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Keys to the genera of Annonaceae

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Identification keys are provided for all genera currently recognized in Annonaceae. Separate keys are presented for the Neotropics (34 genera), Africa-Madagascar (40 genera) and Asia-Australasia (42 genera). These keys are based on a combination of vegetative and fertile characters. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 74–83.

ADDITIONAL KEYWORDS: identification – synonymy – taxonomy.

INTRODUCTION

Annonaceae are a pantropical family of trees, shrubs and lianas. They play an important ecological role in terms of species diversity, especially in tropical rainforest ecosystems. To date, there are 109 validly described and recognized genera and c. 2440 species (Chatrou *et al.*, 2012; Erkens, Mennega & Westra, 2012). Several family-wide keys to the genera have been published in the past (Engler & Diels, 1901; Hutchinson, 1923; Fries, 1959), with the most recent one by Keßler (1993) published almost 20 years ago. Since then, significant taxonomic changes at the generic level have been made, most of them based on molecular phylogenetic studies at the species and generic levels, with the justification to conserve strictly monophyletic genera (see Table 1 for a complete list). Several different types of changes can be identified, including description of genera new to science (Verdcourt, 1996; Couvreur *et al.*, 2009),

elevation to the rank of genus of previously described species from different genera (Chatrou, 1998; Mols *et al.*, 2008), reinstatement of generic names formally sunken into other genera (Surveswaran *et al.*, 2010) and generic names reduced to synonymy with other genera (van Heusden, 1994b; Kenfack *et al.*, 2003; Erkens *et al.*, 2007; Rainer, 2007; Zhou, Su & Saunders, 2009; Zhou *et al.*, 2010). Two new generic names were also described and subsequently synonymized: *Craibella* R. M. K. Saunders, Y. C. F. Su & Chalermglin (Saunders, Su & Chalermglin, 2004), now synonymized with *Pseuduvaria* Miq. (Su, Smith & Saunders, 2008), and *Cleistopetalum* Okada (Okada, 1996), which was synonymized into *Polyalthia* Blume (Turner, 2010). However, *Polyalthia*, one of the largest genera in Annonaceae, has been shown to be polyphyletic (Mols *et al.*, 2004; Xue *et al.*, 2011) with the species previously described under *Cleistopetalum* belonging to a clade (Xue *et al.*, 2011) associated with the conserved name *Enicosanthum* Becc. (Saunders & Xue, 2011). Finally, some genera still have an uncertain status. *Oncodostigma* Diels was listed as

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Table 1. Changes in generic status and new genera within Annonaceae since the publication of the last family-wide key of Annonaceae by Keßler (1993). A-AUS, Asia and Australia. NA, not applicable

	Genus	Accepted name	Region	Reference
New genera				
	<i>Cleistopetalum</i>	<i>Enicosanthum</i>	A-AUS	(Okada, 1996)
	<i>Craibella</i>	<i>Pseuduvaria</i>	A-AUS	(Saunders <i>et al.</i> , 2004)
	<i>Klarobelia</i> Chatrou	NA	Neotropics	(Chatrou, 1998)
	<i>Maasia</i> Mols, Kessler & Rogstad	NA	A-AUS	(Mols <i>et al.</i> , 2008)
	<i>Mosannonna</i> Chatrou	NA	Neotropics	(Chatrou, 1998)
	<i>Mwasumbia</i> Couvreur & D. M. Johnson	NA	Africa	(Couvreur <i>et al.</i> , 2009)
	<i>Pseudomalmea</i> Chatrou	NA	Neotropics	(Chatrou, 1998)
	<i>Sanrafaelia</i> Verdc.	NA	Africa	(Verdcourt, 1996)
Reinstated generic names				
	<i>Drepananthus</i> Maingay ex Hook.f.	NA	A-AUS	(Surveswaran <i>et al.</i> , 2010)
	<i>Fenerivia</i> Diels*	NA	Madagascar	(Saunders, Su & Xue, 2011)
Genera reduced to synonymy				
	<i>Ancana</i> F. Muell.	<i>Meiogyne</i>	A-AUS	(van Heusden, 1994b)
	<i>Anomianthus</i> Zoll.	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2009)
	<i>Atopostema</i> Boutique	<i>Monanthotaxis</i> Baill.	Africa	(Verdcourt, 1971)
	<i>Balanga</i> Le Thomas	<i>Uvaria</i>	Africa	(Zhou <i>et al.</i> , 2010)
	<i>Chieniodendron</i> Tsiang & P. T. Li	<i>Meiogyne</i>	A-AUS	(van Heusden, 1994b)
	<i>Cleistopetalum</i> †	<i>Enicosanthum</i>	A-AUS	(Turner, 2010)
	<i>Craibella</i>	<i>Pseuduvaria</i>	A-AUS	(Su, Chaowasku & Saunders, 2010)
	<i>Cyathostemma</i> Griff.	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2009)
	<i>Dasoclema</i> J. Sinclair	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2010)
	<i>Deeringothamnus</i> Small	<i>Asimina</i> Adans.	USA	Abott <i>et al.</i> in prep
	<i>Dennettia</i> Baker f.	<i>Uvariopsis</i> Engl. & Diels	Africa	(Kenfack <i>et al.</i> , 2003)
	<i>Ellipeia</i> Hook.f. & Thomson	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2009)
	<i>Ellipeiopsis</i> R. E. Fr.	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2009)
	<i>Enantia</i> Oliv.‡	<i>Annickia</i> Setten & Maas	Africa	(van Setten & Maas, 1990)
	<i>Fitzalania</i> F. Muell.	<i>Meiogyne</i>	A-AUS	(Chaowasku, Zijlstra & Chatrou, 2011)§
	<i>Guamia</i> Merr.	<i>Meiogyne</i>	A-AUS	(van Heusden, 1994b)
	<i>Guattertiella</i> R. E. Fr.	<i>Guatteria</i> Ruiz. & Pav.	Neotropics	(Erkens <i>et al.</i> , 2007)
	<i>Guattertiopsis</i> R. E. Fr.	<i>Guatteria</i>	Neotropics	(Erkens <i>et al.</i> , 2007)
	<i>Heteropetalum</i> Benth.	<i>Guatteria</i>	Neotropics	(Erkens <i>et al.</i> , 2007)
	<i>Mezzettiopsis</i> Ridl.	<i>Orophea</i> Blume	A-AUS	(Keßler, 1988)
	<i>Oreomitra</i> Diels	<i>Pseuduvaria</i>	A-AUS	(Su <i>et al.</i> , 2010)
	<i>Pachypodanthium</i> Engl. & Diels	<i>Duguetia</i>	Africa	(Chatrou, 1998)
	<i>Papualthia</i> Diels	<i>Haplostichanthus</i> F. Muell.	A-AUS	(van Heusden, 1994a)
	<i>Petalolophus</i> K. Schum.	<i>Pseuduvaria</i>	A-AUS	(Su <i>et al.</i> , 2005)
	<i>Polyaulax</i> Backer	<i>Meiogyne</i>	A-AUS	(van Heusden, 1994b)
	<i>Raimondia</i> Staff.	<i>Annona</i>	Neotropics	(Rainer, 2001)
	<i>Rauwenhoffia</i> Scheff.	<i>Uvaria</i>	A-AUS	(Zhou <i>et al.</i> , 2009)
	<i>Richella</i> A. Gray	<i>Goniotalamus</i> Hook.f. & Thomson	A-AUS	(Nakkuntod <i>et al.</i> , 2009)
	<i>Rollinia</i> A. St.-Hil.	<i>Annona</i>	Neotropics	(Rainer, 2007)

*This name was officially reduced to synonymy with *Polyalthia*, but was nevertheless included in the Keßler (1993) key.

†See Introduction.

‡Although the new name *Annickia* was given in 1990, it was not adopted in the Keßler (1993) key.

§This is a nomenclatural proposal and still has to be validated.

synonym of *Meiogyne* Miq. by van Heusden (1994b), but the types species (*O. leptoneura* Diels) was considered as a 'dubious name' (the holotype appeared to be a mixed collection), making the transfer of the name *Oncodostigma* incomplete. Here, we shall consider *Oncodostigma* as a 'confused name' and will not include it into the key. This issue will require future investigation. Furthermore, the genus *Friesodielsia* Steenis has been shown to be polyphyletic (Richardson *et al.*, 2004; Chatrou *et al.*, 2012): two clades are recognized, an Asian one sister to *Desmos* Lour. and *Dasymaschalon* Dalla Torre & Harms and an African one closely related to the African genus *Monanthotaxis* Baill. The status of both clades of *Friesodielsia* is not officially recognized yet, and we shall treat the concerned species under the same name. Finally, the taxonomy of *Melodorum* Lour., *Sphaerocoryne* Scheff. ex Ridl. and *Mitrella* Miq. is ambiguous and these genera are in great need of a revision. Following the traditional circumscription of these taxa, we include the liana groups *Sphaerocoryne* p.p./*Melodorum* p.p. and the arborescent group of *Melodorum* p.p./*Sphaerocoryne* p.p. in the key.

In total, eight new generic names have been published since 1993, and 31 have been synonymized (Table 1). These changes clearly warrant new keys to the genera of the family. For a complete list of accepted genera, number of species per genus and a family-level classification see Chatrou *et al.* (2012) and for an annotated list of all generic names

ever published in Annonaceae see Erkens *et al.* (2012).

MATERIAL AND METHODS

We provide identification keys following three major geographical regions: the Neotropics and the USA, Africa (including Madagascar) and Asia/Australasia (including India, Sri Lanka and the Pacific Islands). This approach was taken because most genera are endemic to these major regions. Only seven genera are shared between two regions: *Anaxagorea* A.St.-Hil. (Neotropics/Asia), *Annona* L. (Neotropics/Africa), *Artabotrys* R.Br. (Palaeotropics), *Duguetia* A.St.-Hil. (Neotropics/Africa), *Friesodielsia* and *Sphaerocoryne* (Palaeotropics, but see above), *Uvaria* (Palaeotropics); and one between them all: *Xylopia* L. (pantropical). This provides a faster and easier way to identification than a single comprehensive key. For each genus, we also provide an approximate indication of distribution, which can also help with identification. We tried to use vegetative characters as much as possible, but most of these are coupled with fertile ones (flowers and/or fruits). Only macromorphological characters have been retained in the key (e.g. visible with or without a hand lens) in order to make the key useful to a wide range of users. However, in the South-East Asian key an extra pollen character is indicated in parentheses in addition to fertile ones to help identification as these are easily visible using a hand lens (polyads vs. monads).

KEY TO NEOTROPICAL GENERA OF ANNONACEAE (PAUL J. M. MAAS)

1. Leaves spirally arranged; flowers tetra-(to hexa-)merous; indument of stellate hairs; Amazon region and French Guiana in the north and Pacific coast of Colombia in the west.....*Tetrameranthus*
- 1'. Leaves arranged in two rows (distichous); flowers trimerous (rarely dimerous); indument of various types (simple, stellate or scale-like hairs).....2
2. Indument of stellate or scale-like hairs (easily visible with a hand lens); fruit syncarpous; carpels strongly coherent, but only partly connate, lower carpels sterile and often forming a basal collar; from Costa Rica in the north to Bolivia and Paraguay in the south, and Africa.....*Duguetia*
- 2'. Indument of simple hairs or lacking (hairs sometimes stellate in *Annona*, microscopic stellate to furcate hairs occur in *Anaxagorea*); fruit either apocarpous or syncarpous, but not as above.....3
3. Inflorescences axillary (sometimes leaf-opposed in *Anaxagorea brevipes*) or sometimes arising from trunk (cauliflorous); fruit apocarpous.....4
- 3'. Inflorescences leaf-opposed, supra-axillary, or terminal, rarely arising from trunk; fruit apocarpous or syncarpous.....22
4. Upper side of leaves with impressed to flat midrib.....5
- 4'. Upper side of leaves with raised midrib.....14
5. Petals often thick and fleshy (2–10 mm thick) and covered with microscopic, brownish hairs; monocarps club-shaped, explosively dehiscent, two-seeded; throughout Neotropics, except for West Indies, three species in Asia.....*Anaxagorea*
- 5'. Petals generally much thinner and covered with much larger hairs or glabrous; monocarps never club-shaped, generally globose to ellipsoid, indehiscent, or non-explosively dehiscent, one- to several-seeded.....6
6. Pedicels with a suprabasal articulation (a few mm above base of pedicel); throughout Neotropics.....*Guatteria*
- 6'. Pedicels with a basal articulation.....7

7. Sepals two; petals four; carpels one (or two); Mexico.....*Tridimeris*
- 7'. Sepals three; petals six; carpels generally numerous..... 8
8. Monocarps dehiscent; seeds distinctly arillate; young twigs mostly lenticellate; leaves generally small and narrow; throughout Neotropics, Africa and Asia.....*Xylopia*
- 8'. Monocarps indehiscent; aril absent or indistinct; young twigs not lenticellate; leaves mostly much larger and broader..... 9
9. Monocarps several-seeded..... 10
- 9'. Monocarps one-seeded..... 11
10. Petals white, maroon, rarely yellow, large, 10–80 × 10–50 mm, distinctly veined; inner petals much shorter than outer ones; monocarps one to 12; south-east USA to southern Canada.....*Asimina*
- 10'. Petals mostly white, 7–23 × 1–3 mm, with indistinct venation; petals subequal or inner petals longer than outer ones; monocarps one or two; tropical South America, but mainly Amazonian.....*Diclinanona*
11. Upper side of leaves with distinctly impressed venation; monocarps long-stipitate (stipes 5–35 mm long); petals 8–12 mm long; tropical South America, but mainly in north-east Brazil.....*Ephedranthus*
- 11'. Upper side of leaves with flat, not or slightly impressed venation; monocarps short- to long-stipitate; petals 4–70 mm long..... 12
12. Pedicels bearing three to six tiny bracts; stipes of monocarps < 8 mm long; petals 4–8 mm long; flowers bisexual, rarely androdioecious (*Oxandra venezuelana*), stipes < 10 mm long; throughout Neotropics.....*Oxandra*
- 12'. Pedicels provided with one or two bracts; stipes of monocarps > 10 mm long, generally much more; petals 7–70 mm long; flowers both staminate and bisexual (staminate and bisexual flowers present)..... 13
13. Pedicels with bract above articulation; petals 8–21 mm long, spreading and leaving floral centre uncovered; raphe of seeds raised, straight; western South America and adjacent Panama.....*Pseudomalmea*
- 13'. Pedicels without bract above articulation; petals 10–30 mm long, concave, covering floral centre; raphe of seeds impressed, straight, slightly sinuous or spiral; tropical South America up to Costa Rica in the north.....*Klarobelia*
14. Petals often fleshy (2–10 mm thick), covered with microscopic, brownish hairs; innermost stamens staminodal; monocarps club-shaped, explosively dehiscent, two-seeded; throughout Neotropics, except for West Indies.....*Anaxagorea*
- 14'. Petals generally much thinner, covered with much larger hairs or glabrous; all stamens fertile or outermost stamens staminodal (*Fusaea*); monocarps globose to ellipsoid, indehiscent or non-explosively dehiscent, one- to several-seeded..... 15
15. Leaves with distinct marginal vein, almost touching margin (except in *P. spiritus-sancti*); petals 4–15 mm long; tropical South America.....*Pseudoxandra*
- 15'. Leaves without marginal vein (except in *Oxandra p.p.*, but then much further removed from margin); petals 4–35 mm long..... 16
16. Lower side of leaves glaucous; monocarps transversely ellipsoid, one-seeded; petals 25–35 mm long; western part of South America.....*Ruizodendron*
- 16'. Lower side of leaves not glaucous; monocarps ellipsoid to globose, one- to several-seeded; petals 4–20 mm long..... 17
17. Monocarps one or two, sessile, two- to four-seeded; petals 4.0–8.5 mm long, provided with a small, incurved, tail-like, apical appendage; tropical South America.....*Onychopetalum*
- 17'. Monocarps generally more numerous (up to 30), mostly distinctly stipitate, often one-seeded; petals 2.5–20.0 mm long, without apical appendage..... 18
18. Leaves asymmetrical; petals 2.5–4.5 mm long; monocarps one-seeded (except in *B. pleiosperma*), shortly stipitate; tropical South America.....*Bocageopsis*
- 18'. Leaves symmetrical; petals mostly > 5 mm long; monocarps one- to several-seeded, mostly distinctly stipitate..... 19
19. Upper side of leaves with distinctly grooved midrib; from Costa Rica in the north to Bolivia in the south, eastwards up to the Guianas, and south of the Amazon River.....*Crematosperma*
- 19'. Upper side of leaves with non-grooved midrib..... 20
20. Leaves with distinctly raised veins on both sides; petals 10–15 mm long; seeds 25–30 mm long; Amazonian south-west Venezuela and adjacent Brazil.....*Pseudephedranthus*
- 20'. Leaves with veins on upper side (except for raised midrib) not or indistinctly raised; petals 4–10 mm long; seeds 8–20 mm long..... 21
21. Inflorescences often one-flowered and shortly pedicellate, flower stalk densely beset with 3–6 bracts; apical prolongation of connective tongue-shaped; monocarps one-seeded; throughout Neotropics.....*Oxandra*
- 21'. Inflorescences often branched, if one-flowered, flower stalk not densely beset with bracts; apical prolongation of connective discoid; monocarps one- to several-seeded; seeds striate to pitted; from Mexico (Oaxaca) in the north to Bolivia, north Paraguay, and southern Brazil in the south.....*Unonopsis*
22. Bracts absent..... 23
- 22'. Bracts present..... 29

23. Flowers pendent on long (40–60 mm) pedicels; inner petals boat-shaped; throughout Neotropics, except for West Indies *Cymbopetalum*
- 23'. Flowers non-pendent and pedicels much shorter; inner petals not boat-shaped 24
24. Leaves asymmetrical; monocarps 20–90 × 30–40 mm, thick-walled (wall 2.5–4.0 mm thick); from Costa Rica in the north through western South America to Bolivia, and south-east Brazil *Porcelia*
- 24'. Leaves symmetrical; monocarps smaller, thin-walled 25
25. Petals basally connate 26
- 25'. Petals free 27
26. Petals basally connate into 2–4 mm long tube; monocarps dehiscent, falciform, yellow or orange; aril fleshy, two-lobed; tropical South America *Cardiopetalum*
- 26'. Petals free; monocarps indehiscent, fusiform to linear, green; aril fibrous; western South America *Froesiodendron*
27. Leaves often triplinerved at base; monocarps three to nine; flower buds globose; stamens c. 40; tropical South America, absent from central Amazon basin *Trigynaea*
- 27'. Leaves not triplinerved at base; monocarps one to three; flower buds globose or conical; stamens < 20; east and south-east Brazil 28
28. Flower buds conical; petals linear, recurved to patent; calyx cup-shaped, without distinct lobes; flowers solitary or in many-flowered inflorescences; inflorescences often flagellate and produced from main stem; east and south-east Brazil *Hornschuchia*
- 28'. Flower buds globose; petals ovate to elliptic, erect; calyx distinctly three-lobed; flowers solitary; east and south-east Brazil *Bocagea*
29. Upper side of leaves with raised midrib 30
- 29'. Upper side of leaves with impressed to flat midrib 31
30. Fruit apocarpous, monocarps distinctly stipitate; seeds pitted; sepals < 5 mm long; inner base of inner petals with food bodies; from Mexico in the north to Bolivia in the south *Mosannona*
- 30'. Fruit syncarpous, carpels strongly coherent; seeds smooth; sepals > 9 mm long; petals without food bodies; Amazonian Brazil (Upper Rio Negro) *Duckeanthus*
31. Flowers winged; fruit syncarpous (rarely apocarpous); throughout Neotropics and Africa *Annona*
- 31'. Flowers not winged; fruit apocarpous or syncarpous 32
32. Outermost stamens staminodal; fruit syncarpous with almost woody basal collar; tropical South America *Fusaea*
- 32'. All stamens fertile; fruit apocarpous or syncarpous, without basal collar 33
33. Fruit syncarpous, each carpel one-seeded; petals often thick and fleshy; throughout Neotropics *Annona*
- 33'. Fruit apocarpous, each monocarp one- to several-seeded; petals thin 34
34. Pedicels often with one leafy bract; Mexico and Central America and adjacent northern Colombia *Desmopsis*
- 34'. Pedicels without leafy bracts 35
35. Monocarps one-seeded; petals yellow to cream, margins ciliate; from Panama in the north to Peru in the south, also one species in south-east Brazil (Bahia) *Malmea*
- 35'. Monocarps one- to several-seeded; petals red, purple, brown, or rarely cream, margins not ciliate 36
36. Petals distinctly veined, length/width ratio 2–5; flowers often with a foetid scent; monocarps 13–100 mm long; seeds with lamellate rumination; Mexico and Central America *Sapranthus*
- 36'. Petals not distinctly veined, length/width ratio 5–20; flowers without a foetid scent; monocarps 10–30 mm long; seeds with spiniform rumination; Mexico, Central America to Pacific coast of Colombia *Stenanona*

KEY TO AFRICAN AND MALAGASY GENERA OF ANNONACEAE (THOMAS L. P. COUVREUR & DAVID M. JOHNSON)

1. Indument of stellate or scale-like hairs (easily visible with a hand lens) 2
- 1'. Indument of simple hairs or lacking 7
2. Lower surface of leaf completely covered with silver scale-like hairs; West and Central Africa *Meiocarpidium*
- 2'. Indument of lower leaf surface sparser, not completely covering surface; hairs more stellate than scale-like 3
3. Outer petal whorl absent; monocarps stipitate, stipe articulated at apex; West and central Africa, one species in East Africa *Annickia*
- 3'. Outer petal whorl present; monocarps sessile, or if stipitate then stipe not articulated at apex 4
4. Trees; fruit syncarpous; West and Central Africa and Neotropics *Duguetia*
- 4'. Scandent shrubs or lianas; fruit of one to many free monocarps 5
5. Carpel one; East Africa *Dielsiothamnus*
- 5'. Carpels more than one 6

6. Inner petals smaller than outer ones; monocarps moniliform, with seeds in a single row; East Africa.....*Friesodielsia* (*F. obovata*)
- 6'. Inner and outer petals subequal; monocarps oblong, with seeds in two rows; throughout tropical Africa, including Madagascar and Asia.....*Uvaria*
7. Lianas; inflorescence peduncle formed into a woody hook; throughout tropical Africa including Madagascar and Asia.....*Artabotrys*
- 7'. Trees, shrubs or lianas; inflorescence peduncle not formed into a woody hook.....8
8. Upper side of leaves with a raised midrib.....9
- 8'. Upper side of leaves with an impressed to flat midrib.....11
9. Petals free; flower and fruit apocarpous, inner petals with brush-like structure on inner side; East Africa.....*Ophrypetalum*
- 9'. Petals fused at base; flowers and fruit syncarpous.....10
10. Corolla lobes equal in length, margins generally straight; throughout tropical Africa including Madagascar.....*Isolona*
- 10'. Outer petals longer than inner, margins generally undulated or crisped; throughout tropical Africa...*Monodora*
11. Calyx reduced and vestigial, present as basal flange (sometimes three-lobed); Madagascar.....*Fenerivia*
- 11'. Calyx not reduced, clearly visible.....12
12. Sepals free but enclosing petals until anthesis, sometimes reduplicate; monocarps multi-seeded.....13
- 12'. Sepals free but exceeded in length by petals well before anthesis, or sepals connate; monocarps one- or multi-seeded.....16
13. Petals connate at base, crumpled in bud; throughout tropical Africa.....*Hexalobus*
- 13'. Petals free to base, not crumpled in bud.....14
14. Receptacle convex but not columnar; West and Central Africa.....*Uvariastrum*
- 14'. Receptacle columnar.....15
15. Small trees; anther connective reduced to a tuft of hairs; West and Central Africa.....*Mischogyne*
- 15'. Scandent shrubs or lianas; anther connective flattened above anthers; Central and East Africa.....*Toussaintia*
16. Sepals completely connate.....17
- 16'. Sepals free, at least at the apex.....18
17. Trees; calyx forming a flat disk at base of flower; petals six in a single whorl; West Africa.....*Monocyclanthus*
- 17'. Lianas; calyx entirely enclosing flower in bud, tearing as flower enlarges; petals six in two whorls; Central Africa.....*Letestudoxa*
18. Flowers with two sepals; throughout tropical Africa.....*Uvariopsis*
- 18'. Flowers with three sepals.....19
19. Lianas with leaf-opposed or terminal inflorescences.....20
- 19'. Trees, or, if lianas, inflorescence axillary.....26
20. Inner petals shorter than outer ones, vaulted and connivent over stamens and carpels.....21
- 20'. Inner and outer petals subequal, erect or spreading.....23
21. Anthers septate; monocarps sessile; Cameroon.....*Boutiquea*
- 21'. Anthers not septate; monocarps stipitate.....22
22. Leaves glaucous beneath; inner petals with short claw; throughout tropical Africa.....*Friesodielsia*
- 22'. Leaves sometimes pale beneath, but not glaucous; inner petals lacking claw; east Africa and Asia.....*Sphaerocoryne*
23. Monocarps sessile, forming a syncarpous fruit; Central Africa, Gabon.....*Pseudartabotrys*
- 23'. Monocarps stipitate.....24
24. Stamens usually < 15; monocarps often many-seeded and moniliform.....25
- 24'. Stamens numerous; monocarps one-(or two-)seeded; Democratic Republic of the Congo.....*Afroguatteria*
25. Petals connivent (or rarely imbricate) in bud; stamens obconical; throughout tropical Africa including Madagascar.....*Monanthotaxis*
- 25'. Petals completely separate in bud; stamens linear; Democratic Republic of the Congo.....*Gilbertiella*
26. Flowers with three petals.....27
- 26'. Flowers with six petals.....28
27. Petals opposite sepals, wood bright yellow, monocarps one-seeded; West and central Africa, one species in East Africa.....*Annickia*
- 27'. Petals alternate with sepals, wood not bright yellow, monocarps multi-seeded; Central Africa.....*Uvariopsis* (*U. tripetala*)
28. Petals connate at base.....29
- 28'. Petals free.....30
29. Young branches glabrous; flowers small (< 1 cm), carpels and monocarps solitary; Tanzania, Usambara Mountains.....*Sanrafaelia*
- 29'. Young branches hairy; flowers large (> 2 cm), carpels and monocarps 5–20; East Africa.....*Asteranthe*
30. Monocarps stipitate, stipe articulated at apex.....31

30'. Monocarps sessile, or, if stipitate, stipe not articulated at apex.....	34
31. Inner petals shorter than outer ones.....	32
31'. Inner and outer petals subequal.....	33
32. Anthers septate; monocarps one-seeded, with stipe longer than seed-containing portion; seeds smooth; West and Central Africa.....	<i>Neostenanthera</i>
32'. Anthers not septate; monocarps two-seeded, with stipe equal in length to or shorter than seed-containing portion; seeds tuberculate; West and Central Africa.....	<i>Cleistopholis</i>
33. Petals linear, acute; introduced in Africa, South-East Asia.....	<i>Cananga</i>
33'. Petals ovate, obtuse; East Africa.....	<i>Lettowianthus</i>
34. Inner petals much longer than outer ones; West and Central Africa.....	<i>Piptostigma</i>
34'. Inner petals shorter than or equal in length to outer petals.....	35
35. Fruits syncarpous.....	36
35'. Fruits apocarpous.....	37
36. Flowers bisexual, borne in leaf-opposed and terminal inflorescences on leafy branches; throughout tropical Africa including Madagascar and Neotropics, introduced in Asia.....	<i>Annona</i>
36'. Flowers both staminate and bisexual, borne in long pendant leaf-opposed or axillary inflorescences on old branches or stems; West and Central Africa, one doubtful species in East Africa.....	<i>Anonidium</i>
37. Inflorescences leaf-opposed, supra-axillary, or terminal.....	38
37'. Inflorescences axillary, or plant cauliflorous.....	39
38. Flowers bisexual; petals ovate; anthers septate; monocarps fusiform, sessile; East Africa.....	<i>Mkilua</i>
38'. Androdioecious; petals linear; anthers non-septate; monocarps globose, stipitate; throughout tropical Africa.....	<i>Greenwayodendron</i>
39. Anthers septate; monocarps dehiscent; throughout tropical Africa, Madagascar, Asia and the Neotropics.....	<i>Xylopia</i>
39'. Anthers non-septate; monocarps indehiscent.....	40
40. Inner petals smaller than outer ones, deeply concave; monocarps globose with up to 20 seeds in two rows; Central Africa.....	<i>Exellia</i>
40'. Inner and outer petals subequal, flat or concave; monocarps elongate, or if globose then containing only one or two seeds.....	41
41. Tertiary veins of leaves percurrent; androdioecious; monocarps elongate, seeds pitted; throughout tropical Africa.....	<i>Polyceratocarpus</i>
41'. Tertiary veins variously curved and anastomosing; flowers bisexual; monocarps elongate or globose; seeds pitted or smooth.....	42
42. Petals < 5 mm long.....	43
42'. Petals ≥ 10 mm long.....	44
43. Flowers borne singly on leafless branches; monocarps stipitate, one-seeded; East Africa.....	<i>Cleistochlamys</i>
43'. Flowers multiple in cymose inflorescences; monocarps sessile, two-seeded; Madagascar.....	<i>Ambavia</i>
44. Monocarps long-stipitate, one-seeded, red; East Africa, including Madagascar and Asia.....	<i>Polyalthia</i>
44'. Monocarps sessile, multi-seeded, green or brown.....	45
45. Carpels 4, ovules and seeds uniseriate; Tanzania, Kimboza Forest Reserve.....	<i>Mwasumbia</i>
45'. Carpels > 20, ovules and seeds biseriate; throughout tropical Africa.....	<i>Uvarioidendron</i>

KEY TO ASIAN AND AUSTRALASIAN GENERA OF ANNONACEAE (SVENJA MEINKE & PAUL J. A. KEBLER)

1. Lianas.....	2
1'. Trees or shrubs.....	10
2. Indument of stellate hairs (easily visible with a hand lens); throughout tropical Australasia and (for <i>Uvaria</i>) tropical Africa including Madagascar.....	<i>Uvaria</i>
2'. Indument of simple hairs or glabrous.....	3
3. Inflorescence peduncle formed into a woody hook; throughout tropical Australasia and tropical Africa including Madagascar.....	<i>Artabotrys</i>
3'. Inflorescence peduncle not formed into a woody hook.....	4
4. Inflorescences supra-axillary or leaf opposed.....	5
4'. Inflorescences axillary.....	7
5. Flowers in multiflowered inflorescences; stamen connective tongue-shaped/acute; throughout tropical Asia.....	<i>Fissistigma</i>
5'. Flowers solitary or in one-flowered inflorescences; stamen connective discoid (uvarioid).....	6
6. Petals coherent above sexual organs; throughout tropical Asia.....	<i>Friesodielsia</i>
6'. Petals not coherent above sexual organs; throughout tropical Australasia.....	<i>Desmos</i>

7. Petals coherent above sexual organs.....	8
7'. Petals not coherent above sexual organs.....	9
8. Petals clawed; stamen connective tongue-shaped/acute; New Guinea.....	<i>Schefferomitra</i>
8'. Petals not clawed; stamen connective discoid (uvarioid); tropical West Asia.....	<i>Sphaerocoryne p.p. / Melodorum p.p.</i>
9. Sepals persisting in fruit; carpels few (10–15); ovules three to five; monocarps globose, < 1 cm in diameter; tropical Australasia except India.....	<i>Mitrella</i>
9'. Sepals not persisting in fruit; carpels six; ovules six or more; monocarps cylindrical, > 2 cm in diameter; Thailand, Malesia.....	<i>Pyramidanthe</i>
10. Flowers in multiflowered inflorescences.....	11
10'. Flowers solitary or in one-flowered inflorescences.....	19
11. Petals coherent above sexual organs.....	12
11'. Petals not coherent above sexual organs.....	16
12. Inner petals longer than outer ones.....	13
12'. Inner petals shorter than or equal in length to outer ones.....	14
13. Stamen connective not prolonged (miliusoid); stamens few (three to 12); throughout tropical Asia.....	<i>Orophea</i>
13'. Stamen connective discoid (uvarioid); stamens many (> 30); throughout tropical Australasia.....	<i>Pseuduvaria</i>
14. Petals clawed; ovule one; seed one; tropical Asia except India.....	<i>Neo-uvaria</i>
14'. Petals not clawed; ovules two to many; seeds two to many.....	15
15. Midrib on upper surface of leaf raised; carpel one; throughout tropical Asia.....	<i>Cyathocalyx</i>
15'. Midrib on upper surface of leaf flat/impressed; carpels few (two to 20); throughout tropical Asia.....	<i>Drepananthus</i>
16. Flowers unisexual, with carpellate inflorescences at base of main trunk; West Malesia.....	<i>Stelechocarpus</i>
16'. Flowers bisexual.....	17
17. Stamens many (> 30); carpels many (> 20); throughout tropical Asia.....	<i>Maasia</i>
17'. Stamens few (< 20); carpel one.....	18
18. Trees up to 30 m tall; sepals and petals valvate; West Malesia.....	<i>Mezzettia</i>
18'. Treelets up to 5 m tall; sepals and petals imbricate; West Malesia.....	<i>Dendrokingstonia</i>
19. Sepals imbricate.....	20
19'. Sepals valvate.....	21
20. Inner petals shorter than outer ones; tropical Asia except New Guinea.....	<i>Sageraea</i>
20'. Inner and outer petals subequal in length; throughout tropical Asia except New Guinea.....	<i>Enicosanthum</i>
21. Petals in one whorl.....	22
21'. Petals in two whorls.....	23
22. Petals three; anthers not septate, with pollen in monads; monocarps without abscission zone between seed bearing part and stalk (without a stipe); throughout tropical Asia except New Guinea.....	<i>Dasymaschalon</i>
22'. Petals four to nine; anthers septate, pollen in polyads; monocarps with abscission zone between seed bearing part and stalk (with a stipe); South China to Sumatra and Borneo.....	<i>Disepalum</i>
23. Anthers septate, with pollen in tetrads or polyads.....	24
23'. Anthers not septate, with pollen in monads.....	28
24. Inner petals coherent above sexual organs.....	25
24'. Inner petals not coherent above sexual organs.....	27
25. Inner petals spoon-shaped; throughout tropical Asia, Africa and Neotropics.....	<i>Xylopia</i>
25'. Inner petals clawed.....	26
26. Inflorescences leaf-opposed; throughout tropical Asia.....	<i>Mitrephora</i>
26'. Inflorescences axillary to slightly supra-axillary or plant cauliflorous; throughout tropical Australasia.....	<i>Goniothalamus</i>
27. Fruits syncarpous; without abscission zone between seed bearing part and stalk (without a stipe); cultivated for its fruits; Neotropics and Africa, introduced throughout tropical Australasia.....	<i>Annona</i>
27'. Monocarps not connate, with abscission zone between seed bearing part and stalk (with a stipe); cultivated for its flowers; throughout tropical Australasia, introduced in Africa.....	<i>Cananga</i>
28. Ovules three to many.....	29
28'. Ovule(s) one or two.....	33
29. Petals coherent above sexual organs.....	30
29'. Petals not coherent above sexual organs.....	31
30. Sepals free; throughout tropical Asia, except New Guinea.....	<i>Meiogyne</i>
30'. Sepals connate; South Thailand and West Malesia.....	<i>Platymitra</i>
31. Petals saccate; stamen connectives not prolonged (miliusoid); throughout tropical Asia.....	<i>Alphonsea</i>
31'. Petals not saccate; stamen connectives discoid (uvarioid).....	32
32. Inflorescences axillary; ovules three to five; tropical Australia.....	<i>Meiogyne</i> (ex <i>Fitzalania</i>)
32'. Inflorescences supra-axillary; ovules about 10; West Malesia except Philippines.....	<i>Monocarpia</i>

33. Petals clawed.....	34
33'. Petals not clawed.....	35
34. Petals coherent above sexual organs; carpels few (< 20); throughout tropical Australasia.....	<i>Popowia</i>
34'. Petals not coherent above sexual organs; carpels many (> 20); West Malesia.....	<i>Trivalvaria</i>
35. Petals connate.....	36
35'. Petals free.....	37
36. Petals coherent above sexual organs; ovules two; Philippines, East Malesia, tropical Australia.....	<i>Haplostichanthus</i>
36'. Petals not coherent above sexual organs; ovule one; Borneo.....	<i>Woodiellantha</i>
37. Inner petals longer than outer ones.....	38
37'. Inner petals shorter than or equal in length to outer ones.....	40
38. Inflorescences axillary; ovules two; throughout tropical Australasia.....	<i>Miliusa</i>
38'. Inflorescences supra-axillary or leaf-opposed; ovule one.....	39
39. Petals coherent above sexual organs; tropical West Asia.....	<i>Marsypopetalum</i>
39'. Petals not coherent above sexual organs; throughout tropical Asia.....	<i>Phaeanthus</i>
40. Stamens few ($\leq$ nine); Sri Lanka.....	<i>Phoenicanthus</i>
40'. Stamens many (> 30).....	41
41. Petals spoon-shaped; monocarps dehiscent; throughout tropical Asia, except New Guinea, and throughout Neotropics.....	<i>Anaxagorea</i>
41'. Petals not spoon-shaped; monocarps indehiscent.....	42
42. Petals coherent above sexual organs; Thailand, Indochina.....	<i>Melodorum</i> p.p./ <i>Sphaerocoryne</i> p.p.
42'. Petals not coherent above sexual organs; throughout tropical Australasia.....	<i>Polyalthia</i>

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REFERENCES

- Chaowasku T, Zijlstra G, Chatrou LW. 2011. Proposal to conserve the name *Meiogyne* against *Fitzalania* (Annonaceae). *Taxon* **60**: 1522–1523.
- Chatrou LW. 1998. Changing genera. Systematic studies in Neotropical and West African Annonaceae. Unpublished PhD Thesis, Utrecht University.
- Chatrou LW, Pirie MD, Erkens RHJ, Couvreur TLP, Neubig KM, Abbott RJ, Mols JB, Maas JW, Saunders RMK, Chase MW. 2012. A new higher-level classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics. *Botanical Journal of the Linnean Society* **169**: 5–40.
- Couvreur TLP, Van der Ham RWJM, Mbele YM, Mbogo FM, Johnson DM. 2009. Molecular and morphological characterization of a new monotypic genus of Annonaceae, *Mwasumbia*, from Tanzania. *Systematic Botany* **34**: 266–276.
- Engler A, Diels L. 1901. Anonaceae. In: Engler A, ed. *Monographien afrikanischer Pflanzen-Familien und -Gattungen*. Leipzig: Engelmann, 1–96.
- Erkens RHJ, Chatrou LW, Koek-Noorran J, Maas JW, Maas PJM. 2007. Classification of a large and widespread genus of Neotropical trees, *Guatteria* (Annonaceae) and its three satellite genera *Guatterella*, *Guatteropsis* and *Heteropetalum*. *Taxon* **56**: 757–774.
- Erkens RHJ, Mennega EA, Westra LYT. 2012. A concise bibliographic overview of Annonaceae. *Botanical Journal of the Linnean Society* **169**: 41–73.
- Fries RE. 1959. Annonaceae. In: Melchior H, ed. *Die natürlichen Pflanzenfamilien: nebst ihren Gattungen und wichtigeren Arten, insbesondere den Nutzpflanzen*, 2nd edn. Berlin: Duncker & Humblot, 1–171.
- van Heusden ECH. 1994a. Revision of *Haplostichanthus* (Annonaceae). *Blumea* **39**: 215–234.
- van Heusden ECH. 1994b. Revision of *Meiogyne* (Annonaceae). *Blumea* **38**: 487–511.
- Hutchinson J. 1923. A contribution towards a phylogenetic classification of flowering plants. II. The genera of Annonaceae. *Bulletin of Miscellaneous Information* **1923**: 241–261.
- Kenfack D, Goseline G, Gereau RE, Schatz GE. 2003. The genus *Uvariopsis* (Annonaceae) in tropical Africa with a recombination and one new species from Cameroon. *Novon* **13**: 443–449.
- Keßler PJA. 1988. Revision of the genus *Orophea* Blume (Annonaceae). *Blumea* **33**: 1–80.
- Keßler PJA. 1993. Annonaceae. In: Kubitzki K, Rohrer JG, Bittrich V, eds. *The families and genera of vascular plants*, Vol. 2. *Magnoliid, Hamamelid and Caryophyllid families*. Berlin: Springer Verlag, 93–129.
- Mols JB, Gravendeel B, Chatrou LW, Pirie MD, Bygrave PC, Chase MW, Keßler PJA. 2004. Identifying clades in Asian Annonaceae: monophyletic genera in the polyphyletic Miliuseae. *American Journal of Botany* **91**: 590–600.
- Mols JB, Keßler PJA, Rogstad SH, Saunders RMK. 2008. Reassignment of six *Polyalthia* species to the new genus *Maasia* (Annonaceae): molecular and morphological congruence. *Systematic Botany* **33**: 490–494.
- Nakkuntod M, Su YCF, Seelanan T, Saunders RMK. 2009. Molecular phylogenetic and morphological evidence

- for the congeneric status of *Goniothalamus* and *Richella* (Annonaceae). *Taxon* **58**: 127–132.
- Okada H. 1996.** New genus and new species of the Annonaceae from the Malesian wet tropics. *Acta Phytotaxonomica et Geobotanica* **47**: 1–9.
- Rainer H. 2001.** Nomenclatural and taxonomic notes on *Annona* (Annonaceae). *Annalen des Naturhistorischen Museums in Wien, Serie B Botanik und Zoologie* **103**: 513–524.
- Rainer H. 2007.** Monographic studies in the genus *Annona* L. (Annonaceae): inclusion of the genus *Rollinia* A.St. Hil. *Annalen des Naturhistorischen Museums in Wien, Serie B Botanik und Zoologie* **108**: 191–205.
- Richardson JE, Chatrou LW, Mols JB, Erkens RHJ, Pirie MD. 2004.** Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philosophical Transactions of the Royal Society of London, series B* **359**: 1495–1508.
- Saunders RMK, Su YCF, Chalermglin P. 2004.** *Craibella phuyensis* (Annonaceae): a new genus and species from Thailand. *Systematic Botany* **29**: 42–49.
- Saunders RMK, Su YCF, Xue B. 2011.** Phylogenetic affinities of *Polyalthia* species (Annonaceae) with columellar-sulcate pollen: enlarging the Madagascan endemic genus *Fenerivia*. *Taxon* **60**: 1407–1416.
- Saunders RMK, Xue B. 2011.** Proposal to conserve the name *Enicosanthum* against *Monoon* (Annonaceae). *Taxon* **60**: 236–237.
- van Setten AK, Maas PJM. 1990.** Studies in Annonaceae. XIV. Index to generic names of Annonaceae. *Taxon* **39**: 675–690.
- Su YCF, Chaowasku T, Saunders RMK. 2010.** An extended phylogeny of *Pseuduvaria* (Annonaceae) with descriptions of three new species and a reassessment of the generic status of *Oreomitra*. *Systematic Botany* **35**: 30–39.
- Su YCF, Mols JB, Takeuchi W, Kessler PJA, Saunders RMK. 2005.** Reassessing the generic status of *Petalolophus* (Annonaceae): evidence for the evolution of a distinct sapromyophilous lineage within *Pseuduvaria*. *Systematic Botany* **30**: 494–502.
- Su YCF, Smith GJD, Saunders RMK. 2008.** Phylogeny of the basal angiosperm genus *Pseuduvaria* (Annonaceae) inferred from five chloroplast DNA regions, with interpretation of morphological character evolution. *Molecular Phylogenetics and Evolution* **48**: 188–206.
- Surveswaran S, Wang RJ, Su YCF, Saunders RMK. 2010.** Generic delimitation and historical biogeography in the early-divergent ‘ambavioid’ lineage of Annonaceae: *Cananga*, *Cyathocalyx* and *Drepananthus*. *Taxon* **59**: 1721–1734.
- Turner IM. 2010.** A consideration of *Cleistopetalum* and a new combination in *Polyalthia* (Annonaceae). *Phytotaxa* **8**: 41–45.
- Verdcourt B. 1971.** Notes on African Annonaceae. *Kew Bulletin* **25**: 1–24.
- Verdcourt B. 1996.** *Sanrafaelia*, a new genus of Annonaceae from Tanzania. *Garcia de Orta, Série de Botanica* **13**: 43–44.
- Xue B, Su YCF, Mols JB, Keßler PJA, Saunders RMK. 2011.** Further fragmentation of the polyphyletic genus *Polyalthia* (Annonaceae): molecular phylogenetic support for a broader delimitation of *Marsypopetalum*. *Systematics and Biodiversity* **9**: 17–26.
- Zhou L, Su YCF, Chalermglin P, Saunders RMK. 2010.** Molecular phylogenetics of *Uvaria* (Annonaceae): relationships with *Balanga*, *Dasoclema* and Australian species of *Melodorum*. *Botanical Journal of the Linnean Society* **163**: 33–43.
- Zhou L, Su YCF, Saunders RMK. 2009.** Molecular phylogenetic support for a broader delimitation of *Uvaria* (Annonaceae), inclusive of *Anomianthus*, *Cyathostemma*, *Ellipeia*, *Ellipeiopsis* and *Rauwenhoffia*. *Systematics and Biodiversity* **7**: 249–258.