The Families and Genera of Vascular Plants

Edited by K. Kubitzki

Volume XI

Flowering Plants. Eudicots

Malpighiales

Springer

THE FAMILIES
AND GENERA
OF VASCULAR PLANTS

Edited by K. Kubitzki

For further volumes see list at the end of the book and:
http://www.springer.com/series/1306

The Families and Genera of Vascular Plants

Edited by K. Kubitzki

XI

Flowering Plants · Eudicots

Malpighiales

Volume Editor:
K. Kubitzki

With 74 Figures

Springer

Editor
Professor Dr. Klaus Kubitzki
Universität Hamburg
Biozentrum Klein-Flottbek und Botanischer Garten
22609 Hamburg
Germany

ISBN 978-3-642-39416-4 ISBN 978-3-642-39417-1 (eBook)
DOI 10.1007/978-3-642-39417-1
© Springer Heidelberg New York Dordrecht London

Library of Congress Control Number: 2013954369

© Springer-Verlag Berlin Heidelberg 2014
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed. Exempted from this legal reservation are brief excerpts in connection with reviews or scholarly analysis or material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work. Duplication of this publication or parts thereof is permitted only under the provisions of the Copyright Law of the Publisher's location, in its current version, and permission for use must always be obtained from Springer. Permissions for use may be obtained through RightsLink at the Copyright Clearance Center. Violations are liable to prosecution under the respective Copyright Law.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
While the advice and information in this book are believed to be true and accurate at the date of publication, neither the authors nor the editors nor the publisher can accept any legal responsibility for any errors or omissions that may be made. The publisher makes no warranty, express or implied, with respect to the material contained herein.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

Preface

It is with great satisfaction that, with this volume, the major part of the families of the order Malpighiales is now published within this book series. Malpighiales are a relatively new ordinal concept because the member families have few evident common characters and, therefore, could be recognised as a monophyletic group only after the application of DNA sequence studies. Submission of manuscripts for the families belonging to this order extended over a very long time, and I regret the long delay in publication for those authors who complied early. Now, all but three families of the order (Achariaceae, Malpighiaceae and Salicaceae) are treated in this series and a concise overview of all families is given in the introduction to this volume, including those (the Clusiaceae Alliance and Passifloraceae Alliance) already published in Vol. IX of this series.

My deep thanks go to all authors of this volume for their interesting and scholarly contributions, and to all those who have freely shared additional information and/or have commented on earlier drafts. Dr. C.C. Davis is warmly thanked for permission to prepare a simplified version of his consensus tree of malpighialean families for the introduction of this volume. I am also most grateful to all copyright holders who so kindly gave permission to reproduce illustrations published under their responsibility, including the Director and Board of Trustees, Royal Botanic Gardens, Kew, and the editors of Blumea (Leiden, The Netherlands) and Austrobaileya (Brisbane, Queensland). The artist Bobby Angell, New York, deserves my continued appreciation for her generous authorization to use illustrations published under her authorship.

The volume has greatly profited from the critical eyes of the copy editor, Dr. Monique Delafontaine, whose dedicated work deserves my warmest thanks. I would also like to gratefully acknowledge the pleasant collaboration with Dr. Andrea Schlitzberger from the staff of Springer Verlag, and with SPi Technologies India PvT Limited.

Hamburg
13 October 2013

Klaus Kubitzki

List of Contributors

Amaral, Maria do Carmo E. do	Depto de Biología Vegetal, Instituto de Biología, Universidade Estadual de Campinas, Cx. P. 6109, Campinas SP 13083-970, Brazil, mceamaral2009@gmail.com
Ballard, Jr., Harvey E.	Ohio University, Environmental and Plant Biology, Athens, OH 45701-2979, USA, ballardh@ohio.edu
Bayer, Clemens	Palmengarten der Stadt Frankfurt, Siesmayerstr. 61, 60323 Frankfurt/M., Germany, clemens.bayer@stadt-frankfurt.de
Bittrich, Volker	Rua Mário de Nucci, 500, Campinas SP 13083-290, Brazil, folcar2007@gmail.com
Dickison, William C.†	Formerly at University of North Carolina, Chapel Hill, NC, USA, folcar2007@gmail.com
Dressler, Stefan	Forschungsinstitut Senckenberg, Senckenberganlage 25, 60325 Frankfurt/M., Germany, stefan.dressler@senckenberg.de
Kubitzki, Klaus	Biozentrum Klein-Flottbek, Ohnhorststr. 18, 22609 Hamburg, Germany, klaus.kubitzki@gmail.com
Levin, Geoffrey A.	Illinois Natural History Survey, University of Illinois, 1816 South Oak Street, Champaign, IL 61820, USA, glevin@inhs.illinois.edu
Paula-Souza, Juliana de	Universidade de São Paulo, Instituto de Biosciências, Rua de Matão 277, Ed. Sobre as Ondas, São Paulo SP 05508-090, Brazil, jupsouza@gmail.com
Prance, Sir Ghillean T.	Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AS, UK, siriain01@yahoo.co.uk
Repplinger, Miriam	Johannes Gutenberg-Universität, Institut für Spezielle Botanik, Mainz 55099, Germany, siriain01@yahoo.co.uk
Schwarzbach, Andrea	Dept. of Biological Sciences, University of Texas, 80 Fort Brown St., Brownsville, TX 78520, USA, andrea.schwarzbach@utb.edu
Wahlert, Gregory	University of Utah, 257 South 1400 East, Salt Lake City, UT 84112, USA, rinorea@gmail.com
Webster, Grady L.†	Formerly at Section of Plant Biology, University of California, Davis, CA, USA, rinorea@gmail.com

Contents

Introduction to Malpighiales

K. Kubitzki

Conspectus of Families including those treated in previous volumes and those not received for inclusion into this volume

1\. Plants with unclear differentiation of stems, roots, and leaves, or even lacking these completely 2

– Green land plants with stems, roots, and leaves 3

2\. Echlorophyllous endophytic stem or root parasites on *Tetrastigma* [Vitac.]; flowers often very large; stamens 12–40 adnate to a central column; ovary inferior; loculi irregular; ovules very many/carpel; embryo undifferentiated. 3/20, SE Asia, W Malesia

For the time being treated as **Rafflesiaceae** but perhaps to be included into Euphorbiaceae
[see **Tribe Rafflesieae** in Vol. II: 560–561]

– Green cataract-dwellers with unclear differentiation of stems, roots and leaves; fertile pollen and fertilisable embryo sacs developed underwater. 49/280, worldwide in tropical and warm-temperate regions
Podostemaceae [see Vol. IX: 304–344]

3\. Monoecious lianes, climbing by leaf tendrils; vessel elements with simple perforations; leaves alternate, serrulate to crenate; stipules knob-like; flowers 5-merous, disk of 5 connate circumgynoecial glands; ovary 5(4)-locular, each locule with 2 apical axile ovules surmounted by small obturator-like appendages; stylodia 5 (4), minute, subulate, stigmatic; fruit 5-winged, 1-seeded, indehiscent. 1/1, from Malay Peninsula to Melanesia **Lophopyxidaceae**

– No lianes climbing by leaf tendrils 4

4\. Plants producing glucosinolates, woody; dioecious; vessel elements with scalariform perforation plates; leaves alternate, entire, stipulate; sepals 3–6, petals 0; stamens 2–50; disk intrastaminal or 0; ovary 1–3(–6)-locular, stylodia as many as locules; ovules 2 per locule embedded in massive obturator; placentation axile; fruit drupaceous; seeds 1 per locule (or fruit, by abortion); contain glucosinolates, cucurbitacines. 2/225, pantropical and subtropical, mostly in Africa and Malesia **Putranjivaceae**

– Glucosinolates 0 5

5\. Stamen filaments vesiculate towards apex; leaves long-petiolate, trifoliolate, serrate to entire, stipulate, alternate to opposite; plants woody; vessel elements with simple (scalariform) perforations; stamens numerous, inner stamens staminodial; ovary locules and stylodia 4–20; ovule 1 per locule. 1/27, neotropical **Caryocaraceae**

– Stamen filaments not vesiculate; leaves rarely 3-foliolate but then not long-petiolate 6

6\. Plants with the combination of epitropous ovules, nucellar beaks and obturators; fruit structure basically a septicidal/loculicidal capsule/schizocarp, also splitting from the persistent columella; mesocarp often splitting from endocarp. **Euphorbiaceae** s. l.
[as circumscribed in this volume] 7

– Not this combination of embryological traits and fruit structure [although epitropus ovules are common and nucellar beaks have a scattered occurrence in Malpighiales] 9

7\. Ovule 1/locule; laticifers + or 0; stems sometimes succulent; vessel elements mostly with simple perforations; leaves alternate, less often opposite or verticillate; stipules + or 0, with axillary colleters, sometimes transformed into glands or spines; petals 1–8; stamens 1–many; pollen grains usually 3-colporate; inner integument vascularized. 213/c. 5,900. Worldwide
Euphorbiaceae [s. str., "uniovulate euphorbs"]

– Ovules 2/locule; laticifers 0; stems not succulent ["biovulate euphorbs"] 8

8\. Vessel elements usually with scalariform perforation plates; leaves simple and entire (trifoliolate and dentate); petals + or 0; stamens usually 3–8; pollen grains 3–7-colporate (-porate), lacking spines; caruncle mostly 0. 59/1,750, pantropical, most in Malesia, some temperate
Euphorbiaceae subfam. **Phyllanthoideae**
[alternatively: **Phyllanthaceae**]

– Vessel elements usually with simple perforations; leaves simple or palmately compound; petals mostly 0; stamens 2–30; pollen grains 3–7-zono-brevicolporoidate or -porate or 10–40-pantoporate, echinate to verrucose; caruncle mostly +. 26/95, pantropical, preferably S Hemisphere
Euphorbiaceae subfam. **Oldfieldioideae**
[alternatively: **Picrodendraceae**]

9\. Carpels sometimes producing false septa; flowers mostly diplostemonous; lamina vernation usually involute 10

– False septa 0, except for some Salicaceae 11

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_1, © Springer-Verlag Berlin Heidelberg 2014

10. Woody; vessel elements with simple perforations; stamen filaments and style folded in bud; nectary disk usually conspicuous; ovary 5(2)-locular; ovules 2 (1) per locule; style simple; seeds winged or arillate. 4/23, pantropical **Ixonanthaceae**

– Herbaceous and woody; vessels with simple or scalariform perforations; stamen filaments not folded in bud; nectary weakly developed; ovary 2–8-locular; stylodia distinct, as many as carpels; ovules 2/locule; seeds sometimes arillate. 13/255, widely distributed in tropical and mostly northern temperate regions **Linaceae**

11. Flowers obliquely monosymmetric; fertile stamens abaxial, ± connate, staminodes adaxial; plants woody; vessel elements mostly with simple perforations; leaves alternate, entire 12

– Flowers not obliquely monosymmetric or only slightly so (Malpighiaceae) 15

12. Flowers with distinctive floral cup lined by a nectary 13

– Flowers lacking distinctive floral cup 14

13. Corolla of 3 petals; androecium with a large anterior pointed staminode flanked by 2 stamen pairs and 2 posterior groups of 2–3 tooth-like staminodes; ovary 3-locular; ovules 2 per carpel, syntropous, collateral, axile; style simple; capsule septicidal. 1/3, northern South America **Euphroniaceae**

– Corolla of 5 (0) petals; androecium of (2–)8–20 to very numerous stamens, abaxially best developed; ovary 1-locular with 2 ovules or 2-locular with 1 ovule in each locule; style ± gynobasic; drupe 1-seeded. 18/531, pantropical, mostly neotropical **Chrysobalanaceae**

14. Inflorescence sometimes adnate to petiole or midvein of leafblade; stamens 5 (4), up to 3 of them sometimes lacking anthers; pollen grains 3-colporate; disk lobate or a ring; ovary 2–5-locular; ovules 2 per locule; stylodia distinct or more often connate into a single style provided with distal style branches; fruit a drupe; plants contain the poisonous fluoracetic acid. 3/170, pantropical, also subtropical regions of India and South Africa **Dichapetalaceae**

– Inflorescence not adnate to petiole or midvein; fertile stamens 4–8 in abaxial part of the flower, staminodes 0 or up to 6 in adaxial part; pollen grains 3–5-porate; nectary glands [staminodial?] at base of standard + or 0; ovary 3(4)-locular; ovules 1–numerous per locule; style simple; capsule septicidal. 5/28, Neotropics, Madagascar, Malesia **Trigoniaceae**

15. Pistillate flowers with the naked ovary surrounded by spirally arranged cupular bracts; staminate flowers in catkins, the perianth reduced to one or several bracts or vestigial perianth lobes; ovary 2–3-locular; ovules 2 per locule, axile, basal; stylodia repeatedly bifurcate; plants woody; dioecious; vessel elements with scalariform perforation plates; leaves alternate, toothed; stipules minute. 1/9, Queensland to Fiji **Balanopaceae**

– The naked ovary not surrounded by spirally arranged cupular bracts 16

16. All or 4 of the 5 calyx lobes with paired abaxial glands producing fat oil [Neotropics] or sometimes nectar [Palaeotropics]; ovary multilocular (inferior), with axile placentas and a solitary ovule in each locule; stylodia mostly distinct, rarely connate into a common style; woody, often lianescent; secondary growth often anomalous; hairs T-, V- or Y-shaped; leaves usually opposite, entire, with paired stipules. $x = 6$ and 9. 68/1,250, worldwide tropical/subtropical, most in America **Malpighiaceae**

[not yet in this volume but see the website of W.R. Anderson et al., Malpighiaceae, http://herbarium.lsa.umich/edu/malpigh/index.html]

– Calyx lobes without glands producing fat oil 17

17. Plants produce a brownish resin which is also excreted as granulous exudate on the stems; annual and perennial herbs or subshrubs; leaves opposite, entire or serrate, with scarious stipules; ovary 2–5-locular; ovules many per locule; placentation axile or basal; stylodia 3–5; capsule septicidal; endosperm scant or 0. $x = 6$. 2/35, nearly worldwide **Elatinaceae**

– Plants lacking superficial granulous exudate 18

18. Leaves opposite or alternate, entire, estipulate, with colleters; schizogenous canals or cavities often + and containing clear, black or coloured exudate; vessel elements with simple perforations 19

– Leaves usually stipulate, plants usually lacking schizogenous canals or cavities containing exudates 22

19. Woody or herbaceous; leaves opposite (alternate); sepals and petals 3–5; stamens distinct or fasciculate; ovary 3–5-locular; ovules 1–many per locule; stylodia distinct, at least distally, or style simple; aril 0; trichomes, if multicellular, stellate. 9/540, worldwide **Hypericaceae** [see Vol. IX: 194–201]

– Strictly woody; leaves opposite or alternate 20

20. Anthers often with complex or simple apical glands; leaves alternate to opposite, entire, often with resin canals; stamens not obviously fasciculate; ovary 1–15-locular; ovules 1–many per locule; style simple, usually long; seeds exarillate, small to large, when large, consisting almost entirely of the huge cotyledons. 13/460, pantropical **Calophyllaceae**

[see Vol. IX under Clusiaceae subfam. Kielmeyeroideae, pp. 48–66]

– Anthers lacking apical glands 21

21. Leaves alternate, supervolute, serrulate-setose; ovary 3–5-locular; stylodia distinct or connate into a simple or distally branched common style; capsule with persistent column. 3/35, SE Asia and Neotropics **Bonnetiaceae** [see Vol. IX: 36–39]

– Leaves opposite, entire, often with resin canals, vernation often flat; stamens sometimes fasciculate; plants mostly dioecious; ovary 1–5-locular; stylodia widely separate or connate into a common short style; seeds arillate or not; hypocotyl much enlarged, cotyledons 1/10 or less length of embryo. 14/595, pantropical **Clusiaceae** (s. str.)

[see Vol. IX under Clusiaceae subfam. Clusioideae and Symphonioideae, pp. 48–66]

22. Placentation axile 23

– Placentation parietal 33

23. Leaves opposite 24

– Leaves alternate 27

24. Style simple; vessel elements with simple and scalariform perforation plates 25

– Common style 0; stylodia as many as carpels; vessel elements mostly with simple perforations 26

25. Leaves often serrate; plants sometimes with subepidermal laticiferous idioblasts; vessel elements with scalariform and/or simple perforations; hairs simple; petals usually with a terminal arista and filiform appendages on two lobes, enwrapping 1–5 stamens; nectary disk intrastaminal, entire or lobed; ovary often ± inferior, 2–20-locular with the locules often incompletely separated at anthesis; ovules 2–6 per locule; style simple. 14/145, pantropical **Rhizophoraceae**

– Leaves opposite, entire; vessel elements with scalariform perforation plates; hairs tufted, stellate and simple; nectary disk extrastaminal; petals unappendaged; ovary 2-locular; ovules 2 per locule, placentation apical; style simple, apically bifurcate; fruit a capsule; seed solitary, persistent on columella, with hairy-papillose arillode. 1/2(3?), W Africa, Malesia **Ctenolophonaceae**

26. Leaves opposite, simple, toothed, stipules 0; phloem stratified; cristarque cells 0; pollen 3-porate; ovary 16–25-carpellate, each carpel with a short stylodium; ovules 2 per locule; fruit capsular, with persistent columella. 1/1, endemic to Mahé, Seychelles Islands **Medusagynaceae**

– Leaves opposite/whorled, simple, sometimes lobed or compound, stipulate; cristarque cells and lysigenous mucilage canals +; tertiary veins parallel or plumose reticulate and very closely spaced; ovary 2–14-locular (gynoecium apocarpous), ovules 2 per locule; fruit baccate (folliculate). 4/51, neotropical **Quiinaceae**

27. Nectary disk 0 28

– Nectary disk + 29

28. Flowers unisexual, actinomorphic; stamens 5–15; plants dioecious; woody, vessel elements with scalariform (simple) perforation plates; leaves alternate, vernation involute; nectary 0; ovary 2–5-locular; ovule strictly 1/locule, pendulous; stylodia 2–5, short, or 0; stigmas spreading; fruit a drupe. 3/15, Old World tropics **Pandaceae**

– Flowers bisexual, actinomorphic to zygomorphic, often polystemonous; woody; vessel elements mostly with simple perforations; cristarque cells +; leaves alternate, ± simple, entire to serrate, stipulate; anthers dehiscing by slits or 1 or 2 pores; nectary 0; ovary 1–15-locular, either entire and provided with a simple apical style, or divided into 5 or more uniovulate lobes and the style gynobasic; ovules 1–many per locule; fruit capsular or drupaceous, or separating into several drupelets. 27/495, pantropical, mostly in Brazil **Ochnaceae**

29. Ovary 2–3-locular 30

– Ovary 4–5(–7)-locular 31

30. Flowers often heterostylous; petals sometimes with fringed bilobed ligule; woody; vessel elements with simple perforations; cristarque cells +; leaves alternate, entire, involute, colleters +, stipules mostly intrapetiolar; nectary glands sometimes on outside of staminal tube; ovary 2-locular; ovule 1(2) per carpel; stylodia distinct or style simple; fruit a 1-seeded drupe or 2–3-seeded capsule; seeds rarely arillate. 4/240, pantropical, especially neotropical **Erythroxylaceae**

– Flowers not heterostylous; petals eligulate; woody; vessel elements with scalariform perforation plates [*Bhesa*]; leaves alternate, stipulate, colleters + or 0; flowers bisexual or unisexual, 5-merous, haplostemonous; disk +; ovary 2- or 3-locular; ovules 2 per locule, collateral, obturator 0; stylodia widely divergent; capsule loculicidal; seed 1 per locule, almost completely enveloped by an exostomal fleshy, sheet-like, coloured aril; seed coat exotegmic, thick-walled, ribbon-shaped; endosperm copious; embryo small. 2/7, West Africa, Indo-Malesia **Centrolepidaceae**

31. Stylodia on outer shoulders of the 5 carpels; woody; vessel elements with scalariform perforation plates; inflorescence umbellate; petals induplicate-valvate, slender; nectary annular; stamens 5, with very short filaments; ovary 5-locular; placentation basal-axile; ovules few per locule; fruit a few-seeded berry; seeds not arillate. 1/3, C and N South America **Goupiaceae**

– Pistil with a single style 32

32. Woody, contains balsamic juice; stamen filaments not folded in bud; vessels elements with scalariform perforation plates; leaves alternate, involute; stamens 10–30+; stamen filaments at base connate into a tube; anthers apiculate or linguiform, thecae with separated superposed loculi; nectary disk intrastaminal; ovary 4–7-locular; ovule 1 (2) per locule; style simple; fruit a drupe; endocarp with "resin"-filled cavities, 1(2)-seeded. 8/50, Central and South America to S Brazil, one sp. in W Africa **Humiriaceae**

– Wood; balsamic juice 0; stamen filaments plicately folded in bud; vessel elements with simple perforations; leaves alternate, vernation involute; stipules very large, intrapetiolar, encircling terminal bud; stamens 10 (9), anther loculi parallel; nectary disk obvious; ovary 5–4(2)-locular; ovule 1 per locule; placental obturator +; style simple, short. 3/10, Old World tropics **Irvingiaceae**

33. Flowers usually strongly monosymmetric; sepals and petals 5; stamens 5 (3), distinct or filaments connate into a tube, anthers commonly bearing a dorsal connective appendage; ovary 1-locular, placentation parietal; ovules 1–many; style simple; fruit capsular, usually 3-valvate; woody (herbaceous, lianescent); vessel elements with simple and scalariform perforation plates; leaves alternate (opposite), with salicoid teeth, stipulate. 22 [+ 9 undescr.]/830, worldwide **Violaceae**

– Flowers polysymmetric; connective appendages 0 34

34. (Andro)gynophore often +; calyx and corolla forming a floral tube 35

– Gynophore and floral tube 0 [the latter + in some Flacourtiaceae] 37

35. (Andro)gynophore 0; petals contorted; floral tube campanulate or funnel-shaped, rarely with weakly developed corona; nectary near base of tube; ovules

1–numerous per placenta (1 basal ovule); seeds arillate, pitted; woody and herbaceous; vessel elements with simple and sclariform perforations; hairs sometimes stellate. 10/205, Africa, America
Turneraceae [see Vol. IX: 458–466]

– [Andro]gynophore usually present; petals cochlear; corona often present and strikingly coloured 36

36. Herbaceous to subwoody; vessel elements usually with simple perforations; stamens 5; pollen grains tricolporate; ovules numerous on parietal placentae; stylodia inserted beneath the top of ovary; seeds exarillate; calyx persistent in fruit; tendrils 0. 1/24, Andean region of N Chile and S Peru
Malesherbiaceae [see Vol. IX: 247–249]

– Woody, vessel elements with simple or scalariform perforation plates; branch tendrils often present; stamens 4, 5, or many; pollen grains 3–12-colporate or -foraminate; ovules numerous; stylodia inserted on top of ovary; seeds arillate; contains often cyanogenic compounds. 17/705, pantropical
Passifloraceae [see Vol. IX: 270–281]

37. Woody; vessel elements with simple or simple and scalariform perforation plates; leaves supervolute-curved or involute, alternate, toothed or serrate, often with the distinctive "salicoid teeth"; flowers 3–6-merous; sepals (0)3–15; petals often 0; nectariferous disk or nectar glands intra-, inter- or extrastaminal; stamens (1 in Lacistemateae) 2–many; placentation parietal (axile); fruit a capsule (berry, drupe); seed coat commonly not vascularized; plants contain benzoylated glacosides but lack cyanogenic glycosides (except *Banara*). 55/1010, pantropical and temperate [not received] **Salicaceae**

– Woody (herbaceous and climbing); vessel element with simple, scalariform or simple and scalariform perforations; leaves alternate, entire, rarely toothed or serrate but then leaf teeth not salicoid; petiole often geniculate; sepals 2–5; petals 4–15 (Acharieae: 3–4 and connate), either whitish and papery or with a gland inside at base; nectary 0; stamens 5–many; anthers sometimes [*Chiangiodendron*, *Kiggelaria*] poricidal; seed coat thick; testa commonly strongly vascularized; plants contain cyclopentenoid cyanogenic glucosides and/or cyclopentenyl fatty acids [gynocardin]. 32/145, pantropical [not received] **Achariaceae**

The Ordinal Concept of Malpighiales. The term Malpighiales had already been created but hardly used by nineteenth century botanists, at a time when family and ordinal concepts most generously were proposed for nearly every characteristic family or even genus. In the 19th and practically the whole 20th century, the allocation of the families presently comprised in the Malpighiales was scattered over many different orders. Even the perspicacious botanists of the 19th century, who had the advantage that the herbaria of that time were limited in size and permitted an easier overview than our vast present collections, recognised hardly any relationship among at least some of the Malpighialean families. It remains enigmatic how Hutchinson, who in his "Families of Flowering Plants" used the Malpighialean concept, in the third edition of this work (Hutchinson 1973) included in it 14 families of which only five did not belong there according to the modern ordinal concept. There were no obvious morphological characters uniting these families, and Hutchinson's finding must have been either fortuitous or perhaps due to his vast experience or instinct, but little attention was paid to it until the advent of molecular systematics.

In the first broad-based molecular systematics analysis of the seed plants by Chase et al. (1993), a clade within their rosids was disclosed which comprised representatives of 11 families previously never found in association. This clade was confirmed and expanded by further work, and the Angiosperm Phylogeny Group (APG 1998) adopted the ordinal name Malpighiales for it. Molecular analyses specifically devoted to this group (Davis et al. 2005; Wurdack and Davis 2009; Korotkova et al. 2009) employed an increasing number of gene regions, eventually of all three genomes, and underpinned its monophyly; they also confirmed or provided evidence for family relationships and revealed suprafamilial clades around the Violaceae/Salicaceae, the Ochnaceae and the Chrysobalanaceae, but failed to resolve deeper relationships among the 16 malpighialean subclades previously identified by Wurdack and Davis (2009). More recently, however, the use of phylogenomic approaches and the inclusion of 82 plastid genes led Xi et al. (2012) to the elaboration of a well-resolved, taxon-rich molecular tree for the Malpighiales, in which 12 additional clades and further increased resolution among its deeper nodes were obtained. This new phylogenetic hypothesis also proved helpful for an understanding of the detailed morphological analyses of the Chrysobalanaceae, Rhizophoraceae, Ochnaceae and their presumed relatives by Matthews and Endress (2008, 2011) and Matthews et al. (2012).

Thus, the concept of Malpighiales is the direct outcome of molecular systematics, which may explain its dearth of easily recognisable distinctive marks. It is only recently that P.F. Stevens (2001 onwards) has succeeded in elaborating a list of possible apomorphies for the whole order and its constituent families and family groups, but the order as a whole is characterised by nothing more than "*leaf margin toothed (teeth with a single vein running into a congested ± deciduous apex); stigma dry; exotegmen fibrous*".

According to classificatory concepts, Malpighiales now comprise 37–42 families, 716 genera and 15,935 species (Stevens 2001 onwards), and within the eudicots are resolved as a member of the Fabidae (Rosidae) where they occupy a sister position to the Oxalidales, both these orders being sister to the Celastrales (Wang et al. 2009; Moore et al. 2010).

Phylogeny. Fig. 1 gives the best resolved consensus tree for malpighialean families available at the time of writing (Jan. 2013), which is redrawn from Xi et al. (2012) and will be used to explain the phylogenetic interrelationships among the families. In it, the previously known subclades of Malpighiales, which hitherto were unresolved in relation to one another, are represented in three well-supported major clades. The first of these is composed of two subclades; one contains the euphorbioids and linoids, the other the Humiriaceae, the parietal clade, and the salicoids. The euphorbioid-linoid clade is remarkable because it brings (albeit with weak support) the uniovulate euphorbs close to the biovulate ones (the phyllanthoids), which traditionally have been included in a single family, Euphorbiaceae (s. l.). Based on early results of molecular systematics, the euphorbs have been split into three families, these being the uniovulate Euphorbiaceae, and the biovulate Phyllanthaceae and Picrodendraceae; the latter share many characters and more recently have been resolved as sister clades. Although the three-family classification for the traditional euphorbs is now generally accepted, the common possession of peculiar capsular fruits (p. 58) and a remarkable combination of embryological characters (p. 55) shared by the uniovulate and biovulate euphorbs is a momentous hint that must not be overlooked; it calls for further inquiry into the deeper nodes of the Malpighialean phylogeny. In this volume, euphorbs are treated in the broad circumscription following the concept of the author of the family. The sister group relationship of the biovulate euphorbs with the linoid clade needs attention because their closeness had been considered by several earlier authors, and a relationship between Linaceae and Ixonanthaceae, already recognised by Hallier (1923), is now strongly supported in the analysis of Xi et al. (2012). Previously, there had been much confusion as to the relationships of the Ixonanthaceae, and both morphological and molecular workers had often associated them with the (equally problematic) Irvingiaceae. The Rafflesiaceae (which are not in Xi's consensus tree) are holoparasites living embedded inside their host plants (species of *Tetrastigma*), and cladistically have been found nested in the Euphorbiaceae between the Peroideae and the rest of the uniovulates (Davis et al. 2007). If one should not wish to incorporate the three rafflesiaceous genera into the euphorbs, the reinstatement of the Peroideae at family rank would allow the intercalation of the Rafflesiaceae between them. More recently, however, Xi et al. (2012, in the SI) have placed the Rafflesiaceae as sister to the Euphorbiaceae + Peroideae, which warns against making premature rearrangements; the loss of plastids and the consequences of horizontal gene transfer in the Rafflesiaceae make the issue very complicated.

The sister clade to euphorbioids and linoids comprises the Humiriaceae with the parietal clade and the salicoids. Support for the placement of the Humiriaceae is low; relationships previously suggested for them were quite diverse but never convincing, and their closest relatives may still remain unknown. In the parietal clade, the Achariaceae, reshaped by Chase et al. (2002), are sister to the Violaceae + Goupiaceae, the latter two being strongly divergent in life form and gynoecium structure, but still sharing other floral traits. Further members of this clade are the closely related Malesherbiaceae, Turneraceae and Passifloraceae, and ultimately the Salicaceae, again reshaped by Chase et al. (2002). I cannot see any cogent reason for maintaining Lacistemataceae, Samydaceae and Scyphostegiaceae separately from the Salicaceae into which, in a future treatment for this series, they would be better integrated.

The second principal clade comprises three subclades in a trichotomy strongly supported

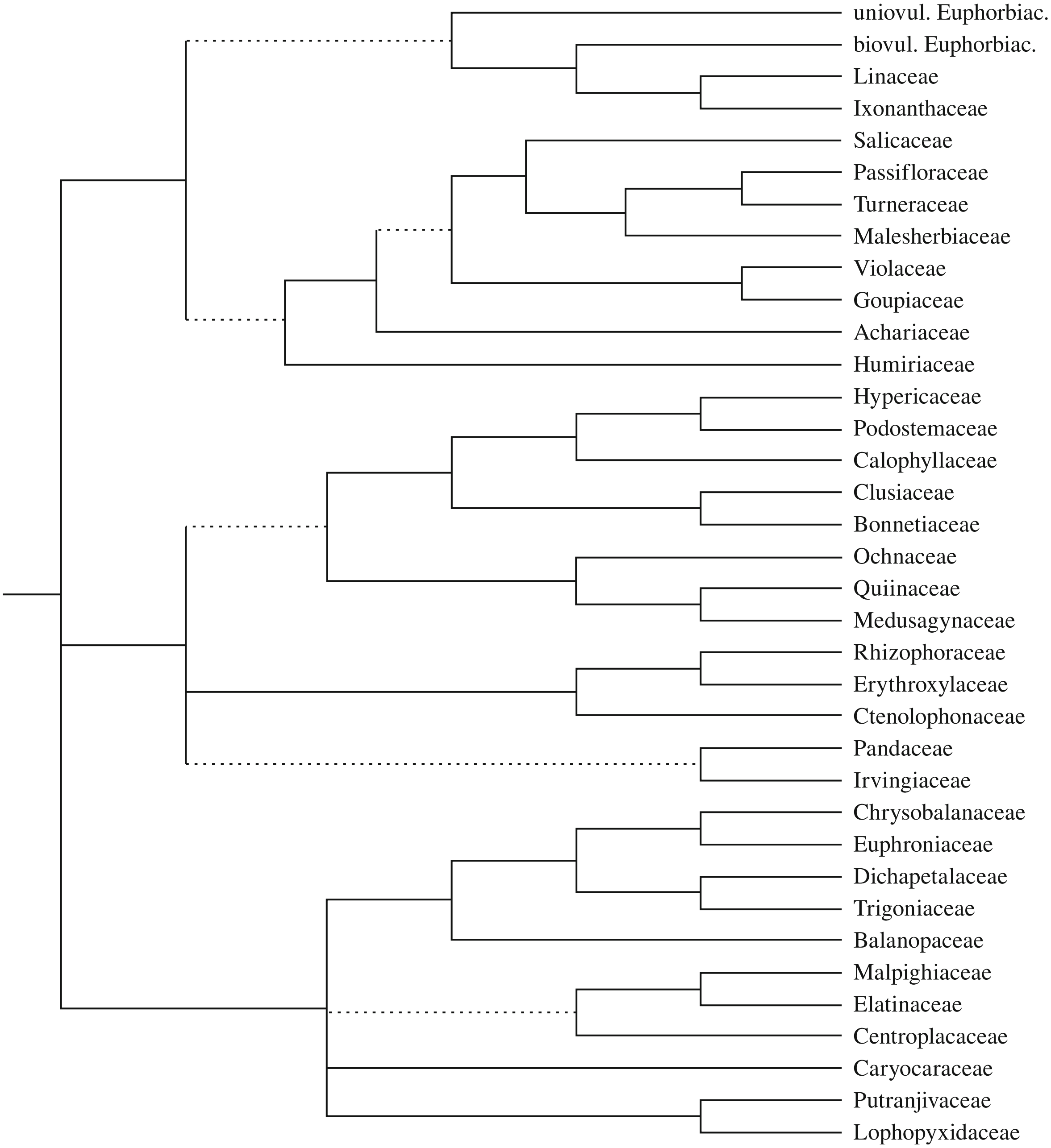

Fig. 1. Maximum likelihood bootstrap consensus tree of the Malpighiales, based on analyses of 82 plastid genes from 58 species added to the existing DNA sequence matrices; redrawn and simplified from Xi et al. (2012) with the kind permission from the authors. Branches with low support hatched.

and characterised by the possession of cristarque cells, with *Medusagyne* as the only exception (elsewhere in Malpighiales, cristarque cells are known from Hugonioideae/Linaceae and Irvingiaceae). The first subclade is composed of the clusioids and the ochnoids, both with a consolidated family classification and containing the interesting association between Hypericaceae and Podostemaceae. Both clusioids and ochnoids usually lack nectar production and are polystemonous; they have brought forth reproductive specialisations like several kinds of floral secretions or simply pollen as reward for pollinators, culminating in buzz pollination. Another subclade, the strongly supported rhizophorids, comprises the Erythroxylaceae, Rhizophoraceae and Ctenolophonaceae, which initially had been recognised as a clade by Wurdack and Davis (2009; see also the morphological work by Matthews and Endress 2011). The third subclade, the pandoids, contains the until recently unplaced Pandaceae, which for lack of a better alternative sometimes had been included in the Euphorbiaceae. They are here in a weakly supported clade with the Irvingiaceae, the latter to date a family of highly controversial placement. This new alliance is backed by several morphological characters listed by Stevens (2001 onwards; see also family treatment of Irvingiaceae).

The third principal clade is composed of four subclades which, except for the position of the Centroplacaceae, had already been recognised by Wurdack and Davis (2009). The five families composing the chrysobalanoids appear in the well-consolidated topology that has already been used as the point of reference for the morphological work by Matthews and Endress (2008). In the malpighioids, Elatinaceae and Malpighiaceae are strongly supported as a clade, whereas their sister position with the Centroplacaceae is only weakly supported. A clade formed by the isolated Putranjivaceae and Lophopyxidaceae and the isolated Caryocaraceae belongs also to the third major clade.

Malpighiales in Time and Space. Davis et al. (2005) used molecular divergence time estimates, calibrated on reliable fossils, to determine the age of the Malpighiales clade. They resolved a much higher age than was expected at that time, i.e. well before the Cretaceous/Tertiary boundary, 112–94 million years ago (Mya) in the Albian and Cenomanian. The extant representatives of this clade are mostly species of shrubs and small trees of the understorey of tropical rain forests, though some of them are tall rain forest trees (*Goupia* and the Irvingiaceae), and various families have extensions into seasonally dry habitats; the Ochnaceae can hardly be seen as a forest family. Davis et al. (2005) extrapolated that the early Malpighiales were shade-tolerant invaders into the understorey of the Cretaceous conifer-dominated forests, where they led to the decline of the light-demanding cycadophytes, pteridophytes and pteridosperms and eventually to the complete disappearance of conifers from tropical biomes. They also suggested that the rise of the Malpighiales might have been paralleled by other tropical clades. Recent broader insights into the age and diversification of the angiosperms have revealed that the Malpighiales were but one part of the vast rosid clade comprising most extant representatives of tropical and temperate tree species (≈70,000 species and 140 families), the lineages of which underwent a rapid diversification within a short period of time in the Cretaceous. The timing of the inferred radiation of the rosids (108 to 91 Mya) and their main branches Fabidae and Malvidae (107–83 Mya) supports a rapid rise of angiosperm-dominated forests in the Cretaceous (Wang et al. 2009; see also Bell et al. 2010; Moore et al. 2010).

With the invasion of modern trees, the habitats of those times underwent profound abiotic and biotic changes. New interactions developed among plants and their substrates, the soil, as well as their pollinators, dispersers, predators, symbiotic partners, etc., thereby triggering an enormous codiversification. The increase of shade reduced the evapotranspiration of the subcanopy including the soil and vegetation, whereas the canopy of the angiospermous forest supplied increased transpiration. This became particularly important for the forest belt of the ever-wet equatorial west wind zone, i.e. the tropical rain forest, the water balance of which is maintained largely by its own transpiration and, to a smaller degree, by the humidity brought by the western winds from the oceans (Salati and Vose 1984). In addition, biogenous aerosol particles in the atmosphere yield condensation nuclei for clouds and precipitation, and sustain the hydrological cycle (Pöschl et al. 2010). Thus, there is an interdependence between vegetation and climate: the equatorial humid west wind zone cannot exist without the humid equatorial forest and vice versa (Kubitzki and Krutzsch 1996; Boyce and Lee 2010).

Very little is known about the place of origin of the Malpighiales and its component lineages. More than half of its families have a pantropical distribution, but in most cases it is unknown whether this is the result of vicariance or dispersal. Lineages that have propagules capable of flotation (Clusiaceae, Chrysobalanaceae and perhaps others) appear prone to long-distance dispersal and, in view of the very many documented intercontinental dispersal events in other groups, it is likely that this may have occurred in the Malpighiales as well. The only pertinent case studies known to me that demonstrate intercontinental dispersal in this plant group are those by Li et al. (2009) on *Bridelia* and by Bardon et al. (2013) on the Chrysobalanaceae. Marked differences in diversification rates among the different Malpighiales clades have been found by Xi et al. (2012), disclosing significant rate decelerations in eight clades, among them Balanopaceae, Ctenolophonaceae, Goupiaceae and Lophopyxidaceae, and rate accelerations in Malpighiaceae, Passifloraceae and three others. Elevated diversification rates may indeed be related to specialised plant–pollinator interactions, as suggested by Xi et al. (2012), whereas each lineage in decline will need its own specific explanation. *Lophopyxis*, for instance, because of its highly specialised shoot morphology and anatomy, may hardly have a chance for further diversification.

To finish this section, the story of *Ctenolophon* (for documentation see family account, this vol.) will demonstrate the value of an ample fossil record for an understanding of extant distribution. By the end of the Cretaceous, *Ctenolophon* appears in West Africa, where it survives to the present with a single species, soon followed by several species in southern Arabia. In the Palaeocene the genus enters into northern South America where its record ends by the Eocene. In the Palaeocene the genus starts also drifting northwards on the Indian Plate and there undergoes its greatest diversification (up to 9 pollen types) but disappears from India in the Neogene, after having spread to SE Asia and Malesia where it has survived to the present day in the Malay peninsula, Sumatra, Borneo, the Philippines, and New Guinea. About 50 years ago my unforgettable mentor, Prof. C.G.G.J. van Steenis, alerted me to look for living *Ctenolophon* in the swamp forests of northern South America and, though I did not see it there, I have pleasure in passing his suggestion onto another generation because it still makes sense!

For references, see under General References.

Balanopaceae

Balanopaceae Benth. in Benth. & Hook., Gen. Pl. 3: 341 (1880), nom. cons. ('Balanopseae').

K. Kubitzki

Dioecious small to tall evergreen trees; older bark with white, circular, prominent lenticels; hairs simple, unicellular. Leaves basically alternate, dimorphic, shoots with minute scale leaves proximally and foliage leaves distally, the latter sometimes subverticillate and restricted to the shoot tip; foliage leaves petiolate, with prominently to obscurely toothed margins; stipules a pair of minute teeth at the base of the petiole. Inflorescences usually subtended by scale leaves, less commonly by foliage leaves, in staminate plants a catkin; staminate flowers short-pedicellate and axillary to scales on the catkin axis, subtended by one or several bracts or vestigial perianth lobes, these often fewer than stamens; stamens (1–)3–6(−12), filaments short, anthers dehiscing laterally; a vestigial pistil sometimes present; pistillate plants with solitary subsessile or short-pedicellate flowers in the axils of scale leaves, with numerous densely crowded, spirally arranged deltoid "cupular" bracts subtending the naked ovary, or a terminal flower surrounded by further lateral flowers also subtended by cupular bracts; staminodes 0; gynoecium syncarpous, 2(3)-carpellate; ovary 2(3)-locular, the locules imperfectly septate at anthesis but fully septate in fruit; ovules 2 per carpel, collateral, borne axile-basally, bitegmic and intermediate between apotropous and epitropous; stylodia connate at the base and once or twice bifurcate to form ribbon-like lobes stigmatic on the adaxial surface. Fruit a yellow, orange or brown drupe with rather thin fleshy mesocarp, subtended at the base by a cup of numerous imbricate, concrescent bracts; pyrenes 2–3; endosperm fleshy during fruit maturation, but crushed at maturity, and forming only a thin layer around the embryo; embryo large, green, straight. $n = 20$ (21).

A single genus comprising nine spp., distributed across "old lands" in the S Pacific (N Queensland, New Caledonia, New Hebrides and Fiji), and bound to forest and scrub communities; on New Caledonia growing on both serpentine and gneiss.

Vegetative Morphology and Anatomy. According to the study by Carlquist (1980), the leaves are dimorphic: prior to the fully formed leaves, scale leaves appear on each shoot. In some species (confined to New Caledonia), the foliage leaves form subverticillate clusters at the tips of the shoots only. The leaf margins are toothed to various degrees. The teeth are several cell layers thick, and the cells are filled with a dark content which is thought to be tannins. Both the scale leaves and the foliage leaves are each provided with a pair of lateral, dark-coloured stipules. Hairs are non-glandular, unicellular and early vanishing from the leaves, but persistent in the involucral bracts, which subtend the solitary female flower and fruit and form the "cupule".

Balanops has trilacunar nodes. For leaf anatomy, see Carlquist (1980); a notable anatomical feature is the scattered occurrence of cristarque cells in the leaves. The involucral bracts contain brachysclereids. The wood has no growth rings. The vessel elements are relatively long and possess scalariform or reticulate-scalariform perforation plates. The wood parenchyma is diffuse, and the rays are multiseriate and uniseriate, with a predominance of erect cells.

Reproductive Structures. In contrast to earlier reports to the contrary, Sutter and Endress (2003) have shown that the ovary of *Balanops* is completely septate, that the ovules are weakly crassinucellate, bitegmic with a multilayered inner integument (in contrast to all previous indications), and intermediate between apotropus and epitropous, and that an obturator is not present.

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_2, © Springer-Verlag Berlin Heidelberg 2014

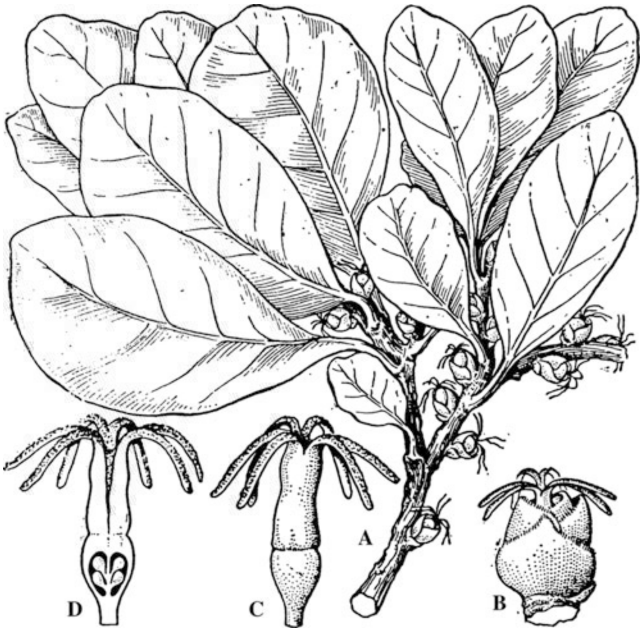

Fig. 2. Balanopaceae. *Balanops sparsiflora*. **A** Branchlet with pistillate flowers. **B** Pistillate flowers enclosed by cupular bracts. **C** Pistillate flower. **D** Same, transversally sectioned. (Takhtajan 1980)

Embryology. Unknown.

Pollen Morphology. The pollen is 3–5-colpate, with colpi that show no sign of an endoaperture. The exine sculpturing consists of small spinules. The exine structure is tectate-granular to columellate. The tectum is traversed by microperforations (Erdtman 1952; Zavada and Dilcher 1986).

Pollination. Probably by wind.

Fruit and Seed. The pericarp consists mostly of thin-walled parenchyma cells, but below the epidermis two or three layers of thick-walled brachysclereids have been observed (Guillaumin 1925; Carlquist 1980). Dispersal is probably by birds (Carlquist 1980).

Phytochemistry. Carlquist (1980) and Sutter and Endress (2003) mention idioblasts containing dark-coloured substances, supposedly tannins, but it is unknown of which type these are. The occurrence of trivial triterpenes gives no clue for affinities (Hegnauer 1964).

Affinities. The affinities of *Balanops* were dubious to early workers such as Engler (1897) and have remained so for a long time. After discussing all taxa that had been suggested as candidates for a relationship to *Balanops*, Carlquist (1980) focused on Hamamelidaceae, Myricaceae, Pittosporales sensu Thorne, and particularly Daphniphyllaceae. Takhtajan (1997) combined Balanopaceae and Daphniphyllaceae in monotypic orders in a superorder Daphniphyllanae, but in sequence analyses of the *rbc*L gene (Litt and Chase 1999; Savolainen, Fay et al. 2000; Chase et al. 2002) Balanopaceae appeared within the Malpighiales in a clade in which they are sister to Dichapetalaceae/Trigoniaceae plus Chrysobalanaceae/Euphroniaceae. In contrast, Sutter and Endress (2003) and Matthews and Endress (2008) argued that features of *Balanops* such as the unisexual flowers, the lack of a perianth, the repeatedly bifurcate stylodia and the weakly crassinucellar ovules would fit much better with a euphorbialean than the chrysobalanoid relationship. However, the multi-gene analyses of Wurdack and Davis (2009), Soltis et al. (2011) and Xi et al. (2012) provide strong support for the earlier molecular findings.

Only one genus:

Balanops **Baill.** Fig. 2

Balanops Baill., Adansonia 10: 117 (1871); Carlquist, Allertonia 2: 191–246 (1980), rev.
Trilocularia Schlechter (1906).

Description as for family. Nine species, for distribution see above.

Selected Bibliography

Carlquist, S. 1980. Anatomy and systematics of Balanopaceae. Allertonia 2(3): 191–246.
Carlquist, S. 1989. Balanopaceae. In: Flora of Australia, vol. 3: 93–95. Canberra: Government Publishing Service.
Chase, M.W. et al. 2002. See General References.
Engler, A. 1897. Balanopsidaceae. In: Engler & Prantl, Nat. Pflanzenfam., Nachtr. I zu T. III, 1. Leipzig: W. Engelmann, pp. 114–116.
Erdtman, G. 1952. See General References.
Guillaumin, A. 1925. Recherches sur l'anatomie et la classification des Balanopsidacées. Rev. Gén. Bot. 37: 433–449.
Hegnauer, R. 1964. See General References.

Hjelmquist, H. 1948. Studies on the floral morphology and phylogeny of the Amentiferae. Bot. Not. Suppl. 2: 1–171.

Litt, A., Chase, M.W. 1999. The systematic position of *Euphronia*, with comments on the position of *Balanops*: an analysis based on *rbc*L sequence data. Syst. Bot. 23: 401–409.

Matthews, M.L., Endress, P.K. 2008. See General References.

Nemirovich-Dachenko, E.N. 1991. Balanopaceae. In: Takhtajan, A. (ed.) Anatomia seminum comparativa, vol. 3. Leningrad: Nauka, pp. 115–116.

Savolainen, V., Fay, M.F. et al. 2000. See General References.

Soltis, D.E. et al. 2000. See General References.

Soltis, D.E. et al. 2011. See General References.

Sutter, D.M., Endress, P.K. 2003. Female flower and cupule structure in Balanopaceae, an enigmatic rosid family. Ann. Bot. 92: 459–469.

Takhtajan, A.L. 1980. See General References.

Takhtajan, A.L. 1997. See General References.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Zavada, M.S., Dilcher, D.L. 1986. Comparative pollen morphology and its relationships to phylogeny in the Hamamelidae. Ann. Missouri Bot. Gard. 73: 348–381.

Caryocaraceae

Caryocaraceae Voigt (1845), nom. cons.

G.T. Prance

Trees or shrubs. Leaves trifoliolate, opposite or alternate, the margins of the leaflets serrate, dentate or crenate or rarely entire, often with stipels at base of leaflets; stipules 2–4, usually caducous, or 0. Inflorescences of terminal racemes; pedicels articulated. Flowers large, hermaphrodite, actinomorphic; sepals 5(6), imbricate; petals 5(6), imbricate, caducous, distinct or rarely slightly connate at base or connate at apex to form a calyptra in *Anthodiscus*; stamens numerous, 55–750; filaments usually connate in a ring at the base, long and slender and usually with some much shorter sterile interior ones which are often recurved, apical portion with numerous vesicles, the sterile filaments often with spirally arranged vesicles along entire length, or the filaments with a row of sterile staminodes at base of interior; anthers basifixed or attached at middle, bilocular; the stamens frequently caducous as a unit together with the petals after pollination; ovary compound, superior, 4(–6)-carpellate in *Caryocar* and 8–20-carpellate in *Anthodiscus*, with as many stylodia as carpels (a common style being absent), each with a distal punctiform stigma; the carpels unilocular each with a single ovule; the ovules basal, erect, anatropous or atropous, bitegmic or unitegmic. Fruit a drupe, with 1–4 seeds developing in *Caryocar* or 8–20 in *Anthodiscus*; mesocarp indehiscent, usually fatty or fleshy; endocarp hard and woody, muricate, tuberculate or spinulose on outer surface, eventually splitting into 1-seeded pyrenes or mericarps. Seeds often reniform, endosperm thin or lacking, the embryo with a straight, arcuate or spirally twisted radicle, a fleshy hypocotyle, and two small cotyledons.

Two genera and 27 spp., in the American tropics from Costa Rica to southern Brazil but not native to the West Indies.

Anatomy and Morphology. A summary of anatomical features with an emphasis on leaf structure is given in Prance and Silva (1973). Brochidodromous and camptodromous nervation are the usual patterns, although *Anthodiscus trifoliatus* is hyphodromous. Branched sclerenchymatous idioblasts are present in the leaf mesophyll and petioles of both genera. The palisade cells frequently contain crystals. Stomata are confined to the abaxial leaf surface, and are usually anomocytic and occasionally either anisocytic or paracytic.

The wood of *Anthodiscus* can easily be distinguished from that of *Caryocar* by the greater abundance (±15/sq. mm) of vessels (3/sq. mm in *Caryocar*), the quantity of gum deposits in the ray cells, and the fibers without septa. The vessels of *Caryocar* vary from 74–577 µm in tangential diameter and are solitary or in radial multiples of 2–5 cells. The vessels of *Anthodiscus* have 50–100 µm mean tangential diameter and are solitary or in multiples of 2–6 cells. Wood of *Caryocar* is described in Barghoorn and Renteria (1967), Loureiro and Silva (1968), Mello (1970) and Araújo and Mattos Filho (1973).

Floral Structure. In *Anthodiscus* the five petals fall as a unit, whereas in *Caryocar* petals and stamens fall as a unit. The floral structure was studied by Dickison (1990) who found that *Caryocar* has bitegmic ovules and simple stylodia, and *Anthodiscus* has unitegmic ovules and compound stylodia (formed by complete coalescence of the upper ventral halves of adjacent carpels). There is also more fusion of major traces in *Anthodiscus*. The gynoecia are richly vascularised by a complex network of wall veins but dorsal or median carpellary bundles are absent. Small prismatic crystals and large deposits of resin-like material are widely distributed throughout all floral parts. The filaments have unique vesicles which are enlarged epidermal cells with numerous membrane-covered wall perforations. Dickison suggests that these cells

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_3,

function in the rapid release and uptake of water during filament erection and subsequent anther dehiscence.

The inner staminodes and the inner side of the floral tube of *Caryocar* are nectariferous, whereas a nectary has not been found in *Anthodiscus* (Vogel 1968; Dickison 1990; Matthews and Endress 2011). On the outside of the sepals of *Caryocar*, Matthews and Endress (2011) found a glandular structure reminiscent of an oil gland, in which the cuticle is separated from the epidermis and the latter is differentiated into small-celled tissue rich in cytoplasm. It remains unknown whether it is a nectary or an oil gland.

Fig. 3. Caryocaraceae. **A**–**C** *Caryocar harlingii*. **A** Branch with inflorescence. **B** Flower bud. **C** Section of fruit; note spiny endocarp. **D**–**F** *Anthodiscus peruanus*. **D** Flowering branchlet. **E** Petals forming a single caducous unit. **F** Ovary and stylodia. (Orig.)

KARYOLOGY. The chromosome number of three species of *Caryocar* is $2n = 46$ (Ehrendorfer et al. 1984).

POLLINATION. The genus *Caryocar* is bat-pollinated (Vogel 1968), and *C. brasiliense*, which is pollinated mainly by glossophagine bats, is self compatible but sets more fruits when crossed (Barradas 1972; Gribel and Hay 1993). Sphingids may also act as pollinators of *Caryocar* (Gribel and Hay 1993), and *Anthodiscus* is probably insect-pollinated (Prance and da Silva 1973).

FRUIT AND SEED. The fruits are drupes with 1–4 seeds in *Caryocar* splitting into 1-seeded cocci and 8–20 seeds in *Anthodiscus*. In *Caryocar* the mesocarp is soft and fleshy and the endocarp is protected by a layer of spines in most species.

DISPERSAL. Little is known about dispersal of the seeds but agoutis have been reported as dispersers of several species of *Caryocar*. Gribel (1986) found that rheas eat and defecate the stone and seed of *C. brasiliense*, and were the main agent of dispersal before they became so rare.

PHYTOCHEMISTRY. Since the oil of the fruit is comestible, there are many papers about the fatty acid content of *Caryocar* oils, for *C. villosum* Georgi (1929) and Hilditch and Rigg (1935), for *C. brasiliense* Ferreira and Motidome (1962) and Handro and Barradas (1971), and for *C. coriaceum* Sales (1973), Lima et al. (1981) and Alencar et al. (1983). *Caryocar* oils are rich in palmitic and oleic acids, and there is a difference between the mesocarp and kernel oils but little difference between species.

The leaves of *Caryocar brasiliense* contain various triterpenes, ellagic acid (Oliveira et al. 1968) and large amounts of condensed tannins (K. Kubitzki, pers. comm.).

AFFINITIES. Caryocaraceae have been placed in the Theales in most traditional systems of classification and are there still in Takhtajan (2009). Molecular studies have placed the family firmly in the Malpighiales, but no close relatives could be revealed in the vast sequence analyses from many gene regions of Wurdack and Davis (2009) and Soltis et al. (2011). In a 3-gene analysis Soltis et al.

(2007) recovered a clade, albeit with low support, in which Caryocaraceae + [Linaceae + Irvingiaceae] were sister to Erythroxylaceae + Rhizophoraceae. From their careful comparative study of the floral structure of these families, however, Matthews and Endress (2011) concluded that a clade of Linaceae, Irvingiaceae and Caryocaraceae is not well supported by floral morphology, and that Caryocaraceae are morphologically most divergent among these families. This has been confirmed by the analysis of Xi et al. (2012) in which Caryocaraceae are somewhat lost in a moderately supported tetratomy where they stand alongside the chrysobalanoids, malpighioids and putranjivoids.

Distribution and Habitats. Both genera range from Costa Rica to eastern Brazil. *Anthodiscus* occurs in the Guianas and western Amazonia but is absent from central and eastern Amazonia. Most species are found in lowland rainforest and flooded riverside habitats, but species of *Caryocar* occur in other habitats. *C. brasiliense* is common throughout the cerrados of central Brazil and *C. cuneatum* in the arid caatinga of the Brazilian northeast. *C. montanum* occurs at about 1,000 m in the Guayana Highland and *C. gracile* is endemic to white sand areas of north-western Amazonia.

Economic Importance. The uses of *Caryocar* are summarised in Prance (1990). The wood of most species is durable and finishes well, is resistant to insect attack and is much used in boat building. The fruit of most species have an edible mesocarp and a kernel that is used like a nut or for the extraction of a comestible oil rich in oleic acid. The fruit of *C. glabrum* is also used as a fish poison (Prance 1973; Kawanishi et al. 1986), the mesocarp of *C. brasiliense* to prepare a liqueur, and there are many other local indigenous uses.

Conservation. *Caryocar costaricense* has been seriously overexploited for its wood and is listed in Appendix 2 of the CITES Treaty, and therefore requires permits for trade.

Key to the Genera

1. Leaves opposite, calyx deeply lobed; ovary and fruit 4 (–6)-locular; stylodia 4; radicle of embryo straight **1. *Caryocar***
– Leaves alternate; calyx truncately dentate and reduced; ovary and fruit 8–20-locular, stylodia 8–15; radicle of embryo spirally twisted **2. *Anthodiscus***

1. ***Caryocar*** L. Fig. 3

Caryocar L., Mant. plantarum 2: 247 (1771); Prance & Silva, Fl. Neotrop. Monogr. 12: 1–75 (1973), rev.

Large trees or rarely shrubs or suffrutices. Leaves opposite, often with 2–4 stipels at base of leaflets; stipules absent or present and soon caducous. Flowers large; calyx distinctly 5(–6)-lobed; petals fused at base together with the base of the filaments and often caducous with the filaments; stamens 55–750, the inner often staminodial and basally with glandular nectar-secreting tissue; ovary 4(–6)-locular; ovules bitegmic. Fruit 4–6-locular, a drupe with 1–4 loculi developing, and dehiscing into 1-seeded cocci; endocarp tuberculate or spinous on exterior. Seeds reniform or subreniform, the embryo with a straight to arcuate radicle.

Eighteen spp., from Costa Rica, Colombia, Peru, Ecuador, Venezuela, the Guianas to central and Atlantic coastal Brazil.

2. ***Anthodiscus*** G.F.W. Meyer

Anthodiscus G.F.W. Meyer, Prim. Fl. Esseq. 193–195 (1818); Prance & Silva, Fl. Neotrop. Monogr. 12: 1–75 (1973).

Trees or shrubs. Leaves alternate; stipels 0; stipules 0. Flowers medium sized; calyx cupuliform with very small, reduced, indistinct dentate lobes; petals circumscissile at base and fused at apex to form a caducous calyptra; stamens 100–280; ovary 8–12(–15)-locular; ovules unitegmic. Fruit an 8–15-locular drupe with most loculi developing. Seeds small, laterally compressed.

Nine spp. in Guyana, Venezuela, Colombia, Peru and western Amazonia, with one sp. in

Costa Rica and Chocó, Colombia and one in Atlantic coastal Brazil.

Selected Bibliography

Alencar, J.W., Alves, P.B., Craveiro, A.A. 1983. Pyrolysis of tropical vegetable oils. J. Agric. Food Chem. 31: 1368–1270.

Araújo, P.A. de M., Mattos Filho, A. de 1973. Estrutura das madeiras de Caryocaraceae. Arch. Bot. Rio de Janeiro 19: 5–47.

Barghoorn, A.W., Renteria, R.M. 1967. Estudio anatomico y fisico-mecanico del cagui (*Caryocar costaricense* Donn. Sm.). Bol. Inst. Forest. Lat.-Amer. Merida 24: 35–57.

Barradas, M.M. 1972. Informação frutificação e dispersão do piqui *Caryocar brasiliense* Camb. (Caryocaraceae). Ciência e Cultura 24: 1063–1068.

Dickison, W.C. 1990. A study of the floral morphology and anatomy of the Caryocaraceae. Bull. Torrey Bot. Club 117: 123–137.

Ehrendorfer, F., Morawetz, W., Dawe, J. 1984. The neotropical angiosperm families Brunelliaceae and Caryocaraceae: first karyosystematical data and affinities. Pl. Syst. Evol. 145: 183–191.

Ferreira, P.C., Motidome, M. 1962: Estudo quimico do óleo de piquí. An. Fac. Farm. Odont. Univ. São Paulo 19: 25–30.

Georgi, C.D.V. 1929. Piqui-a fruit oils. Malayan Agric. J. 17: 166–170.

Gribel, R. 1986. Ecologia da polinização e da dispersão de *Caryocar brasiliense* Camb. (Caryocaraceae) na região do Distrito Federal. M. Sc. thesis, Univ. de Brasília, xii + 109 pp.

Gribel, R., Hay, J.D. 1993. Pollination ecology of *Caryocar brasiliense* (Caryocaraceae) in Central Brazil cerrado vegetation. J. Trop. Ecol. 9: 199–211.

Handro, W., Barradas, M.M. 1971. Sôbre os óleos do fruto e da semente do pique – *Caryocar brasiliense* Camb. (Caryocaraceae), pp. 110–113. In: III Simpósio sôbre o Cerrado. Ed E. Blücher, Univ. São Paulo.

Hilditch, T.P., Rigg, J.G. 1935. The component glycerides of piqui-a fats. J. Soc. Chem. Indust. 54: 109.

Kawanishi, K., Raffauf, R.F., Schultes, R.E. 1986. The Caryocaraceae as a source of fish poisons in the northwest Amazon. Bot. Mus. Leafl. 30: 247–253.

Lima, M.T., Maia, G.A., Guedes, B.L., Oria, H.F. 1981. Composição de acidos graxos da fração lipidica do piqui (*Caryocar coriaceum* Wittm.). Ciencia Agron. 12: 93–96.

Loureiro, A.A., Silva, M.F. 1968. Catálogo das madeiras do Amazônia 1: 154–164. Belém.

Matthews, M.L., Endress, P.K. 2011. See General References.

Mello, E.C. 1970. Estudo anatômico das madeiras do gênero *Caryocar* Linn. Brasil Florestal 1: 54–62.

Oliveira, M.M. de, Gilbert, B., Mors, W.B. 1968. Triterpenes in *Caryocar brasiliense*. An. Acad. Brasil. Ciências. 40: 451–452.

Prance, G.T. 1973. Ethnobotanical notes from Brazil. Econ. Bot. 26: 221–237.

Prance, G.T. 1990. The genus *Caryocar* L. (Caryocaraceae): an underexploited tropical resource. Adv. Econ. Bot. 8: 177–188.

Prance, G.T., Silva, M.F. da 1973. Monograph of Caryocaraceae. Flora Neotropica 12: 1–75. New York: Hafner.

Sales, F.J.M. 1973. O oleo no fruto de piquizeiro, *Caryocar coriaceum* Wittm. Turrialba 23: 108–109.

Soltis, D.E., Gitzendanner, M.A., Soltis, P.S. 2007. A 567-taxon data set for angiosperms: the challenges posed by Bayesian analyses of large data sets. Int. J. Pl. Sci. 168: 137–157.

Soltis, D.E. et al. 2011. See General References.

Takhtajan, A. 2009. See General References.

Vogel, S. 1968, 1969. Chiropterophilie in der neotropischen flora. Flora 157: 562–602; 158: 195–202, 289–323.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. 2012. See General References.

Centroplacaceae

Centroplacaceae Doweld & Reveal (2005).

K. Kubitzki

Trees. Leaves alternate, stipulate, colleters + or 0. Inflorescences racemose; pedicels articulated. Flowers bisexual or unisexual and then plants dioecious, 5-merous, haplostemonous, stamens antesepalous; gynoecium syncarpous, ovary 2- or 3-locular; stylodia widely divergent, with slightly expanded stigmas; ovules 2 per locule, collateral. Capsule loculicidal. Seed 1 per locule, almost completely enveloped by an exostomal fleshy, sheet-like, coloured aril; seed coat exotegmic, thick-walled, ribbon-shaped; endosperm copious; embryo small.

A family comprising two genera and seven spp., West Africa, Indo-Malesia.

Morphology and Anatomy. *Bhesa* has vessel elements with scalariform perforation plates and paratracheal parenchyma +; stomata are anisocytic (*Centroplacus*) and laterocytic (*Bhesa*); the ovules are epitropous (*Centroplacus*) and apotropous (*Bhesa*).

Pollen Morphology. The pollen is tricolporate, that of *Centroplacus* tectate and microperforate and very similar to that of (uniovulate!) *Microdesmis* (see also the discussion by Punt 1962: 89), whereas that of *Bhesa* is finely striate (Wurdack and Davis 2009).

Fruit and Seed. The loculicidal fruits contain a single seed per locule (one ovule aborts), invested with a coloured, sheet-like, fleshy aril that envelops nearly the entire seed. It is orange or red in *Bhesa* and red in *Centroplacus*; this may be related to bird dispersal. Stuppy (1996) cites a collector's note according to which the valves of the mature fruit of *Centroplacus* fall away completely and leave behind the brown seed wrapped into a fleshy bright orange aril. Wurdack and Davis (2009) believe that the aril arises at the exostome, but Leandri (1957: 207) thought it to be an outgrowth of the "fruit axis".

The seeds of both genera agree in the small size of the embryo, the copious endosperm, and the 1-layered exotegmen of ribbon-like cells (see Corner 1976, figs. 80 and 82; Stuppy 1996: 202 and t. 85; Tokuoka and Tobe 2001). Such a seed coat is also found in genera of the Phyllanthoideae.

Relationships. This family concept is the outcome of recent molecular studies. *Bhesa*, for long considered a strange element within Celastraceae in terms of gross morphology and anatomy, has been recognised as malpighialean by Zhang and Simmons (2006). *Centroplacus*, after having been assigned to Flacourtiaceae and Celastraceae, was referred by Hutchinson (1912) to Euphorbiaceae, where its affinities remained contentious. The absence of an obturator and the minute embryo, together with the presence of an aril may exclude *Centroplacus* from the biovulate Euphorbiaceae. The multi-gene analysis of Wurdack and Davis (2009) provided strong support for a clade consisting of *Centroplacus* and *Bhesa*, which is weakly supported as sister to a clade of Malpighiaceae + Elatinaceae (Xi et al. 2012). These four families share axile placentation, crassinucellar ovules without endothelium, and sepals persistent in fruit (Xi et al. 2012).

Key to the Genera

1. Flowers unisexual, plants dioecious; leaves denticulate; pistillate flowers apetalous; ovary 3-merous **1. *Centroplacus***
– Flowers bisexual; leaves entire; pistillate flowers petaliferous; ovary 2(1)-merous **2. *Bhesa***

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_4, © Springer-Verlag Berlin Heidelberg 2014

1. *Centroplacus* Pierre

Centroplacus Pierre, Bull. Mens. Soc. Linn. Paris II, 14: 144 (1899); Hutch., Fl. Trop. Afr. 6(1): 629 (1912); Webster, Ann. Missouri Bot. Gard. 81: 54 (1994); Radcl.-Sm., Gen. Euphorb. 78, fig. 8 (2001).

Dioecious trees; indumentum simple. Leaves 2-ranked, denticulate, eglandular; stipules minute, persistent. Inflorescences axillary, paniculate. Flowers unisexual, pedicellate; staminate flowers: sepals and petals 5, imbricate; disk extrastaminal, cupular, its lobes antepetalous; stamens 5, anthers basifixed, introrse, dehiscence oblique-apical; pollen oblate-spheroidal, 3-colporate, tectate-microperforate; pistillode columnar; pistillate flowers apetalous; disk annular; ovary 3-locular; ovules subapical, epitropous; stylodia spreading. Fruits septicidal and loculicidal capsules dehiscing from the base; columella 0. Seeds 1 per locule, carunculate, with black and shining testa, exotegmic cells flattened, elongate at right angles to mesotegmic fibres; cotyledons twice as long as radicle.

A single sp., *C. glaucinus* Pierre, rain forests of West Africa (Cameroon to Gabon).

2. *Bhesa* Buch.-Ham. ex Arn.

Bhesa Buch.-Ham. ex Arn., Edinb. New Philos. Soc. J. 16: 315 (1834); Simmons, this book series vol. VI: 41 (2004).

Buttressed trees, glabrous. Leaves spiral, conduplicate, entire; petioles ± pulvinate apically; stipules with colleters, almost encircling the stem, caducous. Inflorescence axillary, thyrsopaniculate to racemose. Flowers bisexual, 5-merous; calyx contorted; anthers extrorse or introrse; pollen spheroidal, 3-colporate, finely striate; disk lobed or not; ovary 2(1)-locular, ovules basal, erect, apotropous. Fruit capsular, fusiform or deeply 2-lobed, loculicidally dehiscent. Seeds with coloured, sheet-like aril; exotegmic cells fibrous.

Six spp., Indo-Malesia.

Selected Bibliography

Corner, E.J.H. 1976. See General References.

Forman, L.L. 1966. The reinstatement of *Galearia* Zoll. & Mor. and *Microdesmis* Hook.f. in the Pandanaceae, with appendices by C. R. Metcalfe and N. Parameswaran. Kew Bull. 20: 309–321.

Leandri, J. 1957. Notes systématiques sur les Euphorbiacées-Phyllanthées de Madagascar. Mém. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 8: 205–261.

Nowicke, J.W. 1984. A palynological study of the Pandaceae. Pollen Spores 26: 31–42.

Pierre, P.J.L. 1894. Flore forestière de la Cochinchine. Vol. 3. Paris: Octave Doin.

Punt, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. Wentia 7: 1–116.

Stuppy, W. 1996. Systematische Morphologie und Anatomie der Samen der biovulaten Euphorbiaceen. Dissert., Univ. Kaiserslautern.

Tokuoka, T., Tobe, H. 2001. Ovules and seeds in subfamily Phyllanthoideae (Euphorbiaceae): structure and systematic implications. J. Plant Res. 114: 75–92.

Wurdack, K.J., Davis, C.C. 2009. See General References.

Xi, Z. et al. (2012). See General References.

Zhang, L.-B., Simmons, M.P. 2006. Phylogeny and delimitation of the Celastrales inferred from nuclear and plastid genes. Syst. Bot. 31: 122–137.

Chrysobalanaceae

Chrysobalanaceae R. Br. (1818), nom. cons.

G.T. Prance

Trees, shrubs or suffrutices. Leaves alternate, simple, margins entire, pinnately nerved; stipules small and caducous to large and persistent, sometimes adnate to petiole. Inflorescence racemose, paniculate or cymose. Flowers bracteate and usually with 2 prophylls, actinomorphic to zygomorphic, bisexual or rarely polygamous or unisexual, markedly perigynous; receptacle short to elongate-cylindrical, sometimes gibbous at base; disk always present, forming a lining to receptacle or an annular or shortly tubular structure at its mouth; sepals 5, imbricate; petals 5, imbricate, often unequal, rarely unguiculate, sometimes absent; stamens 2–100 (–300) inserted on margin of disk or basally adnate to it, forming a complete circle or unilateral in zygomorphic flowers; filaments free, connate at base or ligulately connate, included to far exserted; anthers dorsifixed, longitudinally dehiscent; ovary superior, inserted at base, middle or mouth of the receptacle, either unilocular with 2 ovules, or bilocular with 1 ovule in each loculus; ovules erect, epitropous with micropyle directed towards base; style filiform arising from receptacle at base of ovary; stigma distinctly or indistinctly 3-lobed. Fruit a dry or fleshy drupe; endocarp thin and bony to thick and woody, often with a special mechanism for seedling escape, often densely hairy within. Seed erect, almost exalbuminous; cotyledous plano-convex, fleshy, rarely ruminate; germination cryptocotylar or phanerocotylar.

A pantropical family with eighteen genera and 423 of the 531 spp. in the Neotropics, 56 in Africa and Madagascar, and 43 in Asia and the Pacific. Extending beyond the tropics with one species each into the southern U.S.A. and southern Brazil.

Vegetative Morphology. The majority of species of Chrysobalanaceae are leptocaul trees but there are also many savannah shrubs and understorey shrubs, especially in the genus *Hirtella*. At least six species are geoxylic suffrutices, one in Florida, two in the Cerrado region of Brazil and three (*Parinari capensis* and two species of *Magnistipula*) in southern Africa. Many species are tall trees of the rainforest canopy and a few, especially in *Parinari*, are emergents. A few species of *Dactyladenia* and *Hirtella* have scandent branches, but there are no lianas. Those species which have been studied exhibit the architectural model of Troll. Leaves are simple, alternate and usually medium sized, but very large in a few species (up to 50 cm long in *Licania gentryi*). There are frequently glands on the undersurface or on the petioles. Stipules are always present but sometimes very early caducous. They range from minute to quite large in some species of *Licania*, *Parinari* and *Magnistipula*. They are either axillary or, in many species of *Licania*, inserted on the lower portion of the petiole. Seven species of *Hirtella* section *Myrmecophila* have myrmecophilous inflations at the junction of the leaf lamina with the petiole. These are inhabited by ants of the genera *Allomerus*, *Azteca* or *Solenopsis*. *Magnistipula bimarsupiata* also has two small inflations at the base of the lamina, and some internodes are swollen and perforated. It also has the coarse hispid tomentum characteristic of ant plants. The trunks of tree species may be either cylindric or buttressed. The bark of most species chips into small fragments with a sharp metallic ring when hit with a machete, due to the presence of abundant silica grains.

Flower Structure. The flowers are actinomorphic with the ovary inserted at the base of the receptacle in *Chrysobalanus*, *Licania* and *Parastemon* (Fig. 4), and zygomorphic with the ovary inserted at the mouth or middle of the receptacle in the remaining genera (Fig. 5). The

K. Kubitzki (ed.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 11,
DOI 10.1007/978-3-642-39417-1_5, © Springer-Verlag Berlin Heidelberg 2014

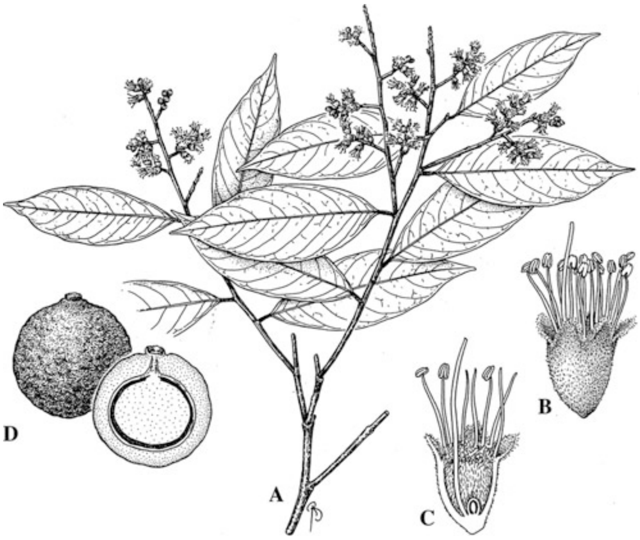

Fig. 4. Chrysobalanaceae. *Licania granvillei*. **A** Flowering branchlet. **B** Flower; note lack of corolla. **C** Medial section of flower showing gynobasic style. **D** Entire and sectioned fruit with attachment scar at top. (Reproduced with kind permission of the artist Bobbi Angell)

calyx is imbricate in bud, 5-lobed, entire; stipitate glands occur in some species of *Dactyladenia* and *Hirtella*. There are usually 5 free, imbricate petals, except in *Licania* subgenus *Licania* and section *Leptobalanus* which are apetalous. In a few species distinctly unguiculate petals occur, especially in *Kostermanthus* where the 2 posterior petals are larger and enclose the stamens in bud. Stamens range from 2 in *Parastemon* to over 300 in some species of *Couepia*. The filaments are usually distinct, but are connate into a unilateral, strap-like ligule in *Acioa*, *Dactyladenia* and *Kostermanthus*; they may be connate for up to half their length in a few species of *Licania* and in *Chrysobalanus*. The stamens may be inserted around a complete circle or unilateral, and the filaments either exserted or included. The anthers are dorsifixed and dehisce laterally. A disk is always present, forming a lining to the receptacle or an annular structure at its mouth. The ovary is superior and inserted at the base, middle or mouth of the receptacle, either unilocular with two ovules or bilocular with one tenuinucellate ovule in each loculus. The ovules are erect and epitropous, with the micropyle directed towards the base. The style is filiform and always arises from the base of the ovary (gynobasic); it usually equals or exceeds the stamens in length.

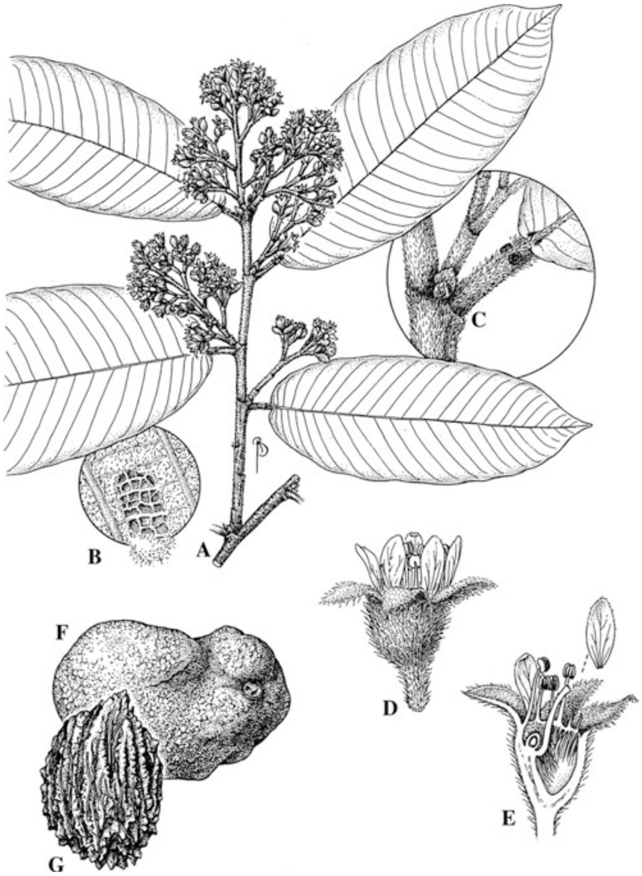

Fig. 5. Chrysobalanaceae. *Parinari montana*. **A** Flowering branchlet. **B** Abaxial leaf surface with part of woolly pubescence removed to show venation. **C** Stipulate node with glandular petiole and base of panicle with prophyll. **D** Flower. **E** Same, medial section, with perched gynoecium, cup-shaped hypanthium and petal. **F** Fruit with attached scar. **G** Seed with corrugated endocarp. (Reproduced with kind permission of the artist Bobbi Angell)

EMBRYOLOGY. The embryology was studied by Tobe and Raven (1984). The tetrasporangiate anthers have five-layered walls including a glandular tapetum with cells two-nucleate. Cytokinesis in the microspore mother cells is simultaneous. The nucellus is very small and the nucellar tissue soon disintegrates, except for the megaspore or embryo sac; antipodal cells are absent. The ovule is bitegmic; the inner integument (ii) and the outer integument (oi) are initiated dermally; the ii is up to five or eight cells thick and the oi more than five cells thick; the inner epidermis of the ii develops into the endothelium, which directly borders the embryo sac and accumulates starch grains; the micropyle is formed by both integuments. Endosperm formation is of the nuclear