

# The Families and Genera of Vascular Plants

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Edited by K. Kubitzki

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*Volume XII*

## Flowering Plants Eudicots

Santalales, Balanophorales

J. Kuijt, B. Hansen

THE FAMILIES  
AND GENERA  
OF VASCULAR PLANTS

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**XII**     *Flowering Plants · Eudicots*  
*Santalales, Balanophorales*

Job Kuijt · Bertel Hansen

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With 82 Figures

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## Foreword

Some years ago I sent Prof. Kuijt a photograph of a mistletoe of a genus that is endemic to southern Chile and Argentina, and largely restricted to the tree genus *Nothofagus* as its host. Upon this first contact we found out that we shared great love for the forests of austral South America, and with some discretion I could familiarize Dr. Kuijt with the scope and objective of my book series. Throughout his career Dr. Kuijt has made significant contributions to the morphology, biology and systematics of Santalales, which in my opinion made him the born author of Santalales for this book series. Nevertheless, because of the difficulties of the contentious family classification resulting from the apparently insurmountable differences between morphological and molecular data sets, he would have shied from this task had I not helped him to overcome these difficulties by pointing to the goal of the series, which is not so much aiming at a definitive family classification but rather trying to provide a broad factual basis that allows the reader to follow the arguments and form an own concept. I am particularly thankful to Dr. Kuijt who apart from the taxonomic treatment of Santalales has also given broad attention to the phenomenon of parasitism with all its manifestations such as primary haustoria and ramal parasitism, secondary haustoria and root parasitism, and the haustorial connection and tissue continuity between host and parasite, important topics that all have been the subject of Dr. Kuijt's lifelong studies. Thus, it remains for me to express to Dr. Kuijt my deepest gratitude for agreeing to author the present treatment and bringing it to a fortunate end. I am sure that the present volume will be the pride of my entire series!

The treatment of Balanophoraceae is based on a manuscript prepared about 35 years ago by the late Dr. B. Hansen as one of the first contributions to this book series. Unfortunately, the author did not live to see publication of his work but his later publications on the subject allowed me to include further original information both from his papers and also from other sources. Dr. Hansen will be remembered by the lasting imprint he left upon this book series, for which his original draft had served as a kind of starter.

I am also most grateful to the copyright holders who so readily allowed us to reprint in this volume most valuable illustrations published under their responsibility, including the Director and Board of Trustees, Royal Botanic Gardens, Kew, the Secretary of The Flora Malesiana Foundation, Leiden, the New York Botanical Garden Press, Bronx, New York, and the University of California Press, Berkeley and Los Angeles.

As usual, the present volume has greatly profited from the critical eyes of the copy editor Dr. Monique Delafontaine, to whom I am continually grateful for her dedicated work. Dr. Sabine von Mering deserves my thanks for compiling the index of the volume. I would also like to gratefully acknowledge the agreeable collaboration with Dr. Andrea Schlitzberger from the staff of Springer Verlag, and with SPi Technologies India TvP Limited for type setting and page laying.



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I am indebted to Valéry Malécot for information on *Brachynema* and *Scleropyrum*, to Daniel Nickrent for answers to various literature questions, and to Jim Reveal for nomenclatural advice. Gerry Allen gave of her time to discuss some technical points on phylogenetic taxonomy. Paul Hiepko contributed significantly to my understanding of Opiliaceae. The editor of this series, Klaus Kubitzki, has been extremely helpful during the preparation of this work. To all, my sincere thanks.

Job Kuijt





# Contents

<b>SANTALALES</b>	
<b>Historical Survey</b>	3
<b>Morphology and Anatomy</b>	7
<b>Chromosome Numbers and Embryology</b>	17
<b>Fruits, Seeds and Seedlings</b>	21
<b>Germination</b>	25
<b>Biological and Structural Aspects of Parasitism</b>	27
<b>Chemosystematics</b>	43
<b>Santalales in Human Affairs and Conservation</b>	49
<b>Family Classification</b>	53
<b>Key to the Families of Santalales</b>	57
<b>Aptandraceae</b>	59
<b>Coulaceae</b>	65
<b>Eremolepidaceae</b>	69
<b>Loranthaceae</b>	73
<b>Misodendraceae</b>	121
<b>Octoknemaceae</b>	125
<b>Olacaceae</b>	127
<b>Opiliaceae</b>	137
<b>Santalaceae</b>	143
<b>Schoepfiaceae</b>	167
<b>Viscaceae</b>	169
<b>Ximeniaceae</b>	187

**BALANOPHORALES**

<b>Balanophoraceae</b>	.....	193
<b>Glossary</b>	.....	209
<b>Index</b>	.....	211

# SANTALES

By J. Kuijt

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## Historical Survey

The order Santalales has had a complex history, its contents and outline undergoing many changes over the years, and significant controversies persist in our days. A very detailed historical account was provided by Reed (1955); innumerable genera have in the past been placed in the order and subsequently been removed. (For a brief history of neotropical mistletoes, see Kuijt 2014; Table 1.)

The affinities between Olacaceae, Loranthaceae and Santalaceae were not beginning to be recognized until Brown (1810) first placed the last two families together. Three years later the “Olacineae” were introduced as a family (Mirbel 1813) but placed remote from Santalaceae and Loranthaceae, a suggestion followed by de Candolle (1824) who also treated Loranthaceae in a separate volume of his *Prodromus* (de Candolle 1830). There are cautious hints in Endlicher’s writing (Endlicher 1837) that the three families might be related, but they remained widely separated in his publication. The three families were for the first time united by A. Brongniart (1850), who placed them together in his *Class Santalineae*, along with some doubtful groups. Planchon and Decaisne (1855), agreeing with these suggested affinities, added Proteaceae, an affinity that is no longer taken seriously today. It is in that publication that we first find the term “calycode” used that, in our contemporary terminology, would probably compare to “calyculus”. Bentham and Hooker did not follow these French workers; both Loranthaceae and Santalaceae are to be found in volume 3, but “Olacineae” (the present Olacaceae and Opiliaceae, but also containing Icacinaceae) were treated in volume 1 of their *Genera Plantarum* (Bentham and Hooker 1862–1883). Baillon

(1892) proposed a much wider concept of Loranthaceae that included genera today placed in Olacaceae, Erythralaceae, Grubbiaceae, Balanophoraceae, and Misodendraceae. While this conception today is of little more than historic interest, we find these families grouped together in the same volume in both editions of *Die Natürlichen Pflanzenfamilien*. Before the end of the 19th century, meanwhile, Van Tieghem proposed a profound fragmentation of what we today know as Santalales (Van Tieghem 1898), basing at least some of his arguments on the variable structure of ovules. Since this proliferation of families and orders has not been followed by any subsequent worker, it remains as no more than a complex series of footnotes with little bearing on our present insights.

A more realistic and modern view of Santalales was not available until Schellenberg’s pivotal work (1932). Here we find Olacaceae at the base of the various families because of having 0–2 integuments, and the Loranthaceae (at that time still including both Viscaceae and Eremolepidaceae) at the order’s terminus because of the lack of differentiated ovules. Part of Schellenberg’s motivation was a perceived gradient of increasing parasitism—an idea that, however, inadequately defined or supported, may have been traceable to Van Tieghem’s publications (none of which are cited in Schellenberg’s work), and was to be repeated by some later students like Reed (1955). However, the resultant more or less linear arrangement of families was not always convincing. Clearly, such ideas have had an influence on later writers, especially in the second edition of *Die natürlichen Pflanzenfamilien*.

**Table 1** Family disposition of genera of Santalales beyond mistletoes and non-contentious Santalaceae. (For contentious members of the Santalaceae, see Table 4 under that family.)

	Sleumer (1935a, 1935b) or others	Nickrent et al. (2010)	Present treatment
<i>Anacolsa</i>	Olacaceae	Aptandraceae	Olacaceae
<i>Aptandra</i>	Olacaceae	Aptandraceae	Aptandraceae
<i>Arjona</i>	Santalaceae	Schoepfiaceae	Santalaceae
<i>Brachynema</i>	Olacaceae	Excluded	Olacaceae
<i>Cansjera</i>	Opiliaceae	Opiliaceae	Opiliaceae
<i>Cathedra</i>	Olacaceae	Aptandraceae	Olacaceae
<i>Chaunochiton</i>	Olacaceae	Aptandraceae	Aptandraceae
<i>Coula</i>	Olacaceae	Coulaceae	Coulaceae
<i>Curupira</i>	Black and Murça Pires (1948): Olacaceae	Ximeniaceae	Ximeniaceae
<i>Diogoia</i>	Excell and Mendonça (1951): Olacaceae	Strombosiaceae	= Strombosiopsis
<i>Douradoa</i>	Sleumer (1984a, 1984b): Olacaceae	Ximeniaceae	Ximeniaceae
<i>Dulacia (Liriosma)</i>	Olacaceae	Olacaceae	Olacaceae
<i>Eganthus</i>	Olacaceae	-	= Minquartia
<i>Endusa</i>	Olacaceae	-	= Minquartia
<i>Engomegoma</i>	Breteler et al. (1996): Olacaceae	Strombosiaceae	Olacaceae
<i>Erythralpalum</i>	Excluded	Erythralpalaceae	Excluded
<i>Harmandia</i>	Olacaceae	Aptandraceae	Aptandraceae
<i>Heisteria</i>	Olacaceae	Erythralpalaceae	Olacaceae
<i>Hondurodendron</i>	Ulloa et al. (2010): Aptandraceae	Aptandraceae	Aptandraceae
<i>Liriosma = Dulacia</i>			
<i>Maburea</i>	Maas et al. (1992): Olacaceae	Erythralpalaceae	Olacaceae
<i>Malania</i>	Lee (1980): Olacaceae	Ximeniaceae	Ximeniaceae
<i>Minquartia</i>	Olacaceae	Coulaceae	Coulaceae
<i>Ochanostachys</i>	Olacaceae	Coulaceae	Coulaceae
<i>Octoknema</i>	Octoknemaceae	Octoknemaceae	Octoknemaceae
<i>Olox</i>	Olacaceae	Olacaceae	Olacaceae
<i>Ongoeka</i>	Olacaceae	Aptandraceae	Aptandraceae
<i>Phanerodiscus</i>	Cavaco (1954): Olacaceae	Aptandraceae	Aptandraceae
<i>Ptychopetalum</i>	Olacaceae	Olacaceae	Olacaceae
<i>Quinchamalium</i>	Santalaceae	Schoepfiaceae	Santalaceae
<i>Schoepfia</i>	Olacaceae	Schoepfiaceae	Schoepfiaceae
<i>Scorodocarpus</i>	Olacaceae	Strombosiaceae	Olacaceae
<i>Strombosia</i>	Olacaceae	Strombosiaceae	Olacaceae
<i>Strombosiopsis</i>	Olacaceae	Strombosiaceae	Olacaceae
<i>Tetrastylidium</i>	Olacaceae	Strombosiaceae	Olacaceae
<i>Ximienia</i>	Olacaceae	Ximeniaceae	Ximeniaceae

As mentioned above, the first detailed, general treatment of Santalales is found in the first edition of *Die natürlichen Pflanzenfamilien*. In the second edition of this work, more up to date accounts were provided for Olacaceae (Sleumer 1935a), Opiliaceae (Sleumer 1935b), Octoknemaceae (Mildbraed 1935), Misodendraceae (Skottsberg 1935), Loranthaceae, s.l. (Engler and Krause 1935), and Santalaceae (Pilger 1935). The order was considered to be allied to some holoparasitic families (Balanophoraceae, Rafflesiaceae, Hydnoraceae), but the role of parasitism appears to have had undue influence in these assignments. In the case of Balanophoraceae, surprisingly, recent molecular data provide some sup-

port for a relationship of that family with the Santalales (Barkman et al. 2007; Su and Hu 2008; Nickrent et al. 2010). In fact, the occurrence and nature of parasitism in some of the families presently included has by no means been fully explored beyond the obviously parasitic mistletoes and Santalaceae, s.l. Considering the highly advanced nature of the haustoria in these genera, it is difficult to conceive of parasitism having evolved in only some genera of a family and not in others. Undoubtedly, much still needs to be explored in this regard. A listing of documented parasitism in Santalales is provided in Tables 2 and 3 on p. 2.

Families for which the exclusion from Santalales is no longer controversial include

Dipentodontaceae (Worberg et al. 2009), Grubiaceae (APG II 2003), and Medusandraceae (Soltis et al. 2007). More details on the convoluted history of Santalales are found in Harms (1935) and Reed (1955).

Undoubtedly the most significant taxonomic development in recent years has been the application of molecular methods to Santalales, as seen in the work of D.L. Nickrent and co-workers, especially in Der and Nickrent (2008) and Nickrent et al. (2010). This work has led to a fundamental revision, at the family level, of the entire order, and to a new tribal and subtribal organization of the largest family, Loranthaceae, as presented under that family below. A number of new families were proposed or reinstated from earlier workers, some of these proposals appearing to be problematic. However, this is not an appropriate place to enter into a detailed consideration of contentious issues in some of those families, for these will be dealt with in the relevant places. The general aim of the present treatment is to try and reconcile molecular data with morphological information wherever resulting in recognizable, definable families. I see it as my task to provide a comprehensible account of this highly complex order even if occasional apparent conflicts with molecular or cladistic indications remain (see Nordal and Stedje 2005; Brummitt 2006; Zander 2011). The main history of contentious genera in the order are indicated in the following table.

## References

- APG II (Angiosperm Phylogeny Group). 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399–436.
- Baillon, H.E. 1892. *Histoire des plantes* 11: 449. Paris: L. Hachette & Cie.
- Barkman, T.L., McNeal, J.R., Lim, S.-H., Croom, H.B., Young, N.D., de Pamphilis, C.W. 2007. Mitochondrial DNA suggests at least 11 origins of parasitism in angiosperms and reveals genomic chimerism in parasitic plants. *BMC Evol. Biol.* 7: 248.
- Bentham, G., Hooker, J.D. *Genera Plantarum*, 1862–1883. London: Reeve.
- Black, G.A., Murça Pires, J. 1948. Dois gêneros novos *Curupira* e *Froesia*, cinco espécies novas, uma nova combinação, chaves e observações sobre plantas da região Amazônica. *Bol. Técn. Inst. Agron. Norte* 15: 1–32.
- Breteler, F.J., Baas, P., Boesewinkel, F.D., Bouman, F., Lobreau-Callen, D. 1996. *Engomegoma* Breteler (Olacaceae), a new monotypic genus from Gabon. *Bot. Jahrb. Syst.* 118: 113–132.
- Brongniart, A.T. 1850. Énumération des genres de plantes cultivés au Muséum d'histoire naturelle de Paris, ed. 2, p. 176.
- Brown, R. 1810. *Prodromus florae Novae Hollandiae*, p. 357.
- Brummitt, R.K. 2006. Am I a bony fish? *Taxon* 55: 268–269.
- Candolle, A.P. de. 1824. *Prodromus systematis naturalis regni vegetabilis*. 1: 531.
- Candolle, A.P. de. 1830. *Mémoire sur les Loranthacées*. *Coll. Mém.* VI: 12.
- Cavaco, A. 1954. Sur le genre *Phanerodiscus* gen. nov. (Olacacées) de Madagascar. *Not. Syst.*, Paris 15: 10–14.
- Der, J., Nickrent, D.L. 2008. A molecular phylogeny of Santalaceae (Santalales). *Syst. Bot.* 33: 107–116.
- Endlicher, S.L. 1837. *Genera plantarum*. Vienna: Fr. Beck.
- Engler, A., Krause, K. 1935. Loranthaceae. In: Engler, A., Harms, H., *Die natürlichen Pflanzenfamilien*, ed. 2, 16b: 98–203.
- Excell, A.W., Mendonça, F.A. 1951. Novidades de flora de Angola. *Bol. Socied. Broter.*, ser. 2, 25: 109–110.
- Harms, H. 1935. Reihen Santalales, Aristolochiales, Balanophorales. In: Engler, A., Harms, H., *Die natürlichen Pflanzenfamilien*, ed. 2, 16b: 1–4.
- Kuijt, J. 2014. Eremolepidaceae, Loranthaceae, and Viscaecae. In: Davidse, G. (ed.) *Flora Mesoamericana*. (in press)
- Lee, S.-K. 1980. *Malania*, a new genus of oil-yielding plant. *Bull. Bot. Lab. North-East Forest Inst.* 6(8): 67–72.
- Maas, P.J.M., Baas, P., Boesewinkel, F.D., Hiepko, P., Lobreau-Callen, D., Van den Oever, L., Ter Welle, B.J.H. 1992. The identity of “Unknown Z”: *Maburea* Maas, a new genus of Olacaceae in Guyana. *Bot. Jahrb. Syst.* 114: 275–291.
- Mildbraed, J. 1935. Octoknemaceae. In: Engler, A., Harms, A., *Die nat. Pflanzenfam.*, 2nd edn, 16b: 42–45.
- Mirbel, C.F.B. de. 1813. Notes pour servir à l'histoire naturelle de la famille des orangers. *Nouveau Bull. des Sciences*, par la Société Philomatique 3: 377–382.
- Nickrent, D.L., Malécot, V., Vidal-Russell, R., Der, J.P. 2010. A revised classification of Santalales. *Taxon* 59: 538–558.
- Nordal, I., Stedje, B. (coordinators). 2005. Paraphyletic taxa should be accepted. *Taxon* 54: 5–6.
- Pilger, R. 1935. Santalaceae. In: Engler, A., Prantl, K., *Die nat. Pflanzenfam.*, 2nd edn, 16b: 52–91.
- Planchon, J.É., Decaisne, J. 1855. (Communication). *Bull. Soc. Bot. France* 2: 86–87.
- Reed, C.F. 1955. The comparative morphology of the Olacaceae, Opiliaceae and Octoknemaceae. *Mem. Soc. Broteriana* 10: 29–79.
- Schellenberg, G. 1932. Über Systembildung und über die Reihe der Santalales. *Festschr. Deutsch. Bot. Ges.* 50a: 136–145.
- Skottsberg, C. 1935. Myzodendraceae. In: Engler, A., Prantl, K., *Die nat. Pflanzenfam.*, 2nd edn, 16b: 92–97.

- Sleumer, H. 1935a. Olacaceae. In: Engler, A., Prantl, K., Die nat. Pflanzenfam., 2nd edn, 16b: 5–32.
- Sleumer, H. 1935b. Opiliaceae. In: Engler, A., Prantl, K., Die nat. Pflanzenfam., 2nd edn, 16b: 33–41.
- Sleumer, H. 1984a. Olacaceae. Flora Malesiana, I, 10: 1–29.
- Sleumer, H. 1984b. Olacaceae. Flora Neotropica 38: 1–159. New York: Organiz. For Fl. Neotrop.
- Soltis, D.E. et al. 2007. Monophyly and relationships of the enigmatic amphitropical family Peridiscaceae. *Taxon* 56: 65–73.
- Su, H.-J., Hu, J.-M. 2008. Phylogenetic relationships of Balanophoraceae and Santalales based on floral B homeotic genes. (Abstract 512). *Botany* 2008. University of British Columbia, Vancouver, B.C.
- <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=512>.
- Ulloa, U.C., Nickrent, D.L., Whitefoord, C., Kelly, D.L. 2010. *Hondurodendron*, a new monotypic genus of Aptandraceae from Honduras. *Ann. Missouri Bot. Gard.* 97: 457–467.
- Van Tieghem, P. 1898. *Éléments de botanique*, ed. 3, 2: 290.
- Worberg, A. et al. 2009. Huerteales sister to Brassicales plus Malvales, and newly circumscribed to include *Dipentodon*, *Gerrardina*, *Huerteia*, *Perrottetia*, and *Tapiscia*. *Taxon* 58: 468–478.
- Zander, R.H. 2011. Structuralism in phylogenetic systematics. *Biol. Theory* 5: 383–394.



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## Morphology and Anatomy

**Stem.** The stems of members of Santalales are mostly terete, less commonly ridged or quadrangular; rarely they are alate or compressed to broadly complanate, as in species of *Dendrophthora*, *Exocarpos*, *Phoradendron*, in *Phthirusa hutchisonii*, and especially in many *Korthalsella*. In *Acanthosyris*, ramal thorns are present; this is also said to be true in *Ximenia* (Sleumer 1935), even though Sleumer's Fig. 11 does not show it.

The great majority of species in Santalales are glabrous or essentially so. Exceptions include *Minquartia* and *Octoknema*, which bear elaborate stellate epidermal hairs, the short-haired, young portions of *Coula*, a few species of *Phoradendron* and *Psittacanthus*, especially a number of Loranthaceae in Africa and Australia, and the genus *Notothixos* of Viscaceae that is characterized by dendritic hairs or peltate scales.

Stomatal types are simple and of the rubiaceous type, the guard cells usually being aligned in slightly oblique positions on stems, as can be seen in *Oryctanthus grammatus* (Kuijt 2011, his Fig. 3a). As in many other plants, abaxial leaf surfaces tend to have more stomata than adaxial ones. In *Misodendrum* subgen. *Gymnophyton*, the surface of young stems bears innumerable raised tubercles that each have a stoma at the top, below which is a large air space.

Little or no cork forms in mistletoes, but lenticels are occasionally prominent features, as in *Peristethium* and stems of *Psittacanthus*. The trees in the order, of course, have well-developed cork when older, which at times is distinctive in texture or color at the generic level.

No comprehensive survey of the internal anatomy of Santalales exists, but Reed (1955) has provided a detailed summary of Olacaceae, Opiliaceae, and Octoknemaceae. The latter family has been updated by Gosline and Malécot (2012), and similar information has been published for some Mexican mistletoes (Gómez-Sánchez et al. 2011). This information is difficult to summarize for a number of reasons, among which is the inclusion of many generic names in Reed's work that are not currently accepted, and the use of a complex wood terminology derived from his mentor, I.W. Bailey.

Stelar organization has rarely been commented on in the literature, but appears to be of the standard siphonostelar type. Wilson and Calvin (1996) have provided information on *Arceuthobium*, where initially a simple siphonostelar arrangement also prevails. However, in at least larger species, the bundles remain separate even though they expand tangentially, each curling somewhat laterally. Most species in the genus, being small or even short-lived, are not likely to show this pattern. Further information is given in several families below, including the unusual stelar structure in *Misodendraceae*. Other stelar modifications are to be expected in species that have evolved phyllodes, as in some species in Viscaceae and *Exocarpos*.

*Nuytsia* stems have prominent gum ducts containing slimy materials.

With regard to Santalalean wood structure, Reed (1955) has provided many details for Olacaceae, Opiliaceae, and Octoknemaceae. The nodal structure in these families is predominantly

trilacunar. *Anacolosa*, *Chaunochiton*, and *Cathedra* have unilacunar nodes, and *Scorodocarpus* is pentalacunar. The arrangement of vessels in the secondary wood in nearly all genera surveyed is radial, usually in short series. *Heisteria* is unusual in having a diffuse-porous vessel distribution, *Schoepfia* shows a tangential pattern, and some Opiliaceae tend to have solitary vessels. Perforation plates are simple except in *Engomegoma* (Breteler et al. 1996) and *Heisteria* (Reed 1955), where oblique, scalariform perforations occur, as they do in Octoknemaceae; lateral walls bear bordered pits. Vessels are surrounded by (sometimes septate) fibers in Octoknemaceae and *Engomegoma*, and by tracheids in *Heisteria* and Opiliaceae, but by libriform fibers or fiber tracheids in Coulaceae, *Chaunochiton*, *Strombosia*, *Strombosiopsis*, *Tetrastylidium*, *Anacolosa*, and *Cathedra*. Wood parenchyma is variously distributed: it is apotracheal in Opiliaceae, paratracheal in *Schoepfia*, and ranges from diffuse to aggregate in *Engomegoma*, *Heisteria*, *Strombosia*, *Strombosiopsis*, *Tetrastylidium*, and Coulaceae. *Octoknema* lacks wood parenchyma entirely. In general, many of such anatomical details are difficult to place in taxonomic context.

Because of the famous oil present in stems and roots of *Santalum album*, its wood structure has received some attention (Metcalf and Chalk 1950). There is little wood parenchyma, and only occasional, scattered vessel members occur, explaining the fine grain of the tree. The xylem consists mostly of fiber tracheids with bordered pits and narrow lumina. The oil of *S. album* is present in all cell types.

Phloem is probably present in all genera but has received little focused attention in the order. The curious near-absence of phloem in *Arceuthobium* is discussed under Viscaceae.

Secondary phloem tissues containing many clusters of thick-walled sclereids and cells containing calcium oxalate crystals and extrastelar fibers are commonly differentiated.

**Leaf.** The leaves of Santalales are uniformly simple, but squamate leaves occur in many groups. The apex is rounded to attenuate, rarely mucronate or emarginate; the base is also variable, mostly being petiolate, occasionally sessile or even clasping, as in some *Phoradendron*, *Psitta-*

*canthus*, *Oryctanthus*, and in various African genera. Linear leaves are found in *Amyema giberulum*, *A. preissii*, *Lysiana linearifolia* and other species in Australia, as well as in some *Thesium* and *Tripodanthus flagellaris*. The fleshy, terete leaves of the xerophytic *Psittacanthus sonorae* and *Amyema linophylla* may be unique in Loranthaceae. Stipules do not exist in the order. The leaf margin is entire in all but two species: *Brachynema ramiflorum* has very shallowly lobed margins, and the leaves of *Jodina rhombifolia* have a prominent marginal spine on each side.

**Cataphylls.** The term *cataphyll*, normally describing much reduced phyllomes at the base of a plant (as in the seedlings of *Ximenia*, Hecke 1899) or its ramifications, has specific taxonomic significance in several genera of Viscaceae (Kuijt 1959, 1996). In *Ginalloa* and (more irregularly) *Notothixos*, lateral branches bear one pair of inconspicuous, acute cataphylls that, however, do not provide criteria to distinguish the species. This contrasts greatly with *Dendrophthora* and *Phoradendron*, where several types of cataphylls occur, supplying major systematic criteria. In both genera, numerous species lack cataphylls completely, especially in the more northern species of *Phoradendron*. Perhaps the majority of species, especially in *Phoradendron*, have one or more pairs of basal cataphylls at the lower end of all lateral branches and often also on inflorescences. In a number of instances, intercalary cataphylls and normal foliage leaves alternate on percurrent stems, in various patterns. Intercalary cataphylls in a few cases subtend inflorescences, as in the common *P. crassifolium*.

**Prophylls**—See under Inflorescences

**Leaf Venation.** The great majority of foliar Santalales have pinnately veined leaves, sometimes very strikingly so, as in *Strombosia* and *Strombosiopsis*. The common venation pattern is of the camptodromous type. Palmately veined leaves are seen occasionally in *Phoradendron*—for example, *P. chrysocladon*—*Dendrophthora*, *Oryctanthus*, *Psittacanthus*, *Maburea*, and elsewhere in some paleotropical loranthaceous genera. The venation in leafy *Misodendrum* species is unique in that there are virtually no cross-connections,

the pattern remaining open (Kuijt 1969). In many species of mistletoe, however, the venation is obscure; a striking instance is the Australian *Amyema mackayense* parasitic on mangroves that has thick, orbicular leaves storing excess salt (Watson 2011, p. 6).

*Leaf Anatomy.* The overall organization of foliar tissues in the order is not unusual, except probably (but unexplored) in leaves like the terete ones of *Psittacanthus sonora*. Sclerenchyma, however, as far as explored, is extremely variable in Loranthaceae, as detailed below. Clusters of storage tracheids are common throughout Loranthaceae, Santalaceae, and Viscaceae, as are crystals of various sorts; cristarque cells have also been noted in Loranthaceae (Kuijt and Lye 2005). The leaf mesophyll in *Misodendrum* is completely undifferentiated (Skottsberg 1935). Laticifers are present in the leaves of *Chaunochiton*, *Coula*, and *Heisteria* (Baas and Kool 1983), and can be recognized even in dry leaves by holding them up to the light, thus allowing for easy generic identification of sterile materials. In *Nuytsia*, even the leaf contains conspicuous gum ducts.

*Stomata.* Commonly, in the order, stomata are more common in the abaxial leaf surface, as in most dicotyledons; however, they may also be common on young stems. Only rarely are they essentially limited to the abaxial leaf surface, as in Octoknemaceae and *Heisteria* (Baas and Kool 1983; Gosline and Malécot 2012); frequently, the difference is a matter of degree. In Loranthaceae and Viscaceae, their orientation is mostly (approximately) perpendicular to the length direction of the leaf or stem, or slightly oblique. Detailed information on such aspects, however, is lacking.

*Indumentum.* The great majority of species in Santalales have glabrous or essentially glabrous leaves. Here and there, in some of the large genera, a few species have evolved a recognizable indumentum. For example, two closely related, southern *Phoradendron* species are densely short-tomentose (*P. kuntzei*, *P. tucumanense*), and some in northwestern Mexico and western North America also have a distinctive hair cover, including especially *P. robinsonii* and *P. velutinum*. In *Psittacanthus*, species like *P. lasianthus*

and *P. pilanthus* show a distinctive indumentum, and a few other loranthaceous taxa in the Old World have similarly developed special epidermal covering. *Notothixos* may be the only mistletoe genus in which all species are covered with a dense, gray hair cover. A diagnostic, dense cover of short, stellate hairs is seen in *Octoknema* and some other Olacaceae, and the staghorn-like multicellular hairs of *Ximania* are probably unique within the order. But all of these are rather exceptional. There are numerous genera that are completely glabrous, such as *Arceuthobium*, *Dendropemon*, *Korthalsella*, and *Phthirusa* in the mistletoes. This does not deny, of course, the instances of internal floral hairs in some groups, or the setal hairs in *Misodendrum*. *Agonandra* flower buds have minute glandular structures that are not, strictly speaking, hairs.

*Sclerenchyma.* Foliar sclerenchyma in Olacaceae and some related families has been detailed by Baas et al. (1982, and in Maas et al. 1992). Sclereids are widespread, of brachy- and astroclereids as well as columnar types. More infrequent is the occurrence of fibrous to filiform astroclereids. *Maburea* has significant bundles of thick-walled fibers that usually surround the veins (Baas in Maas et al. 1992), but lacks sclereids. The diversity of occurrence of sclerenchyma types, however, does not usually allow convincing taxonomic conclusions to be drawn.

The most detailed presentation of foliar sclerenchyma in the mistletoes has been that of Kuijt and Lye (2005), but was limited to neotropical Loranthaceae. While much infrageneric variation was found, this aspect of leaf anatomy emerged as an important source of systematic information in a number of instances. *Oryctanthus* leaves develop a nearly diagnostic type of stellate fiber bundles that can be recognized even on dry leaves. *Ligaria* shows many isolated, elongated sclereids that are oriented perpendicular to the leaf surface. *Aetanthus* and *Psittacanthus* in many species studied form numerous astroclereids, the length of their arms varying with species, but some other species lack sclereids completely. Astroclereids have emerged as a major generic character in the newly recognized *Peristethium* (Kuijt 2012), which includes the species *Cladocolea roraimensis* and *Struthanthus leptostachyus* as listed in the Kuijt and Lye paper. The most

extraordinary species in this regard is *Notanthera heterophylla*, the foliar mesophyll of which is permeated by innumerable, convoluted, slender serpentine fibers that follow erratic paths through the leaf. (The astro-filiform sclereids in some species of *Heisteria* are superficially similar but mostly have a certain amount of branching; Baas and Kool 1983.) However, one species, *H. coccinea*, has unbranched elements remarkably similar to those of *Notanthera*. The leaves of paleotropical Loranthaceae probably have an equivalent diversity of sclerenchyma, as hinted by Rao and Kelkar (1951). *Amyema pendula* from Australia has spectacular, long-armed astro-sclereids as well as clusters of terminal sclereids. In Viscaceae, leaf sclerenchyma is much more simple or rare, but detailed information is not available. Even simpler is the leaf of *Misodendrum* where no sclerenchyma of any sort is present, while druses are abundant, as in some Loranthaceae and Santalaceae.

**Crystals.** The occurrence of crystals in various tissues has received less attention than that of sclerenchyma, and they are not often of systematic use. There seems to be no report of raphides in the order, but all other crystal forms occur in various groups. Opiliaceae develop no crystals (Hiepko 2000), but cystoliths are consistently present. Cristarque cells, usually in series or clusters associated with foliar veins, have been documented in several Loranthaceous genera (Kuijt and Lye 2005). The abaxial leaf epidermis of *Dio-goa*, *Strombosia*, *Strombosiopsis*, and *Tetrastylidium* contains distinctive, very small cells each of which is provided with a central druse.

**Roots**—See section on Parasitism

**Inflorescences.** Inflorescences in Santalales are exceedingly diverse, and do not allow for generalizations. The relevant comments, therefore, are placed in the descriptions of separate families. Both determinate and indeterminate inflorescences may be found in the same family, or even in the same genus, as in *Cladocolea* and *Struthanthus*. Their position on the plant may be axillary or terminal; there are instances where inflorescences may emerge endogenously in nodal areas of the stem (see *Aetanthus* and *Psittacanthus*), internodes (*Dicymanthes seriata*,

Kuijt 1981, his Fig. 17–3), or even from epicortical roots (*Amyema dilatipes*, Kuijt 1981, his Fig. 25). In certain instances (some *Antidaphne*; staminate *Arceuthobium americanum*) the concept of inflorescence is possibly inappropriate. A few cases are seen in Loranthaceae where inflorescences do not exist, the flowers being solitary (Kuijt 1981). This is perhaps primitively so in *Phthirusa* but, in contrast, through reduction in *Ligaria* and *Sogerialthe*. Finally, the inflorescences of *Dendrophthora* and *Phoradendron* may have a structure that is unique in flowering plants (Kuijt 1959), and several instances of flabellate inflorescences have evolved in the same family.

**Flowers.** As in inflorescence structure, the diversity of flowers in Santalales is better detailed in separate families. It is generally agreed that the order derives from plants with dichlamydeous perianths and one whorl of stamens. However, the nature and origin of the perianth continues to be a controversial subject, and especially prophylls and the calyx or calyculus require separate discussion.

**Prophylls.** Prophylls (also often called bracteoles when associated with flowers) have usually been ignored in Santalalean literature, but need to be taken into account in order to comprehend the morphological architecture of some taxa. In most instances they are not recognizable but, paradoxically, branching patterns may indicate a residual ability to form secondary lateral branching in such positions—as it were, in the axils of “phantom” prophylls. This unusual situation is exhibited clearly in male *Arceuthobium americanum*, the normal branching pattern of which is verticillate (Kuijt 1970), but also in flower position elsewhere in the genus. However, the six branches at a node of this species are not equivalent: the two larger ones are axillary to the two scale-leaves at that node, the four smaller ones in positions corresponding to where prophylls might be expected to exist but are not in evidence. Significantly, another *Arceuthobium* species with the same branching pattern (*A. azoricum*) does indeed show the expected (but unusual) prophylls (Kuijt 2013). In the genus *Psittacanthus*, this type of branching may often be seen in vigorous plants while prophylls are scarcely recognizable except in a few species—for example,

*P. sonora* (Kuijt 2009). In *Thesium*, the axillary flowers of many species are flanked by well-formed prophylls, as is true in *Thesidium*, but other species are without (Pilger 1935), while most other Santalaceae exhibit no evidence of their existence at all. In small-flowered neotropical Loranthaceae, most genera have well-developed prophylls accompanying their flowers, especially in triadic and dyadic taxa, where the two lateral flowers are placed in the axils of conspicuous prophyllar bracteoles, as in *Struthanthus* and *Passovia*, but also in the large-flowered genera *Aetanthus* and *Psittacanthus*. In *Gaiadendron*, both bracts and prophylls are foliaceous. Prophylls are small but taxonomically significant in separating *Oryctanthus* from *Marcacanthus* and certain other genera. In *Cladocolea* and *Peristethium*, however, monads on inflorescences usually lack visible prophylls. In Olacaceae, *Strombosiopsis* may be the only genus having each flower subtended by both a bract and two prophylls (Sleumer 1935).

In Viscaceae other than *Arcuthobium* and *Korthalsella*, especially in *Dendrophthora* and *Phoradendron*, prophylls may be very conspicuous, and are frequently attested to by the placement of secondary branches or inflorescences (Kuijt 1961, 2003). In the latter two genera, it is essential that we distinguish between the frequent basal cataphylls that are the lowest foliar organs on lateral shoots, and the prophylls that flank such branches. The prophylls in these two genera are clearly definable. In fact, in certain species of *Dendrophthora*, the two prophylls associated with a lateral branch may fuse above the branch to form a double organ, as in *D. remotiflora*. In *D. domingensis*, all four prophylls of a node may fuse into a single compound structure. Finally, the multiseriate flower position on inflorescences of many *Dendrophthora* and *Phoradendron* species hints at a latent tendency of the node to produce flowers in prophyllar positions (Kuijt 1961, 2003).

From the above it is clear, as also mentioned elsewhere, that the recent claim (Wanntorp and Ronse de Craene 2009) to the effect that the Santalalean calyculus represents the developmental fusion of the prophylls must be rejected. The separate existence of prophylls and the calyculus in *Oryctanthus* and numerous other genera,

among several other arguments, renders that concept extremely problematic (Kuijt 2013).

*Calyculus*. The nature and, indeed, presence of a calyx in Santalales has engendered much debate. The extremes are scarcely in dispute: in Viscaceae (notwithstanding the comments of Schaeppi and Steindl 1945 for female *Viscum*) and in *Misodendrum* there is no evidence of even a reduced calyx (calyculus). In Santalaceae (ignoring the debatable situation in *Buckleya*) there is no sign of a calyculus. In contrast, in some genera of the order (e.g., *Olex* and *Ongokea*), a large calyx completely envelops the fruit at maturity. The controversy lies in those taxa where there is a more or less discernible rim crowning the ovary, or even merely a constriction between the ovary and the petals. Unfortunately, there are conflicting published reports on some genera, making an accurate summary for the order difficult. As mentioned above, Nickrent et al. (2010) state that *Nanodea* and *Mida* have a calyculus, for example, but the primary literature does not bear this out for the former and is contradictory for the latter. Bhatnagar (1960) speaks of a short and slightly lobed “calyculus” in *Mida* that is an extremely small, rim-like structure but is not at all visible in the fruit; yet the detailed illustrations of the species (as *Fusanus cunninghamii*) in Cheeseman (1914) show nothing of the sort. The morphological nature of the calyculus-like structure in “Strombosiaceae” (Olacaceae) is not clear (Nickrent et al. 2010). In Opiliaceae, a calyculus is said to be lacking (Hiepkö 1984), but a constriction exists just below the petals with very short lobes alternating with the latter. In Aptandraceae this is true also for the accrescent disk that surrounds the mature drupe in some genera, but in both *Aptandra* and *Chaunochiton* a large, late-developing, profusely vasculated funnel would appear to be a true calyculus (see Kuijt 1969, his Figs. 3–20 and 3-23a). In Loranthaceae, the calyculus has been variously interpreted (Kuijt 1969) but is now generally accepted as representing a reduced calyx. In some species it is very inconspicuous, but in others it may be very large, as in *Aetanthus mutisii* (Kuijt 2014) and especially in the recently discovered, second species of *Gaiadendron* (J. Graham and J. Kuijt, in prep.). Significantly, the loranthaceous genera usually