classification of Comandraceae was in tribe Santaleae (= Osyrideae), but molecular evidence (Der & Nickrent, 2008) placed this taxon in a polytomy among the basal Santalaceae s.l. The distinctiveness of this family first noted by Tieghem (1896) was supported by embryological features (Ram, 1957; Johri & Bhatnagar, 1960). *Comandra umbellata* is likely the most widespread species of Santalales, occurring throughout the United States and southern Canada as well as in the Balkan peninsula. Given its phylogenetic position, one may speculate that the genus is old and that its biogeographic history involves vicariance.

13. Family Thesiaceae Vest (1818). — Five genera: *Buckleya* Torr, with one species in the eastern U.S. and four in eastern Asia; *Kunkeliella* Stearn with four species endemic to the Canary Islands; *Osyridicarpos* A. DC. with one species, *O. schimperianus* (A. Rich.) A. DC., of Africa; *Thesidium* Sond. with eight species of South Africa; and *Thesium* L. with ca. 330 species in Europe, Africa, Asia, Australia, and South America.

Root-parasitic shrubs and herbaceous perennials with alternate or opposite leaves. Plants with bisexual flowers or unisexual (then dioecious) in various types of inflorescences. A calyculus may be present and in some cases is developed into actual sepal lobes, e.g., in *Buckleya*, *Osyridocarpos*, *Thesium liberium*. There are 4 or 5 petals that may or may not be formed into a corolla tube and an equal number of stamens. Hairs opposite the stamens are present on the petals of bisexual or male flowers (absent in *Buckleya*). Upon fruit development the embryo sac extends beyond the ovule or placenta. The fruits of *Buckleya*, *Osyridicarpos*, and *Kunkeliella* are drupes (pseudodrupes) whereas in *Thesium* nutlets are seen. The fruiting pedicel becomes swollen in some species of *Thesium* thus functioning as an elaiosome for myrmechochory.

The sister relationship of *Buckleya* to the remaining members of this family was only recently demonstrated using molecular methods (Der & Nickrent, 2008). *Osyridicarpos* and *Thesidium* are South African endemics whereas *Thesium* reaches its greatest diversity there. A molecular phylogeny using nuclear ITS (Nickrent & al., 2008) did not support the recognition of the segregate genera *Austroamericium* Hendrych and *Chrysothesium* (Jaub. & Spach) Hendrych but did show the genetic distinctiveness of *Thesium mauritanicum* Batt. (northern Africa) and *T. lineatum* L. f. (South Africa). Additional work is required to more precisely determine the phylogenetic history of these taxa and then circumscribe genera accordingly. The South American and Malagasy species of *Thesium* appear to be recent introductions via long distance dispersal, not vicariance. In contrast, it appears that *Buckleya* is an old genus, diverging from *Pyrularia* ca. 80 Ma (Vidal-Russell & Nickrent, 2008b). The existence of this genus in eastern North America and eastern Asia supports a vicariance scenario. Because *Osyridicarpos* and *Thesium lineatum* are the next taxa to diverge in the clade, and because they are both South African endemics, movement of this ancestor from Asia to Africa appears to have taken place. A massive radiation subsequently occurred in *Thesium*, producing the highest number of species of any genus in Santalales.

14. Family Cervantesiaceae Nickrent & Der, fam. nov. — Type: *Cervantesia* Ruiz & Pav. Eight genera: *Acanthosyris* (Eichl.) Griseb. with three species from temperate South America; *Cervantesia* Ruiz & Pav. with four species of Andean South America; *Jodina* Hook. & Arn. ex Meisn. with one species, *J. rhombifolia* (Hook. & Arn.) Reiss., of southern Brazil, Uruguay, and Argentina; *Okoubaka* Pellegr. & Normand with two species of tropical Africa; *Pilgerina* Rogers, Nickrent & Malécot with one species, *P. madagascariensis* Rogers, Nickrent & Malécot, of Madagascar; *Pyrularia* Michx. with one species from the southeastern U.S. and two from China; *Scleropyrum* Arn. with ca. six species of India, Southeast Asia, and Malesia; and *Staufferia* Rogers, Nickrent & Malécot with one species, *S. capuronii* Rogers, Nickrent & Malécot, of Madagascar.

Arbores fruticesve in radicibus parasitici, interdum spinis axillaribus armati. Inflorescentia ex spica racemo panicula fasciculo monochasio vel flore solitario constans. Flores bisexuales unisexualesve monochlamydei 4- vel 5-meri campanulati urceolative, disci lobulis glandularibus inter tepala alternantibus, antherarum connectivis ad tepala trichomatibus affixis, ovario supero semi-infero inferove. Fructus ex drupa grandi dehiscente indehiscenteve constans.

Hemiparasitic trees and shrubs, some of which (*Acanthosyris*, *Scleropyrum*) with ramal and axillary thorns. Plant sexual conditions vary among the genera with bisexual flowers (*Acanthosyris*, *Cervantesia*, etc.), dioecy (*Okoubaka*, *Staufferia*) and trioecy (*Scleropyrum*). Similarly, various inflorescence types occur such as solitary flowers, monochasia, spikes, racemes, panicles and fascicles. No evidence of a calyx or calyculus exists. The 4- or 5-merous campanulate or urceolate flowers bear hairs on the petals opposite to and in equal number with the stamens. Staminodes and pistillodes are present in unisexual species. A glandular disk is present, often with large lobes alternating between the petals. Ovary position varies with superior (*Cervantesia*), half-inferior (*Acanthosyris*), or fully inferior (remaining genera) conditions existing. There appears to be a tendency towards becoming fully inferior upon fruiting. The ovary is unilocular throughout with a straight or twisted (*Acanthosyris*, *Cervantesia*, *Jodina*) placental column. The fruits (drupes) in Cervantesiaceae (e.g., in *Okoubaka*) are the largest seen in Santalales. In *Cervantesia*, *Jodina* and *Staufferia* the five perianth valves extend basipetally upon fruiting. In the mature fruit these valves either remain on the fruit (*Cervantesia*, *Staufferia*) or in *Jodina* the outer exocarp dehisces leaving a white, fleshy inner exocarp covering on the stony mesocarp.

The clade that includes the genera of Cervantesiaceae is strongly supported by molecular data and intergeneric relationships are fully resolved (Der & Nickrent, 2008; Rogers & al., 2008). The family is composed of two clades, the first with *Acanthosyris*, *Cervantesia* and *Jodina* (the South American or *Cervantesia* clade) and a second composed of the remaining four genera (*Pyrularia* clade). Biogeographically, *Pyrularia* shows the eastern North American, eastern Asian disjunction also seen in *Buckleya* (Thesiaceae). The large fruits of *Acanthosyris annonagustata* C. Ulloa & P. Jørg are eaten by local people. Parasitism of surrounding vegetation by *A. asipapote* M. Nee and *Okoubaka* has been documented and is sufficiently severe to limit growing crops around the plants.

15. Family Nanodeaceae Nickrent & Der, fam. nov. — Type: *Nanodea* Banks ex C.F. Gaertn. Two genera: *Mida* A. Cunn. ex Endl. with one species, *M. salicifolia* A. Cunn., disjunct from New Zealand to the Juan Fernandez Islands; and *Nanodea* Banks ex C.F. Gaertn. with one species, *N. muscosa* C.F. Gaertn., of temperate South America (Patagonia, Tierra del Fuego, and the Falkland Islands).

Arbores (*Mida*) vel suffrutices (*Nanodea*) in radicibus parasitici. Folia alterna, tenuia carnosave. Flores bisexuales 4-meri calyculo subtenti, disci lobulis glandularibus inter tepala alternantibus, antherarum connectivis ad tepala trichomatibus affixis, ovario semi-infero (*Mida*) vel infero (*Nanodea*). Fructus ex drupa perianthio persistente coronata constans.

Mida is a hemiparasitic tree whereas *Nanodea* is a turf- or mat-forming dwarf shrub that inhabits peat bogs. Both have alternate, simple leaves, but of different forms. *Mida* has expanded "*Salix*-like" leaves whereas in *Nanodea* they are linear and somewhat fleshy. The flowers are bisexual, tetramerous, with a calyculus. Hairs opposite the stamens as well as a lobed glandular disk are present. The one-locular ovary is inferior in *Nanodea* and half inferior in *Mida*. The placental column is straight and, at least in *Mida* extends beyond the ovules apically as a conical projection to the base of the style. Two or three ategmic ovules occur. The embryo sac extends beyond the ovule or placenta. The mature fruit is a drupe (pseudodrupe) crowned by the persistent perianth parts.

Mida presents generalized vegetative and floral characters, thus it is not surprising that it was classified with members of Santaleae such as *Fusanus* and *Eucarya*, both now included in *Santalum* (Pilger, 1935). This relationship was supported by embryological features, such as the *Polygonum* embryo sac that extends beyond the ovule in the 4-nucleate stage. But variations on this "aggressive" embryo sac behavior also occurs in other Santalaceae s.l. as well as in Opiliaceae, Misodendraceae and Loranthaceae, thus this feature cannot be used to link *Mida* to any particular santalalean clade. The geographical distributions of these two genera suggests they may be Gondwanan relicts.

16. Family Santalaceae R. Br. (1810), emend. — Eleven genera: *Antidaphne* Poepp. & Endl. with seven species of South America, the Caribbean, and Mexico; *Colpoon* P.J. Bergius [including *Fusanus compressus* Murr] with two species of South Africa; *Eubrachion* Hook. f. with two species from the Caribbean to South America; *Exocarpos* Labill. with 26 species of Southeast Asia and Malaysia to Hawaii; *Lepidoceras* Hook. f. with two species of Chile; *Myoschilos* Ruiz & Pav. with one species, *M. oblongum* Ruiz & Pav., of Argentina and Chile; *Nestronia* Raf. [including *Darbya* A. Gray] with one species, *N. umbellula* Raf., of eastern U.S.; *Omphacomeria* (Endl.) A. DC. with one species; *O. acerba* (R. Br.) A. DC., of southeastern Australia; *Osyris* L. with two species of Europe, the Mediterranean, Africa to China; *Rhoiacarpos* A. DC. with one species, *R. capensis* (Harv.) A. DC., endemic to South Africa; and *Santalum* L. with 16 species from Indomalaya to Australia and Hawaii. Includes Eremolepidaceae Tiegh. ex Kuijt.

Root-hemiparasitic trees, shrubs and stem hemiparasites (mistletoes). Leaf form is variable with alternate and opposite arrangements, persistent or caducous, expanded lamina or reduced to scales (squamate). Plant sexual conditions are various including bisexual flowers, dioecious, monoecious, andromonoecious, and androdioecious. Inflorescences are axillary and terminal and of various types: solitary flowers, monochasia, spikes, cymes (simple and compound dichasia), panicles, fascicles, and umbels. A calyx is absent or, in *Myoschilos*, present as a calyculus. Petals 3–6, free or fused into a corolla tube that is short and campanulate or urceolate. Petal hairs opposite the stamens may be present or absent (*Exocarpos*, *Omphacomeria*, mistletoes). Staminodes and pistillodes sometimes present (e.g., *Omphacomeria*). A glandular disk is present in *Eubrachion*, *Lepidoceras* and *Nestronia* (male flowers only). The ovary position varies from half-inferior (e.g., *Exocarpos*, *Santalum*) to inferior (e.g., *Colpoon*). In some genera, such as *Colpoon*, *Rhoiacarpos* and *Osyris* the locule is lobed at the base thus suggesting carpel number. Fruits are drupes (pseudodrupes) sometimes with the subtending pedicel swollen and fleshy (e.g., *Exocarpos*). In the aerial parasites the fleshy mesocarp, forms fibrous seed attachment structures.

Santalaceae s.str. were highly supported as monophyletic using molecular data (Der & Nickrent, 2008), a somewhat surprising result given the wide morphological diversity seen among its members. The family includes Eremolepidaceae, a clade containing three genera of New World mistletoes whose members have been assigned to a variety of santalalean families: Loranthaceae (Kuijt, 1968), Eremolepidaceae (Kuijt, 1988), Santalaceae (Wiens & Barlow, 1971), and Viscaceae (Bhandari & Vohra, 1983). Tribe Anthoboleae, formerly containing *Anthobolus*, *Omphacomeria* and *Exocarpos*, is now defunct given that *Anthobolus* has been transferred to Opiliaceae. The other two genera are closely related and sister to the remaining genera in the family.

17. Family Amphorogynaceae (Stauffer ex Stearn) Nickrent & Der, stat. nov. — Based on tribe Amphorogyneae Stauffer ex Stearn (Stearn 1972: 6). Nine genera: *Amphorogyne* Stauff. & Hürl. with three species endemic to New Caledonia; *Choretrum* R. Br. with six species of Australia; *Daenikera* Hürl. & Stauff. with one species, *D. corallina* Hürl., endemic to New Caledonia; *Dendromyza* Danser [including *Cladomyza* Danser] with 21 species of southeastern Asia, Malaysia, Indonesia, and New Guinea; *Dendrotrophe* Miq. [including *Henslowia* Blume] with four species from the Himalayas to the Philippines and Malaysia, Indonesia; *Dufrenoya* Chatin with eleven species of Indonesia and Malaysia; *Leptomeria* R. Br. with 17 species of

Australia; *Phacellaria* Benth. with four species of eastern India to southern China; *Spirogardnera* Stauff. with one species, *S. rubescens* Stauff., endemic to Western Australia.

Root-parasitic small trees and shrubs, amphiphagous (root and stem-parasitic) shrubs, stem dendroparasites (lianas), and stem-parasitic shrubs (mistletoes). *Phacellaria* is a hyperparasite on Loranthaceae and other Amphorogynaceae. Stems with sympodial branching, in some aerial parasites differentiated into vegetative and haustorial shoots. Leaves alternate or subverticillate, either dimorphic or not dimorphic, persistent, caducous or deciduous, developed or as scales (squamate). Plants with bisexual flowers or unisexual (then plants dioecious). Inflorescences various including solitary flowers, monochasia, spikes, racemes, umbels and panicles. Neither a calyx nor a calyculus is present. The uncinate petals number 4–6 and are occasionally fused into a short corolla tube. Hairs on the petals opposite the stamens are present in most genera (*Dendromyza* and *Phacellaria* the exceptions). Stamens same number as petals. Staminodes and pistillodes sometimes present. Filament very short, equal to or slightly shorter or longer than the anther. The anthers are attached to very short filaments in a dorsifixed manner or the anther is sessile. Instead of the locules of the tetrasporangiate anthers being oriented in one plane, two are anterior and two are posterior. The locules are then anisomerous, i.e., of unequal size. Each thecal loculus dehisces independently (as opposed to a longitudinal slit common to both), an unusual feature that compelled Stauffer (1969) to recognize tribe Amphorogyneae. A glandular disk is present on top of the inferior ovary that may or may not be lobed. The style is either very short or absent. A unique “open” condition exists in *Phacellaria* where the style is hollow and opens directly into the ovarian locule. The ovary at the base contains 1–6 semilocules but is unilocular above. The placental column is straight, sometimes extending apically beyond ovules, and bears 2–5 ategmic ovules. The embryo sac sometimes extends beyond the ovule or placenta and a suspensor is present. The mature fruit (drupe) is crowned by persistent perianth parts. In arial parasites (*Dendromyza*, *Dendrotrophe*, *Phacellaria*), the exocarp and mesocarp are fibrous, both combining to form seed attachment structures. In *Dendromyza* and *Dufrenoya* the endocarp divides into segments, hence the fruit is a pyrene with lobed seeds.

Molecular analyses by Der & Nickrent (2008) yielded a strongly supported and fully resolved clade, identical in composition to tribe Amphorogyneae (Stauffer, 1969; Stearn, 1972), that is here recognized at the family rank. These data (and Nickrent, unpub.) indicate that the rare taxon *Spirogardnera* is so closely related to *Leptomeria* that it may be congeneric. When the four trophic modes (above) are optimized on the molecular tree, several evolutionary trends can be seen. When *Daenikera* and *Dendrotrophe* were scored as polymorphic (root parasites and mistletoes), the most parsimonious condition for the spine of the tree is the amphiphagous condition. This suggests that the ancestral Amphorogynaceae, and the common ancestor with Viscaceae, was amphiphagous. Two examples of highly unusual morphological features in Amphorogynaceae are as follows. The Australian root parasite *Leptomeria drupacea* (Labill.) Druce (as *L. billardieri* R. Br.) is possibly unique among angiosperms in having an unusual homeotic mutation—this species forms embryo sac–like structures in its microsporangia (Ram, 1959).

18. Family Viscaceae Batsch (1802). — Seven genera: *Arceuthobium* M. Bieb. with 26 species of North and Central America, Asia, Africa, and the Azores; *Dendrophthora* Eichl. with 68 species from the Caribbean, Mexico, and South America; *Ginalloa* Korth. with five species of Indomalaysia; *Korthalsella* Tiegh. with ca. 30 species of Africa, Madagascar, Mascarenes, from the Himalayas to Japan, Australia, and New Zealand; *Notothixos* Oliv. with eight species from Sri Lanka to southeast Asia and Australia; *Phoradendron* Nutt. with 234 species from North, Central and South America and the Galapagos Islands; and *Viscum* L. with ca. 150 species of temperate and tropical Old World.

Stem-parasitic herbs and shrubs (mistletoes). Stems and leaves often brittle, glabrous or pubescent. Leaves opposite, persistent, curvinerved, either developed or reduced to scales (squamate). Plant sexual conditions may be dioecious, monoecious or andromonoecious. Inflorescences as axillary or terminal spikes and cymes (simple and compound dichasia) and fascicles. Flowers small (less than 3 mm), unisexual, monochlamydous, with no calyx or calyculus present. Petals 2–4, valvate, free or sometimes fused into a short corolla tube, bearing as many stamens. Filament very short or absent. Anther attachment basifixed and anther sessile or nearly so. Anther 2-locular (bisporangiate), more than 2-locular, or the archesporium a ring (synandrium) around a central columella. Anther locule isomerous, dehiscence transverse by slits and by a single or multiple pores. Glandular disk absent or not well-defined on female flowers but present on male flowers. Ovary inferior, unilocular at base and above. Ovules or integuments are often not present, instead the embryo sacs arise from a placental nucellar complex (mamelon). Fruit a berry with one endospermous seed that has chlorophyllous endosperm. Fruit explosively dehiscent in *Arceuthobium*. Fruit mesocarp fibrous, forming seed attachment structures (viscin).

Although past classifications considered Viscaceae as part of Loranthaceae, the recognition that these two families as distinct comes from embryology (Johri & Bhatnagar, 1960), morphology (Kuijt, 1969), cytology (Wiens & Barlow, 1971), the fossil record (Muller, 1981), and biogeography (Barlow, 1983). All molecular phylogenetic analyses conducted to date gave strong support for the monophyly of this family (Nickrent & Soltis, 1995; Nickrent & al., 1998; Nickrent & Malécot, 2001; Der & Nickrent, 2008). To solve the problem of paraphyly among the clades of Santalaceae s.l., Viscaceae were “lumped” with it in both of the Angiosperm Phylogeny Group publications (APG, 1998, 2003, 2009). The present work presents a classification that solves the same problem but by “splitting” Santalaceae s.l. into six monophyletic groups according to clades reported in the multigene molecular phylogenetic analysis by Der & Nickrent (2008). By retaining both names (Viscaceae and Santalaceae s.str.), this option results in less disruption of the existing system where these names are well established and frequently used.

Past molecular phylogenetic work (Nickrent & al., 1998) resolved some relationships among the genera of Viscaceae, e.g., *Viscum* + *Notothixos*, *Phoradendron* + *Dendrophthora*, *Korthalsella* + *Ginalloa* and *Arceuthobium*, but these four groups emerged from a polytomy. More recent work (Mathiasen & al., 2008) reported a study using two nuclear and two chloroplast genes where the *Viscum* + *Notothixos* clade was sister to the remaining taxa and the *Phoradendron* + *Dendrophthora* clade was sister to *Arceuthobium*. The latter relationship gains additional support from the pattern of deletions seen in chloroplast 16S-23S intergenic spacers (Nickrent & García, 2009). Molecular data from Ashworth (2000a,b) indicate both *Phoradendron* and *Dendrophthora* are paraphyletic. With additional taxon sampling the latter may be sunk into the former genus.

■ PERSPECTIVES ON THE NEW SANTALALES CLASSIFICATION

The clades representing all 18 families described in this work received maximum parsimony bootstrap values of 100 and Bayesian inference values of 1.0 in the various molecular phylogenetic studies (Der & Nickrent, 2008; Malécot & Nickrent, 2008; Vidal-Russell & Nickrent, 2008b). Thus, the primary principle of monophyly recommended by Backlund & Bremer (1998) has been adhered to for this rank. Moreover, the secondary principle of support for monophyly has also been followed as support values are high from multiple genes and two methods of analysis.

A modern but premolecular classification such as that of Cronquist (1981) recognized seven "core" families (excluding Balanophoraceae, Dipentodontaceae, and Medusandraceae) in Santalales: Olacaceae, Misodendraceae, Loranthaceae, Opiliaceae, Santalaceae, Eremolepidaceae and Viscaceae. The secondary principle that recommends maximizing stability (minimizing nomenclatural changes) is similar to Stevens' recommendation to preserve groups that are well-established in the literature. Two of the "core" santalalean families were para- or polyphyletic based on morphological and molecular analyses: Olacaceae s.l. and Santalaceae s.l. In both these cases monophyletic groups were split from the assemblages, but in neither case was the original family name lost. One family name, Eremolepidaceae, was not used because its three genera were well-embedded within Santalaceae s.str. Thus six of the seven "core" family names have been retained but in some cases their generic compositions altered. In addition to those six, twelve family names are now applied to clades that differ from those in Cronquist (1981): Erythropalaceae, Strombosiaceae, Coulaceae, Ximeniaceae, Aptandraceae, Octoknemaceae, Schoepfiaceae, Comandraceae*, Thesiaceae, Cervantesiaceae*, Nanodeaceae*, and Amphorogynaceae*. The four families marked with asterisks (*) are proposed here for the first time. The remaining family names have previously been proposed and are being resurrected here.

The principle to maximize phylogenetic information and minimize redundancy was considered as well. For example, there is evidence that Strombosiaceae and Erythropalaceae may be a clade, but bootstrap support for this is low. Thus, to name this clade as a family would violate the primary principle of monophyly. Similarly, bootstrap support is too low to combine Thesiaceae and Cervantesiaceae. In several cases, support values along the portions of the molecular tree are low (polytomies), thus not providing full resolution of interfamilial relationships: Coulaceae, Ximeniaceae, Aptandraceae, Olacaceae, Octoknemaceae, Comandraceae, Thesiaceae, and Cervantesiaceae. Attempts to minimize redundancy with these families (i.e., "lump") would in most cases result in very morphologically heterogeneous assemblages, thus violating the recognizability principle. Similarly, we view the option, taken by APG, to lump Santalaceae s.l. and Viscaceae as undesirable because the resulting clade is extremely morphologically heterogeneous. If this option were taken, there would be little reason not to also include Opiliaceae. We consider the families that arise from polytomies *sedis mutabilis* (position changeable) and expect that their positions will stabilize with additional molecular analyses.

Considering family size, two families are monogeneric under this revised classification: Misodendraceae and Octoknemaceae. One could consider enlarging the former family (containing just *Misodendrum*) by including genera here listed under Schoepfiaceae, but the two families are so distinct morphologically this would be an undesirable action. Similarly, Octoknemaceae (containing just *Octoknema*) is morphologically distinct and, as discussed above, attempts to place this genus with Olacaceae s.l. or more derived groups have been thwarted. Its topological position on the phylogenetic tree, i.e., as sister to many families in the order, does not allow easy placement in a Linnaean classification. The tendency for monogeneric groups to occur as sister to species-rich clades is not unusual within angiosperms (Chase & al., 2000). In situations such as this, Backlund & Bremer (1998) admit that circumscribing monogeneric families appears to be the best solution. Seven of the families contain only two or three genera. In most of these families, several of the component genera are also monospecific, thus suggesting these clades represent isolated and/or relictual cladogenic events.

We believe that the clades obtained from multigene molecular analyses represent the best current hypotheses for the evolutionary lineages within Santalales. From these clades we have proposed a revised classification of the order, yet the resulting families are, in some cases, more difficult to identify and circumscribe using morphological features. Numerous examples can be given where molecular phylogenetic methods have identified a strongly supported clade that lacks morphological synapomorphies (Chase & al., 2000; Smith & al., 2006), but recognition of the group is justified by assuming such synapomorphies (be they micromorphological, chemical or genomic) exist and remain to be discovered. We present below a key that uses available morphological information to identify the 18 families of Santalales. Especially for Olacaceae s.l. and Santalaceae s.l., anatomical and embryological features were sometimes employed because most macromorphological features are polymorphic among clades. Characters such as parasitism mode (stem vs. root), plant sexual condition, ovary position, petal hair tufts opposite stamens, seed viscin tissue, etc. have states that appear multiple times in different clades. As discussed in Der & Nickrent (2008), it seems this variation is fractal in nature, in other words, similar themes appear repeated at different hierarchical levels. In general, unambiguous synapomorphies delimiting families and larger grouping are rare, thus characterization usually requires unique combinations of characters.

KEY TO SANTALALES FAMILIES

1\. Parasitic or not; flowers dichlamydous (except some *Octoknema* of Octoknemaceae); stamens equal to or greater in number than petals; ovules unitegmic or bitegmic; seeds with a thin testa. 2
1\. Parasitic; flowers monochlamydous (sepals absent) or dichlamydous (often with reduced sepals); stamen and petal numbers equal; ovules ategmic; seeds without a testa. . 8
2\. Stellate pubescence present; flowers unisexual (plants dioecious); ovary inferior. . . . .**Octoknemaceae**
2\. Stellate pubescence absent; flowers bisexual (except *Harmandia* and *Hondurodendron* of Aptandraceae); ovary superior (except some *Strombosia* of Strombosiaceae) . . . 3
3\. Not parasitic (haustoria absent) 4
3\. Root-parasitic (haustoria present). 6
4\. Leaf dendritic hairs present; epidermal cells lignified; leaves with schizogenous cavities; stamen whorls two or three . . . . **Coulaceae**
4\. Leaf dendritic hairs absent; epidermal cells not lignified; leaves without schizogenous cavities; stamen whorls one or two 5
5\. Epidermal cell druses present (except *Scorodocarpus*); sepals completely connate . . . . **Strombosiaceae**
5\. Epidermal cell druses absent; sepals partially connate. . . . . **Erythropalaceae**
6\. Inflorescence a simple umbel; calyx not accrescent . . . . **Ximeniaceae**
6\. Inflorescences various but not a simple umbel; calyx accrescent or not. 7
7\. Stamens in one whorl; anther dehiscence by pores or flaps; ovary 1- or 2-locular . . . . **Aptandraceae**
7\. Stamens (including staminodes) in two whorls; anther dehiscence by slits; ovary 1-locular . . . . **Olacaceae**
8\. Stem-parasitic; fruit an achene bearing accrescent feathery staminodes alternate with perianth lobes. . . . . **Misodendraceae**
8\. Stem- or root-parasitic; fruit a drupe, 1-seeded berry, nutlet (not a plumose achene) 9
9\. Distylous; floral bracts and bracteoles fused into a cup in *Quinchamalium* and *Schoepfia*; petals connate into a tube; petal hairs opposite the stamens present in *Arjona* and *Schoepfia* . . . . **Schoepfiaceae**
9\. Not distylous; floral bracts and bracteoles (if present) separate; petals free or connate; petal hairs opposite the stamens present or absent 10
10\. Anterior and posterior anther locules of unequal size, each thecum dehiscing transversely independently; petals with uncinate tips . . . . **Amphorogynaceae**
10\. Anterior and posterior anther locules of equal size, each thecum dehiscing by a common longitudinal slit or (in *Viscum*) anthers fused with porose dehiscence; petals without uncinate tips 11
11\. Leaf cystoliths present (absent in *Anthobolus*); ovary superior. . . . . **Opiliaceae**
11\. Leaf cystoliths absent; ovary half or fully inferior . . . 12
12\. Calyx present as foliaceus sepals (female flowers of *Buckleya*) or a calyculus (calyx remnant). 13
12\. Calyx or calyculus absent. 15
13\. Root and stem parasites; petal hairs opposite stamens absent; seed with viscin tissue . . . . **Loranthaceae**
13\. Root parasites; petal hairs opposite stamens present (absent in *Buckleya*); seed without viscin tissue. 14
14\. Fruit mesocarp fleshy, endocarp wall bony or cartilaginous. . . . . **Nanodeaceae**
14\. Mesocarp bony, endocarp parenchymatous or crustaceous . . . .**Thesiaceae**
15\. Embryo suspensor present . . . . **Santalaceae**
15\. Embryo suspensor absent 16
16\. Stem-parasitic; phyllotaxy decussate; seed with viscin tissue . . . .**Viscaceae**
16\. Root-parasitic; phyllotaxy alternate; seed without viscin tissue 17
17\. Stems and leaves pubescent; trees or shrubs . . . . **Cervantesiaceae**
17\. Stems and leaves glabrous; herbaceous perennials . . . . **Comandraceae**

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