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A new subfamilial and tribal classification of the pantropical flowering plant family Annonaceae informed by molecular phylogenetics

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The pantropical flowering plant family Annonaceae is the most species-rich family of Magnoliales. Despite long-standing interest in the systematics of Annonaceae, no authoritative classification has yet been published in the light of recent molecular phylogenetic analyses. Here, using the largest, most representative, molecular dataset compiled on Annonaceae to date, we present, for the first time, a robust family-wide phylogenetic tree and subsequent classification. We used a supermatrix of up to eight plastid markers sequenced from 193 ingroup and seven outgroup species. Some of the relationships at lower taxonomic levels are poorly resolved, but deeper nodes generally receive high support. Annonaceae comprises four major clades, which are here given the taxonomic rank of subfamily. The description of Annonoideae is amended, and three new subfamilies are described: Anaxagoreoideae, Ambavioideae and Malmeoideae. In Annonoideae, seven tribes are recognized, one of which, Duguetieae, is described as new. In Malmeoideae, seven tribes are recognized, six of which are newly described: Dendrokingstonieae, Fenerivieae, Maasieae, Malmeeae, Monocarpieae and Piptostigmateae. This new subfamilial and tribal classification is discussed against the background of previous classifications and characters to recognize subfamilies are reviewed. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 5–40.

ADDITIONAL KEYWORDS: plastid markers – subfamilies – supermatrix – tribes.

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INTRODUCTION

Inventories of tropical forests on all continents invariably list Annonaceae as one of the most diverse plant families (Phillips & Miller, 2002). In terms of species richness and abundance of individuals, Annonaceae contributes significantly to the diversity of trees in Neotropical forests (e.g. Gentry, 1988; Valencia, Balslev & Paz Y Miño, 1994) and lianas and trees in rain forests of the Old World (e.g. van Gerner *et al.*, 2003; Slik *et al.*, 2003; Tchouto *et al.*, 2006). Around 2400 species in 108 genera are currently recognized in the family (Rainer & Chatrou, 2006), > 300 of which have been described in taxonomic papers, monographs and regional or continental floras since the start of the international Annonaceae project almost 30 years ago (Maas, 1983; Chatrou, 1999). In parallel with renewed taxonomic efforts, recent years have seen increasingly detailed studies of the phylogenetics of Annonaceae (e.g. Doyle & Le Thomas, 1994, 1996; Mols *et al.*, 2004; Pirie *et al.*, 2006; Couvreur *et al.*, 2008; Erkens, Maas & Couvreur, 2009). The polyphyly of notorious 'dustbin' genera, such as *Polyalthia* Blume, has been demonstrated (Mols *et al.*, 2004; Saunders, Su & Xue, 2011), and even easily recognizable genera in morphological terms have been shown to be nonmonophyletic (Chatrou, Koek-Noorman & Maas, 2000; Erkens *et al.*, 2007; Chatrou *et al.*, 2009; Couvreur *et al.*, 2009). On the basis of these results, some generic circumscriptions have been realigned following the primary principle of monophyly (Chatrou *et al.*, 2000; Su *et al.*, 2005; Rainer, 2007; Erkens & Maas, 2008; Mols *et al.*, 2008; Nakkuntod *et al.*, 2009; Su, Chao-wasku & Saunders, 2010; Surveswaran *et al.*, 2010; Xue *et al.*, 2011).

Given the large numbers of species in Annonaceae, a useful and stable infrafamilial classification is necessary to aid communication and information retrieval. Although a number of formal or informal classifications have been proposed (e.g. Baillon, 1868; Hutchinson, 1923; Fries, 1959; Walker, 1971; van Heusden, 1992; van Setten & Koek-Noorman, 1992), none has yet proved to be stable in the face of increasing knowledge of the diversity of the family. These classifications were based on different sources of data, such as floral morphology (van Heusden, 1992), fruit and seed morphology (van Setten & Koek-Noorman, 1992) and palynology (Walker, 1971). In each case, the data were interpreted intuitively, resulting in often contradictory conclusions/classifications. The classification of Fries (1959), primarily based on floral characters, remains perhaps the most widely used. However, with few exceptions, his tribes and informal groups of genera are neither characterized by unequivocal (combinations of) characters nor demon-

strably monophyletic. To quote from a recent monographic work: 'Systems of informal classifications [in Annonaceae] have proliferated to the point that classification of the family into smaller units is in disarray' (Johnson & Murray, 1995: 249).

The phylogenetic reconstruction in Annonaceae was initiated with cladistic analyses of macromorphological and palynological characters (Doyle & Le Thomas, 1994, 1996, 1997). Although indicating the earliest diverging position of *Anaxagorea* A.St.-Hil., such characters showed high levels of homoplasy and limited phylogenetic utility compared with subsequent studies employing DNA sequence data (Doyle, Bygrave & Le Thomas, 2000; Mols *et al.*, 2004; Richardson *et al.*, 2004; Pirie *et al.*, 2006; Couvreur *et al.*, 2008, 2011). To date, a new formal classification based on molecular phylogenetic work has been postponed because of limitations in taxon representation and phylogenetic resolution. Clades are currently referred to by informal names relating to aspects of their molecular evolution [e.g. long branch clade (LBC) and short branch clade (SBC) *sensu* Richardson *et al.*, 2004, in reference to the differing levels of genetic divergence between the two major clades identified in the early molecular phylogenetic studies]. These names are neither comprehensive in scope nor usefully memorable. Improvements in generic classification have thus yet to be matched by an improved higher level classification.

A robust and maximally representative hypothesis of relationships between clades in this important angiosperm family is clearly warranted. In this article, we present a phylogenetic analysis of Annonaceae inferred from multiple plastid DNA loci, representing 94 of the 108 currently recognized genera and marking an important improvement in both the representation of taxa (at the generic level) and phylogenetic resolution in Annonaceae compared with previous efforts (e.g. Richardson *et al.*, 2004; Couvreur *et al.*, 2011). We place this analysis in the context of previous infrafamilial classifications, evaluate the monophyly of the groupings identified and discuss the relative utility of various morphological characters for the diagnosis of groups in Annonaceae. The rank at which monophyletic groups might be classified remains a more or less subjective decision; we discuss the potential classifications that might be adopted given a number of secondary criteria, such as diagnosability and size of the groups. Finally, based on the results, we formally describe four subfamilies and 12 tribes. The subfamilies are Anaxagoreoideae (corresponding to the genus *Anaxagorea*), Ambavioideae (corresponding to the ambavioide clade of Doyle & Le Thomas, 1994, 1996), Annonoideae (corresponding to the LBC of Richardson *et al.*, 2004, and the inaperturate clade of Doyle & Le Thomas, 1994, 1996)

and Malmeoideae (corresponding to the SBC of Richardson *et al.*, 2004, and the malmeoid/piptostigmoid/miliusoid clade of Doyle & Le Thomas, 1994, 1996). Seven tribes are recognized in Annonoideae, of which Duguetieae is described as new, and seven tribes are recognized in Malmeoideae, of which six are newly described, namely Dendrokingstonieae, Fenerivieae, Maasieae, Malmeeae, Monocarpieae and Piptostigmateae.

MATERIAL AND METHODS

TAXON SAMPLING

Most genera sampled were represented by two species. Exceptions were monotypic genera (with just single samples) and genera that have previously been demonstrated to be para- or polyphyletic, for which each segregate clade was represented by two samples. We selected taxa to bracket the crown node of each clade, if known. Of the 108 currently recognized genera (Rainer & Chatrou, 2006), 94 were represented, five of which were sampled for the first time, i.e. they were not represented in Richardson *et al.* (2004), who sampled 79 genera, Pirie *et al.* (2006), who increased sampling for the SBC, Couvreur *et al.* (2008), who increased sampling for the LBC, and Couvreur *et al.* (2011), who added another few unsampled genera (Table 1). Subsequent to analyses performed for this article, the genera *Anomianthus* Zoll., *Balanga* Le Thomas, *Cyathostemma* Griff., *Dasoclema* J.Sinclair, *Ellipeia* Hook.f. & Thomson, *Ellipeiopsis* R.E.Fr. and *Rauwenhoffia* Scheff. have been brought into synonymy with *Uvaria* L. (Zhou, Su & Saunders, 2009; Zhou *et al.*, 2010). With the exception of *Balanga* and *Dasoclema* (which are not sampled), these former genera are thus still represented individually. A list of currently recognized genera of Annonaceae is presented in Table 2, with the numbers of recognized species, representation of species in previous phylogenetic studies (i.e. evidence for monophyly) and representation in this study.

CHARACTER SAMPLING

We used previously published plus unpublished sequence data from up to eight plastid loci: protein coding *rbcL*, *matK* and *ndhF* genes plus an intron, *trnL*, and spacer regions *trnT-L*, *trnL-F*, *trnS-G*, *atpB-rbcL* and *psbA-trnH*. Total genomic DNA was extracted following a protocol adapted from the cetyltrimethylammonium bromide (CTAB) method (Doyle & Doyle, 1987), as described in Erkens *et al.* (2008). Conditions for the polymerase chain reactions (PCRs) and primers for the plastid markers were standard, and are identical to Pirie *et al.* (2006) and Erkens

et al. (2008). PCR products were purified using QIAquick PCR purification kits (Qiagen) and sequenced with the PCR primers.

The relative importance for the phylogenetic accuracy of sampling either characters or taxa has been discussed extensively (Graybeal, 1998; Mitchell, Mitter & Regier, 2000; Cummings & Meyer, 2005; Rokas & Carroll, 2005). We adopted a sampling strategy that addressed both issues at once, specifically by following a supermatrix approach in which missing data are tolerated (Philippe *et al.*, 2004; Wiens, 2005, 2006; Pirie *et al.*, 2008). In this way, we focused sequencing effort on the resolution of relationships between the major clades of Annonaceae, which is of particular relevance to classification in the family. For all 200 taxa, *rbcL*, the *trnL* intron and *trnL-F* spacer were sampled. After phylogenetic analyses of these three markers (results not shown), 56 species were selected, paying particular attention to the inclusion of early diverging species in clades at all levels. These 56 species were selected as placeholders to be sampled for additional characters using the remaining six markers. All data (both taxa and characters) were subsequently combined in a single supermatrix, i.e. a data matrix including incompletely sampled taxa.

DNA sequences were aligned manually using PAUP* version 4.10b (Swofford, 2000) and MacClade (Maddison & Maddison, 2000) following the guidelines in Kelchner (2000). Characters in regions for which alignment was ambiguous were excluded from the analyses. Microsatellites were also excluded, as these regions are variable within species (Kelchner & Clark, 1997; Provan, Powell & Hollingsworth, 2001; personal observations on species for which the same spacer region from different accessions was sequenced). Gaps in the alignment shared by two or more taxa were coded as a single binary character (presence/absence) according to the simple indel coding method of Simmons & Ochoterena (2000). Single-nucleotide indels were verified once more against the tracer files to ensure that they were not sequence editing artefacts. Nucleotide characters included in these indels were excluded from the analyses, with a few exceptions when insertions in clades contained parsimony informative variation at the nucleotide level. Two short sequences, of 15 positions in *psbA-trnH* and of 12 positions in the *trnT-L* spacer, appeared to represent inversions. Around half of the species exhibited the reverse-complement sequence of the other half and transitions between the motifs appeared to be frequent, with different motifs apparent in closely related species (as reported in Pirie *et al.*, 2006). We aligned one motif with the reverse complement of the other and, as the informative base changes that were revealed displayed little

Table 1. Collections and GenBank numbers

Species	Country	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Persea americana</i> Mill.	UUBG	AY841592	–	JQ437545	JQ742021	AY841669	JQ513882	JQ513883	–
<i>Coelocaryon preussii</i> Warb.	Wieringa, J.J. 3640 (WAG)	AY743437	AY743475	JQ437546	–	AY743456	AY841424	–	–
<i>Degeneria vitiensis</i> L.W.Bailey & A.C.Sm./ <i>D. roseiflora</i> J.M.Mill.	Mixed origin	L12643	–	–	–	AY220414 (intron) AY220361 (spacer)	–	–	–
<i>Eupomatia bennettii</i> F.Muell.	Chatrou, L.W. s.n. (U)	DQ861790	JQ437547	–	–	DQ861842	–	–	JQ513885
<i>Galbulimima belgeveana</i> (F.Muell.) Sprague	Mixed origin	L12646	–	–	–	AY220415 (intron) AY220362 (spacer)	–	–	–
<i>Liriodendron chinense</i> Sargent	Chatrou, L.W. 279 (U)	AY841593	–	–	–	AY841670	–	–	–
<i>Magnolia kobus</i> DC.	Chatrou, L.W. 278 (U)	AY743438	–	–	–	AY743457	–	–	–
<i>Alphonsea boniana</i> Finet & Gagnep.	Keßler, P.J.A. 3116 (L)	AY318965	–	–	–	AY319077	–	–	–
<i>Alphonsea elliptica</i> Hook.f. & Thomson	Van Balgooy, M. 5141 (L)	AY318966	–	–	–	AY319078	–	–	–
<i>Ambavia gerrardii</i> (Baill.) Le Thomas	Rabevohitra, R. 2035 (MO)	JQ513886	–	–	–	JQ513889	–	–	–
<i>Anaxagorea phaeocarpa</i> Mart.	Maas, P.J.M. 8592 (U)	AY238952	AY238960	EF179279	DQ861643	AY231284 (intron) AY238944 (spacer)	AY841426	EF179244	EF179321
<i>Anaxagorea silvatica</i> R.E.Fr.	Maas, P.J.M. 8836 (U)	AY743439	AY743477	EF179280	DQ861644	AY743458	AY841427	AY578140	EF179322
<i>Annickia chlorantha</i> (Oliv.) Setten & Maas	Sosef, M.S.M. 1877 (WAG)	AY841594	AY841393	AY841401	AY841571	AY841671	AY841442	AY841370	AY841550
<i>Annickia pilosa</i> (Exell) Setten & Maas	Sosef, M.S.M. 1803 (WAG)	AY743450	AY743488	AY841402	AY841572	AY743469	AY841444	AY841371	AY841551
<i>Annona glabra</i> L.	Chatrou, L.W. 467 (U)	AY841596	DQ125050	EF179281	JQ742022	AY841673	DQ125116	EF179246	EF179323
<i>Annona herzogii</i> (R.E.Fr.) H.Rainer	Chatrou, L.W. 162 (U)	AY841656	DQ125062	EF179308	JQ742023	AY841734	DQ125132	EF179273	EF179350

<i>Annona muricata</i> L.	<i>Chatrou, L.W.</i> 468 (U)	Cultivated in UUBG, of Neotropical origin	AY743440	AY743478	EF179282	DQ861648	AY743459	AY841428	EF179247	EF179324
<i>Anonidium</i> sp.	<i>Cheek, M.</i> 7896 (K)	Cameroon	AY841598	DQ125051	EF179283	JQ742024	AY841675	DQ125117	EF179248	EF179325
<i>Artabotrys hexapetalus</i> (L.f.) Bhandari	<i>UUBG</i> 94GR01614 (U)	Cultivated in UUBG, origin India	AY238953	AY238962	EF179284	DQ861649	AY231286 (intron) AY238946 (spacer)	AY841429	EF179249	EF179326
<i>Artabotrys</i> sp.	<i>Wieringa, J.J.</i> 4018 (WAG)	Gabon	AY841599	DQ125052	EF179285	JQ742025	AY841676	DQ125118	EF179250	EF179327
<i>Asimina angustifolia</i> A. Gray	<i>Weerasooriya,</i> <i>A. s.n.</i> (U)	USA	DQ124939	DQ125053	EF179286	JQ742026	AY841677	DQ125119	EF179251	EF179328
<i>Asimina rugelii</i> B.L. Rob.	<i>J. R. Abbott</i> 22361 (FLAS)	USA	JQ513887	-	-	-	GQ139881	-	-	-
<i>Asimina triloba</i> (L.) Dunal	<i>Chatrou, L.W.</i> 276 (U)	Cultivated in UUBG, origin USA	AY743441	AY743479	EF179287	JQ742027	AY743460	AY841430	EF179252	EF179329
<i>Asteranthe asterias</i> (S. Moore) Engl. & Diels	<i>Robertson, A.</i> 7548 (WAG)	Kenya	EU169757	-	-	-	EU169757	-	-	-
<i>Bocageopsis multiflora</i> (Mart.) R.E.Fr.	<i>Jansen-Jacobs,</i> <i>M.J.</i> 5789 (U)	Guyana	AY841600	-	-	-	AY841678	-	-	-
<i>Bocageopsis pleiosperma</i> Maas	<i>Miralha,</i> <i>J.M.S.</i> 300 (U)	Brazil	AY841601	-	-	-	AY841679	-	-	-
<i>Cananga odorata</i> (Lam.) Hook.f. & Thomson	<i>Chatrou, L.W.</i> 93 (U)	Costa Rica	AY841602	AY841394	AY841403	-	AY841680	AY841431	AY841372	AY841548
<i>Cleistopholis glauca</i> Pierre ex Engl. & Diels	<i>Wieringa, J.J.</i> 3278 (WAG)	Gabon	AY841603	AY841395	AY841404	-	AY841681	AY841432	AY841373	AY841549
<i>Crematosperma brevipes</i> (DC.) R.E.Fr.	<i>Scharf, U.</i> 76 (U)	French Guiana	AY743527	AY743550	AY841405	AY841573	AY743573	AY841447	AY841374	AY841552
<i>Crematosperma</i> <i>cauliflorum</i> R.E.Fr.	<i>Chatrou, L.W.</i> 224 (U)	Peru	AY743519	AY743542	AY841406	AY841574	AY743565	AY841448	AY841375	AY841553
<i>Cyathocalyx martabanicus</i> Hook.f. & Thomson	<i>Mols, J.B.</i> 11 (L)	Cultivated in Kebun Raya Bogor, Indonesia	AY841605	DQ125054	EF179288	JQ742028	AY841683	DQ125120	EF179253	EF179330
<i>Cymbopetalum brasiliense</i> (Vell.) Benth. ex Baill.	<i>UUBG</i> 84GR00275	Cultivated in UUBG, originating from Brazil	AY841608	DQ125055	EF179289	DQ861646	AY841686	DQ125121	EF179254	EF179331
<i>Cymbopetalum torulosum</i> G.E. Schatz	<i>Chatrou, L.W.</i> 54 (U)	Costa Rica	AY743442	-	-	-	AY743461	-	-	-
<i>Dasydaschalon macrocalyx</i> Finet & Gagnep.	<i>Keßler, P.J.A.</i> 3199 (L)	Thailand	AY841610	EF179277	EF179290	JQ742029	AY841688	EF179313	EF179255	EF179332

Table 1. *Continued*

Species	Country	<i>rbcl</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Dasyaschalon sotoepense</i> Craib	Thailand	AY743443	–	–	–	AY743462	–	–	–
<i>Desmopsis microcarpa</i> R.E.Fr.	Costa Rica	AY319059	–	–	–	AY319173	–	–	–
<i>Desmopsis schippii</i> Standl.	Costa Rica	AY319060	–	–	–	AY319174	–	–	–
<i>Desmos chinensis</i> Lour.	Hong Kong	JQ762414	–	–	–	JQ762415	–	–	–
<i>Desmos elegans</i> (Thwaites) Saff.	Sri Lanka	HQ214067	–	–	–	HQ214069	–	–	–
<i>Dielsiothamnus divaricatus</i> (Diels) R.E.Fr.	Tanzania	EU169781	–	–	–	EU169759	–	–	–
<i>Disepalum pulchrum</i> (King) J.Sinclair	Malaysia	JQ513888	–	–	–	GQ139909	–	–	–
<i>Disepalum platipetalum</i> Merr.	Indonesia	AY841612	–	–	–	AY841690	–	–	–
<i>Drepananthus biovulatus</i> (Boerl.) Survesw. & R.M.K.Saunders	Indonesia	HM173779	–	–	–	HM173751	–	–	–
<i>Duguetia hadrantha</i> (Diels) R.E.Fr.	Peru	AY738161	AY740541	EF179293	DQ861650	AY740573	DQ125123	EF179258	EF179335
<i>Duguetia staudtii</i> (Engl. & Diels) Chatrou	Cameroon	AY738178	AY740558	EF179294	JQ742030	AY740590	DQ125124	EF179259	EF179336
<i>Enicosanthum</i> <i>membranifolium</i> J.Sinclair	Thailand	AY318974	–	–	–	AY319086	–	–	–
<i>Enicosanthum paradoxum</i> Becc.	Indonesia	AY318975	–	–	–	AY319087	–	–	–
<i>Ephedranthus boliviensis</i> Chatrou & Pirie	Bolivia	AY841614	–	–	–	AY841692	–	–	–
<i>Ephedranthus</i> sp.	Brazil	AY841616	AY841396	AY841407	AY841575	AY841694	AY841463	AY841376	AY841554
<i>Fissistigma glaucescens</i> (Hance) Merr.	Hong Kong	AY743444	–	–	–	AY743463	AY743444	–	–
<i>Fissistigma uonicum</i> (Dunn) Merr.	Hong Kong	AY841617	–	–	–	AY841695	–	–	–
<i>Fitzalania heteropetala</i> (F.Muell.) F.Muell.	Australia	AY318977	–	–	–	AY319089	AY318977	–	–

<i>Friesodielsia desmoides</i> (Crab) Steenis	Thailand	AY841618	-	-	-	AY841696	-	-	-
<i>Friesodielsia</i> sp.	Gabon	AY841619	-	-	-	AY841697	-	-	-
<i>Fusaea longifolia</i> (Aubl.) Saff.	Peru	AY841620	-	-	-	AY841698	-	-	-
<i>Fusaea peruviana</i> R.E.Fr.	Peru	AY743445	AY743483	EF179295	DQ861652	AY743464	AY841436	EF179260	EF179337
<i>Goniotalamus griffithii</i> Hook.f. & Thomson	Thailand	AY743446	AY743484	EF179296	JQ742031	AY743465	DQ125125	EF179261	EF179338
<i>Goniotalamus tapis</i> Miq.	Thailand	AY841622	DQ125058	EF179297	JQ742032	AY841700	DQ125126	EF179262	EF179339
<i>Greenwayodendron oliveri</i> (Engl.) Verde.	Ghana	AY743451	AY743489	AY841408	AY841576	AY743470	AY841465	AY841377	AY841555
<i>Greenwayodendron</i> <i>suavolens</i> (Engl. & Diels) Verde.	Kenya	AY841524	-	-	-	AY841538	-	-	-
<i>Guatteria anomala</i> R.E.Fr.	Mexico	AY740962	AY740913	EF179298	DQ861657	AY741011	AY841437	EF179263	EF179340
<i>Guatteria pudica</i> N.Zamora & Maas	Costa Rica	AY740994	AY740945	JQ769093	DQ861663	AY741043	DQ125197	JQ513884	FJ842397
<i>Haplostichanthus</i> <i>longirostris</i> (Scheff.) Heusden	Papua New Guinea	AY318979	-	-	-	AY319091	-	-	-
<i>Hexalobus crispiflorus</i> A. Rich.	Gabon	EU169782	-	-	-	EU169760	-	-	-
<i>Hexalobus salicifolius</i> Engl.	Gabon	EU169783	-	-	-	EU169761	-	-	-
<i>Hornschieuchia citriodora</i> D.M.Johnson	Brazil	AY841625	-	-	-	AY841703	-	-	-
<i>Isolona campanulata</i> Engl. & Diels	UUBG, of tropical African origin	AY238954	AY238963	EU169715	JQ742033	AY231287 (intron) AY238947 (spacer) AY841704	DQ125127	EF179266	EU169806
<i>Isolona cooperi</i> Hutch. & Dalziel ex G.P.Cooper & Record	UUBG, originating from Ivory Coast	AY841626	-	-	-	-	-	-	-
<i>Klarobelia inundata</i> Chatrou	Peru	AY743452	AY743490	AY841409	AY841577	AY743471	AY841469	AY841378	AY841556
<i>Klarobelia stipitata</i> Chatrou	Costa Rica	AY841628	-	-	-	AY841706	-	-	-
<i>Letestudoxa bella</i> Pellegr.	Gabon	AY841629	DQ125059	EF179302	DQ861653.	AY841707	DQ125128	EF179267	EF179344

Table 1. *Continued*

Species	Country	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Letestudoxa glabrifolia</i> Chatrou & Repetur	Gabon	AY841630	–	–	–	AY841708	–	–	–
<i>Letouianthus stellatus</i> Diels	Kenya	EU169775	–	–	–	EU169753	–	–	–
<i>Maasia discolor</i> (Diels) Mols, Keßler & Rogstad	Papua New Guinea	AY319021	AY518872	AY841416	AY841584	AY319135	AY841500	AY841385	AY841563
<i>Maasia glauca</i> (Hassk.) Mols, Keßler & Rogstad	Indonesia	AY319023	–	–	–	AY319137	–	–	–
<i>Maasia sumatrana</i> (Miq.) Mols, Keßler & Rogstad	Malaysia	AY319039	AY518873	AY841418	AY841586	AY319153	AY841503	AY841387	AY841565
<i>Malmea dielsiana</i> R.E.Fr.	Peru	AY238955	AY238964	AY841410	AY841578	AY231288 (intron) AY238948 (spacer)	AY841473	AY841379	AY841557
<i>Malmea</i> sp.	Peru	AY841527	AY841397	AY841411	AY841579	AY841541	AY841475	AY841380	AY841558
<i>Marsypopetalum littorale</i> (Blume) B.Xue & R.M.K.Saunders	Indonesia	AY319026	–	–	–	AY319140	–	–	–
<i>Marsypopetalum pallidum</i> (Blume) Kurz	Thailand	AY318980	–	–	–	AY319092	–	–	–
<i>Meiocarpidium lepidotum</i> (Oliv.) Engl. & Diels	Gabon	EU169776	EU169687	–	–	EU169754	EU169731	–	EU169798
<i>Meiogyne cylindrocarpa</i> (Burck) Heusden	Malaysia	AY318981	–	–	–	AY319093	–	–	–
<i>Meiogyne</i> sp.	Mexico	AY841623	–	–	–	AY841701	–	–	–
<i>Meiogyne stenopetala</i> (F.Muell.) Heusden	Australia	AY318971	–	–	–	AY319083	–	–	–
<i>Meiogyne virgata</i> (Blume) Miq.	Indonesia	AY318982	–	–	–	AY319094	–	–	–
<i>Mezzettia parviflora</i> Becc.	Indonesia	AY318983	–	–	–	AY319095	–	–	–
<i>Miliusa horsfieldii</i> (Benn.) Pierre	Indonesia	AY318986	–	–	–	AY319098	–	–	–

<i>Mituisa mollis</i> Pierre	<i>Pholsena</i> 1756 (L)	Thailand	AY318989	-	-	-	AY319101	-	-	-
<i>Mischogyne michelioides</i> Exell	<i>Bamps, P.</i> 4459 (WAG)	Angola	EU169786	-	-	-	EU169764	-	-	-
<i>Mitrella kentii</i> (Blume) Miq.	<i>Gardette, E.</i> 2239 (K)	Malaysia	AY841633	-	-	-	AY841711	-	-	-
<i>Mitrephora polypyrena</i> (Blume) Miq.	<i>Mols, J.B.</i> 7 (L)	Indonesia	AY318997	-	-	-	AY319110	-	-	-
<i>Mitrephora teysmannii</i> Scheff.	<i>Keßler, P.J.A.</i> 3226 (L)	Thailand	AY318996	-	-	-	AY319109	-	-	-
<i>Mkilua fragrans</i> Verdc.	<i>Chatrou, L.W.</i> 474 (U)	Cultivated in UUBG, origin Kenya	AY841634	DQ125060	EF179303	DQ861647	AY841712	DQ861696	EF179268	EF179345
<i>Monanthotaxis whytei</i> (Stapf) Verdc.	<i>UUBG</i> 84GR00388	Cultivated in UUBG, origin Nigeria	AY841635	EF179278	EF179304	JQ742034	AY841713	EF179315	EF179269	EF179346
<i>Monanthotaxis</i> sp.	<i>Wieringa, J.J.</i> 3833 (WAG)	Gabon	AY841636	-	-	-	AY841713	-	-	-
<i>Monocarpia euneura</i> Miq.	<i>Slik, J.W.F.</i> 2002-2931 (L)	Indonesia	AY318998	AY518865	AY841412	AY841580	AY319111	AY841477	AY841381	AY841559
<i>Monocyclanthus vegnei</i> Keay	<i>Jongkind, C.C.H.</i> 6992 (WAG)	Liberia	EU169765	-	-	-	EU169787	-	-	-
<i>Monodora crispata</i> Engl.	<i>UUBG</i> E64GR00066	Cultivated in UUBG, origin Ivory Coast	AY841637	-	-	-	AY841715	-	-	-
<i>Monodora myristica</i> (Gaertn.) Dunal	<i>UUBG</i> E84GR00389	Cultivated in UUBG, origin Ivory Coast	AY743447	EU169700	EU169721	JQ742035	AY743466	DQ125129	EF179270	EU169812
<i>Mosannona costaricensis</i> (R.E.Fr.) Chatrou	<i>Chatrou, L.W.</i> 90 (U)	Costa Rica	AY743510	AY743503	AY841413	AY841581	AY743496	AY841479	AY841382	AY841560
<i>Mosannona papillosa</i> Chatrou	<i>Pitman, N.</i> s.n. (U)	Ecuador	AY743514	-	-	-	AY743500	-	-	-
<i>Muasumbia alba</i> Couvreur & D.M.Johnson	<i>Couvreur, T.L.P.</i> 85 (WAG)	Tanzania	EU747680	-	-	-	EU747674	-	-	-
<i>Neostenanthera myristicifolia</i> (Oliv.) Exell	<i>Wieringa, J.J.</i> 3566 (WAG)	Gabon	AY743448	AY743486	EF179306	JQ742036	AY743467	DQ125130	EF179271	EF179348
<i>Neo-uvaria acuminatissima</i> (Miq.) Airy Shaw	<i>Ridsdale, C.E.</i> DV-SR-4671 (L)	Malaysia	AY318999	-	-	-	AY319112	-	-	-
<i>Neo-uvaria parallelivenia</i> (Boerl.) H.Okada & K.Ueda	<i>Keßler, P.J.A.</i> sub IV-H-73 (L)	Indonesia	AY319000	-	-	-	AY319113	-	-	-
<i>Onychopetalum periquino</i> (Rusby) D.M.Johnson & N.A.Murray	<i>Chatrou, L.W.</i> 425 (U)	Bolivia	AY319065	AY518876	AY841414	AY841582	AY319179	AY841485	AY841383	AY841561

Table 1. *Continued*

Species	Country	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Ophrypetalum odoratum</i> Diels	Kenya	EU169789	–	–	–	EU169767	–	–	–
<i>Oropheia celebica</i> (Blume) Miq.	Indonesia	AY319004	–	–	–	AY319117	–	–	–
<i>Oropheia creaghii</i> (Ridl.) Leonardia & Keßler	Indonesia	AY841632	–	–	–	AY841710	–	–	–
<i>Oropheia enterocarpa</i> Maingay ex Hook.f. & Thomson	Thailand	AY319006	–	–	–	AY319119	–	–	–
<i>Oropheia kerrii</i> Keßler	Thailand	AY319008	–	–	–	AY319121	–	–	–
<i>Oropheia polycarpa</i> ADC.	Thailand	AY319010	–	–	–	AY319123	–	–	–
<i>Oxandra asbeckii</i> (Pulle) R.E.Fr.	Guyana	AY841639	–	–	–	AY841717	–	–	–
<i>Oxandra longipetala</i> R.E.Fr.	Costa Rica	AY841641	–	–	–	AY841719	–	–	–
<i>Oxandra macrophylla</i> R.E.Fr.	Peru	AY841642	–	–	–	AY841720	–	–	–
<i>Oxandra polyantha</i> R.E.Fr.	Peru	AY841643	–	–	–	AY841721	–	–	–
<i>Oxandra venezuelana</i> R.E.Fr.	Costa Rica	AY841645	–	–	–	AY841723	–	–	–
<i>Oxandra xylopioides</i> Diels	Peru	AY841646	–	–	–	AY841724	–	–	–
<i>Phacanthus ebracteolatus</i> (C.Presl.) Merr.	Papua New Guinea	AY319012	–	–	–	AY319125	–	–	–
<i>Piptostigma morrhani</i> De Wild.	Gabon	AY743454	AY743492	AY841415	AY841583	AY743473	AY841498	AY841384	AY841562
<i>Piptostigma pilosum</i> Oliv.	Cameroon	AY841648	–	–	–	AY841726	–	–	–
<i>Platymitra macrocarpa</i> Boerl.	Indonesia	AY319013	–	–	–	AY319127	–	–	–

<i>Polyalthia borneensis</i> Merr.	<i>Ridsdale, C.E.</i> <i>DV-SR-7921</i> (L)	Malaysia	AY319014	-	-	-	-	AY319128	-	-	-
<i>Polyalthia cauliflora</i> Hook.f. & Thomson	<i>Kessler, P.J.A.</i> <i>3114</i> (L)	Singapore	AY319015	-	-	-	-	AY319129	-	-	-
<i>Polyalthia celebica</i> Miq.	<i>Mols, J.B. 9</i> (L)	Indonesia	AY319016	-	-	-	-	AY319130	-	-	-
<i>Polyalthia cerasoides</i> (Roxb.) Benth. & Hook.f. ex Beddome	<i>Chalermglin</i> <i>440214-4</i> (L)	Thailand	AY319017	-	-	-	-	AY319131	-	-	-
<i>Polyalthia cinnamomea</i> Hook.f. & Thomson	<i>Ridsdale, C.E.</i> <i>DV-M1-347</i> (L)	Malaysia	AY319018	-	-	-	-	AY319132	-	-	-
<i>Polyalthia congesta</i> (Ridl.) J. Sinclair	<i>Ridsdale, C.E.</i> <i>DV-S-5105</i> (L)	Malaysia	AY319019	-	-	-	-	AY319133	-	-	-
<i>Polyalthia debilis</i> (Pierre) Finet & Gagnep.	<i>Kessler, P.J.A.</i> <i>3228</i> (L)	Thailand	AY319020	-	-	-	-	AY319134	-	-	-
<i>Polyalthia flagellaris</i> (Becc.) Airy Shaw	<i>Duding</i> 38 (K)	Brunei	AY319022	-	-	-	-	AY319136	-	-	-
<i>Polyalthia</i> cf. <i>glabra</i> (Hook.f. & Thomson) J. Sinclair	<i>Rastini</i> 224 (L)	Indonesia	AY319032	-	-	-	-	AY319146	-	-	-
<i>Polyalthia lateriflora</i> (Blume) King	<i>Hort. Bot.</i> <i>Bog.</i> <i>XII-B-VII-37</i> (L)	Indonesia	AY319024	-	-	-	-	AY319138	-	-	-
<i>Polyalthia longifolia</i> (Sonn.) Thwaites	<i>Johnson, D.M.</i> <i>1965</i> (OWU)	Tanzania	AY319027	-	-	-	-	AY319141	-	-	-
<i>Polyalthia</i> cf. <i>longifolia</i> (Sonn.) Thwaites	<i>Mols, J.B. 14</i> (L)	Indonesia	AY319025	-	-	-	-	AY319139	-	-	-
<i>Polyalthia longipes</i> (Miq.) Koord. & Valet.	<i>Ridsdale, C.E.</i> <i>DV-M2-11443</i> (L)	Malaysia	AY319028	-	-	-	-	AY319142	-	-	-
<i>Polyalthia obliqua</i> Hook.f. & Thomson	<i>Ambriansyah</i> <i>1694</i> (L)	Indonesia	AY319029	-	-	-	-	AY319143	-	-	-
<i>Polyalthia pendula</i> Capuron ex G.E. Schatz & Le Thomas	<i>Rabevohitra</i> <i>2386</i> (K)	Madagascar	AY319030	-	-	-	-	AY319144	-	-	-
<i>Polyalthia rumphii</i> (Blume ex Hensch.) Merr.	<i>Van Balgooy,</i> <i>M. 5654</i> (L)	Indonesia	AY319031	-	-	-	-	AY319145	-	-	-

Table 1. *Continued*

Species	Country	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Polyalthia sclerophylla</i> Hook.f. & Thomson	Indonesia	AY319033	–	–	–	AY319147	–	–	–
<i>Polyalthia stenopetala</i> (Hook.f. & Thomson)	Thailand	AY319034	–	–	–	AY319148	–	–	–
<i>Polyalthia stuhlmannii</i> Finet & Gagnep. (TISTR)	Kenya	AY319035	–	–	–	AY319149	–	–	–
<i>Polyalthia subcordata</i> (Engl.) Verdc.	Indonesia	AY319037	–	–	–	AY319151	–	–	–
<i>Polyalthia suberosa</i> (Roxb.) Thwaites	Cultivated in UUBG, origin India	AY238956	AY238965	AY841417	AY841585	AY231289 (intron) AY238949 (spacer) AY319154	AY841502	AY841386	AY841564
<i>Polyalthia viridis</i> Craib	Thailand	AY319040	–	–	–	–	–	–	–
<i>Polyalthia xanthopetala</i> Merr.	Malaysia	AY319041	–	–	–	AY319155	–	–	–
<i>Polyceratocarpus</i> <i>microtrichus</i> (Engl. & Diels) Ghesq. ex Pellegr. <i>Polyceratocarpus pellegrinii</i> Le Thomas	Cameroon	EU747683	–	–	–	EU747677	–	–	–
<i>Popovia odoardi</i> Diels	Cameroon	EU747684	–	–	–	EU747678	–	–	–
<i>Popovia pisocarpa</i> (Blume) Endl.	Malaysia	AY319043	–	–	–	AY319157	–	–	–
<i>Porcelia steinbachii</i> (Diels) R.E.Fr.	Indonesia	AY319044	–	–	–	AY319158	–	–	–
<i>Pseudartabotrys letestui</i> Pellegr.	Cultivated in UUBG, origin Bolivia	AY841649	–	–	–	AY841727	–	–	–
<i>Pseudephedranthus fragrans</i> (R.E.Fr.) Aristeg.	Gabon	AY841650	DQ125061	EF179307	–	AY841728	DQ125131	EF179272	EF179349
<i>Pseudomalmea diclina</i> (R.E.Fr.) Chatrou	Venezuela	AY841651	–	–	–	AY841729	–	–	–
	Peru	AY319068	AY841398	AY841419	AY841587	AY319128	AY841506	AY841388	AY841566

<i>Pseudomalmea</i> sp.	<i>Idarraa</i> , A. 13 (U)	Colombia	AY841652	-	-	-	AY841730	-	-	-
<i>Pseudoxandra polypheba</i> (Diels) R.E.Fr.	<i>Maas</i> , P.J.M. 8227 (U)	Peru	AY841654	JQ769091	JQ742037	AY841732	AY841512	-	-	-
<i>Pseudoxandra spiritus-sancti</i> Maas	<i>Maas</i> , P.J.M. 8833 (U)	Brazil	AY841533	AY841399	AY841421	AY841547	AY841513	AY841390	AY841568	-
<i>Pseudoxaria megalopus</i> (K.Schum.) Y.C.F.Su & Mols	<i>Takeuchi</i> 15599 (L)	Papua New Guinea	AY319011	-	-	AY319124	AY319011	-	-	-
<i>Pseudoxaria panattonis</i> (Miq.) Y.C.F.Su & R.M.K.Saunders	<i>Slik</i> , J.W.F. 2002-2911 (L)	Indonesia	AY319049	-	-	AY319163	AY319049	-	-	-
<i>Pseudoxaria phuyensis</i> (R.M.K.Saunders, Y.C.F.Su & Chalermglin)	<i>Keßler</i> , P.J.A. 3221 (L)	Thailand	AY319001	-	-	AY319114	AY319001	-	-	-
<i>Pseudoxaria rugosa</i> (Blume) Merr.	<i>Keßler</i> , P.J.A. .3209 (L)	Thailand	AY319048	-	-	AY319162	AY319048	-	-	-
<i>Ruizodendron ovale</i> (Ruiz & Pav.) R.E.Fr.	<i>Maas</i> , P.J.M. 8600 (U)	Ecuador	AY841657	HQ214070	-	AY841735	AY841514	-	-	-
<i>Sageraea lanceolata</i> Miq.	<i>Ridsdale</i> , C.E. DV-M2-1692 (L)	Malaysia	AY319050	-	-	AY319164	-	-	-	-
<i>Sanrafaelia ruffonammari</i> Verdc.	<i>Kayombo</i> 3027 (MO)	Tanzania	EU169790	-	-	EU169768	-	-	-	-
<i>Sapranthus microcarpus</i> (Donn.Sm.) R.E.Fr.	<i>Maas</i> , P.J.M. 8457 (U)	Honduras	AY319052	-	-	AY319166	-	-	-	-
<i>Sapranthus viridiflorus</i> G.E.Schatz	<i>Chatrou</i> , L.W. 55 (U)	Costa Rica	AY319051	AY743493	AY841422	AY319165	AY841515	AY841391	AY841569	-
<i>Sphaerocoryne gracilis</i> (Oliv. ex Engl. & Diels) Verdc.	<i>Robertson</i> , A. 7554 (WAG)	Kenya	EU169755	-	-	EU169777	-	-	-	-
<i>Sphaerocoryne</i> sp.	<i>Chalermglin</i> 440214-2 (L)	Thailand	AY319071	-	-	AY319185	-	-	-	-
<i>Stelechocarpus burahol</i> (Blume) Hook.f. & Thomson	<i>Mols</i> , J.B. 13 (L)	Indonesia	AY319053	-	-	AY319167	-	-	-	-
<i>Stelechocarpus cauliflorus</i> (Scheff.) J.Sinclair	<i>Hort. Bot. Bog.</i> XV-A-196 (L)	Indonesia	AY319054	-	-	AY319168	-	-	-	-

Table 1. *Continued*

Species	Country	<i>rbcL</i>	<i>matK</i>	<i>ndhF</i>	<i>trnTL</i>	<i>trnLF</i>	<i>psbA-trnH</i>	<i>atpB-rbcL</i>	<i>trnSG</i>
<i>Stenagona costaricensis</i> R.E.Fr.	Costa Rica	AY319069	–	–	–	AY319183	–	–	–
<i>Stenagona panamensis</i> Standl.	Costa Rica	AY319070	–	–	–	AY319184	–	–	–
<i>Tetrameranthus duckei</i> R.E.Fr.	Brazil	AY841658	–	–	–	AY841736	–	–	–
<i>Tetrameranthus laonae</i> D.R.Simpson	Peru	AY841659	–	–	–	AY841737	–	–	–
<i>Toussaintia orientalis</i> Verdc.	Tanzania	EU169778	–	–	–	EU169756	–	–	–
<i>Tridimeris</i> sp.	Mexico	AY319055	–	–	–	AY319169	–	–	–
<i>Trigynaea duckei</i> (R.E.Fr.)	Peru	AY841660	–	–	–	AY841738	–	–	–
<i>Trigynaea lanceipetala</i> R.E.Fr.	Peru	AY743449	AY743487	EF179309	JQ742038	AY743468	–	EF179274	EF179351
<i>Trigynaea lanceipetala</i> D.M.Johnson & N.A.Murray	Peru	AY743449	AY743487	EF179309	JQ742038	AY743468	–	EF179274	EF179351
<i>Trivalvaria macrophylla</i> (Blume) Miq.	Indonesia	AY319056	–	–	–	AY319170	–	–	–
<i>Unonopsis pittieri</i> Saff.	Costa Rica	AY841661	–	–	–	AY841739	–	–	–
<i>Unonopsis stipitata</i> Diels	Peru	AY841662	AY841400	AY841423	AY841591	AY841740	AY841519	AY841392	AY841570
<i>Uvaria chamae</i> P.Beauv.	Cultivated in UUBG, origin Togo	AY841663	–	–	–	AY841741	–	–	–
<i>Uvaria cherreensis</i> (Pierre ex Finet & Gagnep.) L.L.Zhou, Y.C.F. Su & R.M.K. Saunders	Thailand	FJ743823	–	–	–	FJ743858	–	–	–
<i>Uvaria clementis</i> (Merr.) Attanayake, I.M.Turner & R.M.K.Saunders	Thailand	AY841606	–	–	–	FJ743853	–	–	–
<i>Uvaria cuneifolia</i> (Hook.f. & Thomson) L.L.Zhou, Y.C.F.Su & R.M.K. Saunders	Indonesia	FJ743822	–	–	–	FJ743857	–	–	–
<i>Uvaria dulcis</i> Dunal	Thailand	FJ743815	–	–	–	FJ743849	–	–	–

<i>Uvaria grandiflora</i> Roxb. ex Hornem.	Saunders 05/11 (HKU)	Thailand	FJ743836	-	-	-	FJ743870	-	-	-
<i>Uvaria griffithii</i> L.L.Zhou, Y.C.F.Su & R.M.K.Saunders	Chalermglin 440402-2 (TISTR)	Thailand	FJ743820	-	-	-	FJ743855	-	-	-
<i>Uvaria lucida</i> Benth. subsp. virens (N.E.Br.) Verdec.	UUBG 84GR00334	Cultivated in UUBG, origin West African	AY238957	AY238966	EF179310	JQ742039	AY231290 (intron) AY238950 (spacer) FJ743859	AY841440	EF179275	EF179352
<i>Uvaria siamensis</i> (Scheff.) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders	Saunders 07/13 (HKU)	Cultivated in Hong Kong Botanic Gardens	FJ743824	-	-	-	FJ743859	-	-	-
<i>Uvariastrum insculptum</i> (Engl. & Diels) Sprague & Hutch.	Jongkind, C.C.H. 4707 (WAG)	Ivory Coast	EU169791	-	-	-	EU169769	-	-	-
<i>Uvariastrum pyraeartii</i> De Wild.	Wieringa, J.J. 2620 (WAG)	Gabon	EU169792	-	-	-	EU169770	-	-	-
<i>Uvariadendron kirkii</i> Verdec.	Robertson, A. 7550 (WAG)	Kenya	EU169793	-	-	-	EU169771	-	-	-
<i>Uvariadendron molundense</i> (Diels) R.E.Fr.	Sosef, M.S.M. 2219 (WAG)	Gabon	EU169794	-	-	-	EU169772	-	-	-
<i>Uvariopsis korupensis</i> Gereau & Kenfack	Richardson, J.E. 212 (WAG)	Gabon	EU169796	-	-	-	EU169774	-	-	-
<i>Uvariopsis vanderystii</i> Robyns & Ghesq.	Sosef, M.S.M. 2241 (WAG)	Gabon	EU169773	-	-	-	EU169795	-	-	-
<i>Uvariopsis tripetala</i> (Baker.f.) G.E.Schatz	Jongkind, C.C.H. 4356 (WAG)	Ivory Coast	EU169780	-	-	-	EU169758	-	-	-
<i>Woodiellantha</i> sp.	Lugas 311 (K)	Malaysia	AY841665	-	-	-	AY841743	-	-	-
<i>Xylopia ferruginea</i> (Hook.f. & Thomson) Hook.f. & Thomson	Slik, J.W.F. 2002-S 558 (L)	Indonesia	AY841666	DQ125063	EF179311	JQ742040	AY841744	DQ125133	-	-
<i>Xylopia hypolemptra</i> Mildbr. & Diels	Wieringa, J.J. 3748 (WAG)	Gabon	AY841668	-	-	-	AY841746	-	-	-
<i>Xylopia peruviana</i> R.E.Fr.	Chatrou, L.W. 483 (U)	Cultivated in UUBG, origin Peru	AY238958	AY238967	EF179312	DQ861654	AY231291 (intron) AY238951 (spacer)	DQ125134	EF179276	EF179353

Table 2. Currently recognized genera of Annonaceae, number of species and number of species sampled in phylogenetic analyses, demonstrating (lack of) monophyly. Unless indicated otherwise, studies that demonstrate monophyly are given, including the sampling size. A dash indicates either a lack of presence altogether in any phylogenetic study or the presence of a single species only. Genera followed by an asterisk were not included in the phylogenetic analyses presented in this paper

Genus	No. of recognized species	Evidence for monophyly: no. of species sampled and reference	Genus	No. of recognized species	Evidence for monophyly: no. of species sampled and reference
<i>Afroguatteria</i> *	2	—	<i>Meiogyne</i>	15	4 ^a (paraphyletic)
<i>Alphonsea</i>	25	4 ^g	<i>Melodorum</i> *	10	—
<i>Ambavia</i>	2	—	<i>Mezzettia</i>	3	—
<i>Anaxagorea</i>	30	25 ⁿ	<i>Miliusa</i>	50	9 ^g
<i>Annickia</i>	8	3 ^{i,d}	<i>Mischogyne</i>	2	—
<i>Annona</i>	162	22 ^b	<i>Mitrella</i>	8	—
<i>Anonidium</i>	4	—	<i>Mitrephora</i>	47	14 ^s
<i>Artabotrys</i>	102	25 ^a	<i>Mkilua</i>	1	—
<i>Asimina</i>	7	—	<i>Monanthotaxis</i>	56	2 ^{k,r}
<i>Asteranthe</i>	3	—	<i>Monocarpia</i>	1	2 ^a
<i>Bocagea</i> *	2	—	<i>Monocyclanthus</i>	1	—
<i>Bocageopsis</i>	4	2 ^j	<i>Monodora</i>	16	13 ^e
<i>Boutiquea</i> *	1	—	<i>Mosannona</i>	14	7 ⁱ
<i>Cananga</i>	2	2 ^p	<i>Mwasumbia</i>	1	—
<i>Cardiopetalum</i> *	3	—	<i>Neostenanthera</i>	4	—
<i>Cleistochlamys</i> *	1	—	<i>Neo-uvaria</i>	5	2 ^{a, g}
<i>Cleistopholis</i>	4	—	<i>Onychopetalum</i>	2	—
<i>Crematosperma</i>	29	19 ^j	<i>Ophrypetalum</i>	1	—
<i>Cyathocalyx</i>	7	7 ^p	<i>Orophea</i>	50	9 ^g
<i>Cymbopetalum</i>	27	3 ^k	<i>Oxandra</i>	28	11 ^d (polyphyletic)
<i>Dasymaschalon</i>	21	22 ^r	<i>Phaeanthus</i>	9	2 ^{a, g}
<i>Dendrokingstonia</i> *	2	2 ^a	<i>Phoenicanthus</i> *	2	—
<i>Desmopsis</i>	14	2 ^g (unresolved)	<i>Piptostigma</i>	14	4 ^d
<i>Desmos</i>	26	7 ^r	<i>Platymitra</i>	2	2 ^a
<i>Diclinanona</i> *	3	—	<i>Polyalthia</i>	135	26 ^j (polyphyletic)
<i>Dielsiothamnus</i>	1	—	<i>Polyceratocarpus</i>	8	4 ^d
<i>Disepalum</i>	9	8 ^m	<i>Popowia</i>	26	3 ^g
<i>Drepananthus</i>	26	15 ^p	<i>Porcelia</i>	7	—
<i>Duckeanthus</i> *	1	—	<i>Pseudartabotrys</i>	1	—
<i>Duguetia</i>	93	32 ^j	<i>Pseudephedranthus</i> *	1	—
<i>Encicosanthum</i>	18	4 ^g (unresolved)	<i>Pseudomalmea</i>	4	—
<i>Ephedranthus</i> *	6	3 ^j	<i>Pseudoxandra</i>	23	6 ^j
<i>Exellia</i>	1	—	<i>Pseuduvaria</i>	57	54 ^o
<i>Fenerivia</i> *	10	10 ^l	<i>Pyramidanthe</i> *	1	—
<i>Fissistigma</i>	48	2 ^k	<i>Ruizodendron</i>	1	—
<i>Fitzalania</i>	2	2 ^a	<i>Sageraea</i>	9	4 ^a
<i>Friesodielsia</i>	51	5 ^r	<i>Sanrafaelia</i>	1	—
<i>Froesiodendron</i> *	3	—	<i>Sapranthus</i>	6	2 ^g
<i>Fusaea</i>	2	2 ^k	<i>Schefferomitria</i> *	1	—
<i>Gilbertiella</i>	1	—	<i>Sphaerocoryne</i>	3	2 ^u
<i>Goniiothalamus</i>	134	20 ^h	<i>Stelechocarpus</i>	3	3 ^a
<i>Greenwayodendron</i>	2	2 ^j	<i>Stenanona</i>	14	2 ^g
<i>Guatteria</i>	210	145 ^f	<i>Tetrameranthus</i>	6	2 ^k
<i>Haplostichanthus</i>	11	—	<i>Toussaintia</i>	4	—
<i>Hexalobus</i>	5	2 ^c	<i>Tridimeris</i>	1	—
<i>Hornschuchia</i>	10	—	<i>Trigynaea</i>	12	2 ^k
<i>Isolona</i>	20	14 ^e	<i>Trivalvaria</i>	4	2 ^{a, t}
<i>Klarobelia</i>	12	6 ⁱ , 2 ^a	<i>Unonopsis</i>	48	3 ^j
<i>Letestudoxa</i>	3	2 ^k	<i>Uvaria</i>	187	59 ^u
<i>Lettowianthus</i>	1	—	<i>Uvariastrum</i>	8	2 ^c
<i>Maasia</i>	6	5 ^l	<i>Uvarioidendron</i>	15	2 ^c
<i>Malmea</i>	6	4 ⁱ	<i>Uvariopsis</i>	16	2 ^c
<i>Marsypopetalum</i>	6	5 ^t	<i>Woodiellantha</i>	1	—
<i>Meiocarpidium</i>	1	—	<i>Xylopia</i>	157	4 ^k

^aT. Chaowasku *et al.* (unpubl. data).

^bChatrou *et al.* (2009).

^cCouvreur *et al.* (2008).

^dCouvreur *et al.* (2009).

^eCouvreur (2009).

^fErkens *et al.* (2007).

^gMols *et al.* (2004).

^hNakkuntod *et al.* (2009).

ⁱPirie *et al.* (2005).

^jPirie *et al.* (2006).

^kRichardson *et al.* (2004).

^lSaunders, Su & Xue (2011).

^mR. M. K. Saunders (unpubl. data).

ⁿScharaschkin & Doyle (2005).

^oSu & Saunders (2009).

^pSurveswaran *et al.* (2010).

^qThongpairaj (2008).

^rWang (2009).

^sWeerasooriya & Saunders (2010).

^tXue *et al.* (2011).

^uZhou *et al.* (2012).

or no homoplasy, we assumed them to be effectively homologous and included them in the analyses (following Pirie *et al.*, 2006).

PHYLOGENETIC ANALYSES

As plastid DNA is inherited as a unit, individual markers were not analysed separately to look for incongruence; we excluded a paralogous second copy of the *trnL-F* region from these analyses (Pirie *et al.*, 2007). For the combined analyses, a supermatrix approach was adopted, i.e. including all taxa, even where data were not available for particular markers, which were coded as missing.

Parsimony analysis

Analyses were performed using PAUP* version 4.10b (Swofford, 2000) with the heuristic search option, tree bisection–reconnection (TBR) branch swapping, the accelerated transformation (ACCTRAN) criterion and the multiple parsimonious trees (MULPARS) option invoked. Character states were specified as unordered and equally weighted (Fitch parsimony; Fitch, 1971). Alignment gaps were treated as missing data, but larger indels were coded as above. The search strategy consisted of 10 000 replicates of random addition sequence, saving 25 trees per replicate. To ensure that the tree island with the globally shortest tree had been visited, we performed a parsimony ratchet (Nixon, 1999) search as implemented in PAUPRat (Sikes & Lewis, 2001), with 1000 ratchet iterations, perturbing 25% of the characters in each round. The robustness of the phylogenetic relationships was assessed by nonparametric bootstrapping of the data. Following Müller (2005), the number of bootstrap replicates was set at a high level (50 000), whereas the thoroughness of searches and computing time per bootstrap replicate were minimized by limiting the number of random addition sequence replicates to one, saving a single tree. When evaluating the results, we used the following descriptions of support by bootstrap values: 50–74% represents weak support, 75–84% moderate support and 85–100% strong support.

Maximum likelihood (ML) analysis

In recent years, ML algorithms have become more efficient, allowing for fast and accurate estimation of ML trees and even bootstrapping, which is especially useful for large datasets (Guindon & Gascuel, 2003; Stamatakis, 2006; Zwickl, 2006; Morrison, 2007). For this study, we used the RAxML web-server program available at the CIPRES portal in San Diego, CA, USA (<http://www.phylo.org/portal2>), which implements an efficient and rapid heuristic bootstrap in RAxML (Stamatakis, Hoover & Rougemont, 2008).

For each analysis, the ‘maximum likelihood search’ and ‘estimate proportion of invariable sites’ boxes were selected, with a total of 1000 bootstrap replicates performed. The dataset was not partitioned, as the number of missing data per marker (excluding *trnL-F* and *rbcL*) resulted in aberrant results. Indel characters were necessarily excluded from the analyses, resulting in a total of 7657 included characters.

Bayesian inference

Bayesian analysis was performed on the combined dataset using MrBayes 3.2 (Huelsenbeck *et al.*, 2001; Ronquist & Huelsenbeck, 2003). We used the 56 completely sampled species to identify the best partitioning of the data, employing the Bayes factor criterion (2ln Bayes factor > 10; Kass & Raftery, 1995; Sinsheimer, Lake & Little, 1996) following Brandley, Schmitz & Reeder (2005). Bayes factors were calculated as the ratio of the harmonic means of each partitioning strategy, which are produced by MrBayes in the output from the *sump* command. We tested the following partitioning strategies: 1, combined protein coding (‘coding’) regions/combined intron and spacer (‘noncoding’) regions/combined binary coded indel characters (‘indels’) (three partitions); 2, codon positions for the three coding regions (*rbcL*, *matK*, *ndhF*) separately/noncoding/indels (11 partitions); 3, nucleotide and indel characters for each marker separately (14 partitions). Values of the 2ln Bayes factor were all between 0 and 1, showing no preference for any of the partitioning strategies. This being the case, the data were partitioned according to strategy 1. This relatively simple strategy represents an attempt to best reflect differences between markers whilst maximizing the proportion of topology relative to substitution parameter change proposals in the Markov Chain Monte Carlo (MCMC) chains. Both rates and substitution models were allowed to vary across partitions. Priors for the number of parameters in the DNA substitution models were applied to each partition [as determined using ModelTest 3.06 (Posada & Crandall, 1998), with the topology in each case derived from a randomly selected most parsimonious tree]. In each case, this corresponded to models with NST = 6, gamma distributed rates and proportion of invariable sites. Runs were set to continue indefinitely, and the outputs were tested periodically for convergence through both visual inspection of cumulative clade posterior probabilities (PPs) (using AWTY; Nylander *et al.*, 2008) and according to effective sample sizes (ESS) calculated using Tracer 1.4 (Rambaut & Drummond, 2007).

RESULTS

A small number of our sequencing attempts were unsuccessful, e.g. in the case of *trnT-L* for *Cananga*

Table 3. Characteristics of individual markers, which have been assessed using all data available for each locus, i.e. 193 sequences for *rbcL* and *trnL-F* and 59–61 sequences for the remaining loci. Outgroup taxa were excluded from the calculations. Consistency index (CI) includes all (i.e. variable and invariant) nucleotide characters

Marker	Number of characters in aligned matrix	Number of potentially parsimony informative characters (%)	Number of indel characters	CI	RI	Model selected by MrModeltest
<i>rbcL</i>	1376	284 (20.6)	0	0.40	0.80	GTR + I + G
<i>matK</i>	831	247 (29.7)	1	0.61	0.70	GTR + G
<i>ndhF</i>	1956	715 (36.6)	4	0.50	0.70	GTR + I + G
<i>atpB-rbcL</i>	747	206 (27.6)	27	0.70	0.82	GTR + G
<i>trnT-L</i>	673	225 (33.4)	0	0.68	0.73	GTR + G
<i>trnL</i> intron	520	197 (37.9)	23	0.60	0.83	GTR + G
<i>trnL-F</i>	377	214 (56.8)	32	0.56	0.84	GTR + G
<i>psbA-trnH</i>	433	209 (48.3)	24	0.54	0.69	GTR + G
<i>trnS-G</i>	744	241 (32.4)	19	0.70	0.81	GTR + G

RI, retention index.

odorata (Lam.) Hook.f. & Thomson, *Meiocarpidium lepidotum* (Oliv.) Engl. & Diels and *Cleistopholis glauca* Pierre ex Engl. & Diels, *psbA-trnH* and *trnS-G* for *Pseudoxandra polyphleba* (Diels) R.E.Fr. and *Ruizodendron ovale* (Ruiz & Pav.) R.E.Fr. and *ndhF* for *Meiocarpidium lepidotum*. The database contained a total of 7787 characters after alignment and exclusion of ambiguous regions of the alignment. Table 3 shows the number of positions in the aligned data matrix and the number of indel characters per marker.

The heuristic search resulted in 20 960 most parsimonious trees with a tree length of 9806 steps, an overall consistency index (Kluge & Farris, 1969) of 0.55 and an overall retention index (RI; Farris, 1989) of 0.77. The ratchet search did not find shorter trees. The total number of potentially parsimony informative characters was 2729 (35.0%). The greatest number of parsimony informative characters was for *ndhF* (715) and then *atpB-rbcL* (206); *psbA-trnH* (209) had the least (Table 3). The final ML optimization likelihood was -67 480.27. The two MrBayes runs were terminated after ten million generations, having reached the same likelihood plateau after c. 350 000 generations, which were discarded as burn-in. Analysis of the tree output using AWTY (Nylander *et al.*, 2008) showed that the clade PPs of the two runs were consistent with each other, and clade PPs of each run had reached values that no longer changed with additional generations. The effective sampling size of all parameters of the combined output, minus burn-in, as estimated using Tracer (Rambaut & Drummond, 2007), exceeded 200.

PHYLOGENETIC RELATIONSHIPS

The monophyly of Annonaceae (clade A; Fig. 1A) and the sister group relationship between *Anaxagorea* and the remaining Annonaceae (clade B; Fig. 1A) are maximally supported in all three analyses. Clade C (Fig. 1) is weakly supported in the parsimony analyses [parsimony bootstrap percentage (PBP), 66], mainly because of a degree of uncertainty in the position of *Meiocarpidium* Engl. & Diels. Both parametric analyses, however, assign high support [ML bootstrap percentage (MBP), 97; Bayesian PP, 0.95] to this node. The rest of the strongly supported relationships in clade C are the same among all three analyses.

The monophyly of the remainder of Annonaceae, representing >97% of the species diversity of the family, is well supported in all analyses (clade D; PBP, 99; MBP, 100; PP, 1.00; Fig. 1A). The sister clades E and F receive maximum support in all three analyses.

Most of the relationships in Annonoideae, clade E, receive strong support (maximum parsimony, ML and Bayesian; Fig. 1B). Bocageae (clade G) receives maximum support (maximum parsimony, ML and Bayesian), as does the sister relationship between Bocageae and the remaining Annonoideae (clade H). The latter splits into five strongly supported, species-rich clades, the relationships of which, however, are mostly unresolved: *Xylopia* L./*Artabotrys* R.Br. (clade I: c. 250 species; PBP, 97; MBP, 100; PP, 1.00); *Duguetia* A.St.-Hil., *Fusaea* (Baill.) Saff., *Letestudoxa* Pellegr. and *Pseudartabotrys* Pellegr. (clade J: c. 100 species; PBP, 100; MBP, 100; PP, 1.00); *Guatteria* Ruiz & Pav. (clade K: c. 250 species; PBP, 100; MBP, 100;

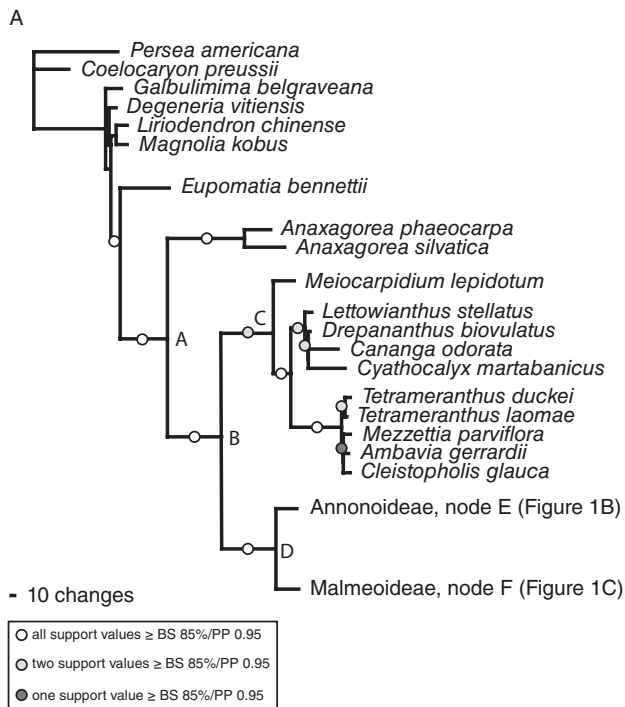


Figure 1. Phylogram showing one of many most parsimonious tree topologies, with support [maximum parsimony bootstrap (BS) percentages, maximum likelihood BS percentages and Bayesian posterior probabilities (PP) indicated in the key]. A, Phylogenetic relationships among the outgroup taxa and species of Anaxagoreoideae and Ambavioideae. B, Phylogenetic relationships in Annonoideae. C, Phylogenetic relationships in Malmeoideae.

PP, 1.00); *Annona* L., *Anonidium* Engl. & Diels, *Asimina* Adans., *Disepalum* Hook.f., *Goniothalamus* (Blume) Hook.f. & Thomson and *Neostenanthera* Exell (clade M; PBP, 100; MBP, 100; PP, 1.00); and a clade containing Palaeotropical species only (clade N: c. 600 species; PBP, 100; MBP, 100; PP, 1.00). Clade M is sister to clade N (PBP, 100; MBP, 100; PP, 1.00). Clade N consists of three maximally supported clades: clade O, including two monotypic African genera *Ophrypetalum* Diels and *Sanrafaelia* Verdc.; clade P, including c. 80 African tree species; and clade Q, including c. 475 Palaeotropical climbing species. A small number of more shallow nodes in the tree are much more strongly supported by Bayesian PPs compared with the results of the maximum parsimony and ML analyses. For example, the sister group relationship between *Toussaintia* Boutique and a clade containing *Friesodielsia* Steenis and *Monanthotaxis* Baill. (clade R; PBP, 62; MBP, 78; PP, 1.00) and the monophyly of a clade of five African genera (clade S; PBP, 62; MBP, 85; PP, 1.00).

Resolution and support in Malmeoideae (clade F) are lower than in Annonoideae and Ambavioideae

(Fig. 1C) across all methods. The first dichotomy in Malmeoideae divides five African genera (clade T; PBP, 74; MBP, 88; PP, 0.97) from the remaining Malmeoideae (clade U; maximally supported). The latter comprises three major clades: V, including c. 175 Neotropical species (PBP, 85; MBP, 95; PP, 1.00); W, comprising the genus *Maasia* Mols, Keßler & Rogstad; and X (PBP, 99; MBP, 100; PP, 1.00), in which the Asian genus *Monocarpia* Miq. is sister to the rest of the c. 525 species (PBP, 71; MBP, 78; PP, 1.00), mainly distributed in Asia, with four genera endemic to Central America [*Desmopsis* Saff., *Sapranthus* Seem., *Stenanona* Standl. and *Tridimeris* Baill. (35 species in total) plus a small number of species of *Polyalthia* from Madagascar (e.g. *P. pendula* Capuron ex G.E.Schatz & Le Thomas) and eastern Africa (e.g. *P. stuhlmannii* (Engl.) Verdc.).

Overall resolution in this clade is poor in all three analyses, but, nevertheless, the nonmonophyly of *Polyalthia*, with c. 135 currently recognized species, is indicated.

DISCUSSION

Molecular phylogenetic studies, such as this, benefit in part from the availability of many more characters (Chase & Cox, 1998). A further benefit of DNA sequence data over morphological characters that have been used previously to infer phylogenetic relationships is the ability to isolate conflicting phylogenetic signals that can be confounded in patterns of inheritance of morphological variation. We used sequence data from eight plastid loci, representing a large number of characters that are always inherited as a single unit (the plastid genome) without recombination (Birky, 2001). In one instance, differing phylogenetic signals caused by paralogy have been identified for putative plastid sequences in Annonaceae (Pirie *et al.*, 2007), but, in general, congruence of plastid loci has been demonstrated. Congruence between low-copy and plastid loci analyses has been documented in other families (e.g. Górniak, Paun & Chase, 2010). In the absence of contradictory evidence (in the form of independent DNA loci), we assume that this plastid tree (Fig. 1) broadly reflects the potentially more complex phylogenetic history underlying the complete genomes of the taxa involved. Support for this topology is largely robust, at least for the purposes of defining major clades, although resolution in these clades is, in some cases, poor. Poor resolution does not affect the creation of an infrafamilial classification for Annonaceae because weakly supported/resolved clades are not given taxonomic recognition. The supermatrix approach employed here works well, particularly for the resolution of deeper nodes, and the generally higher Bayesian PPs (com-

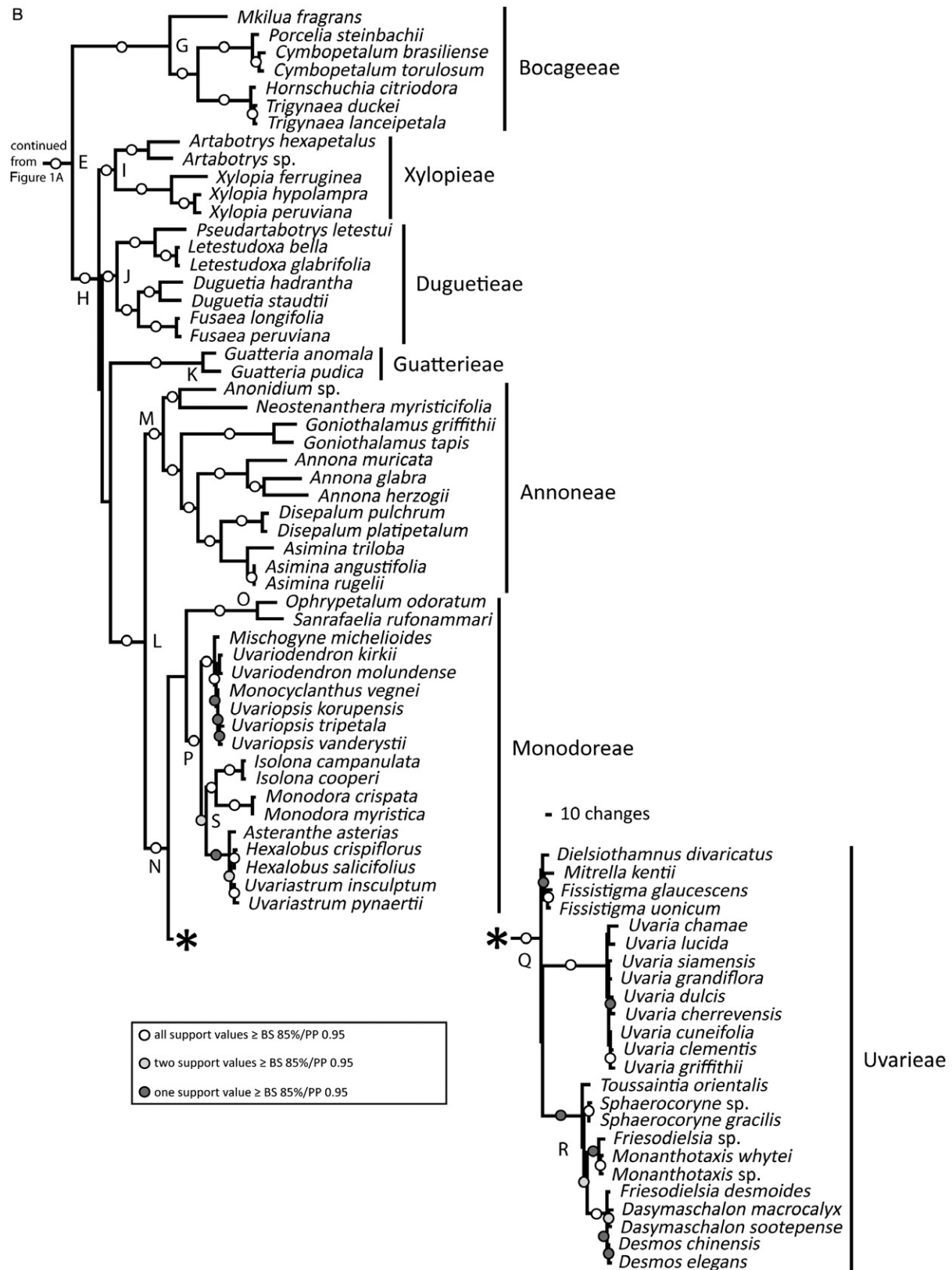
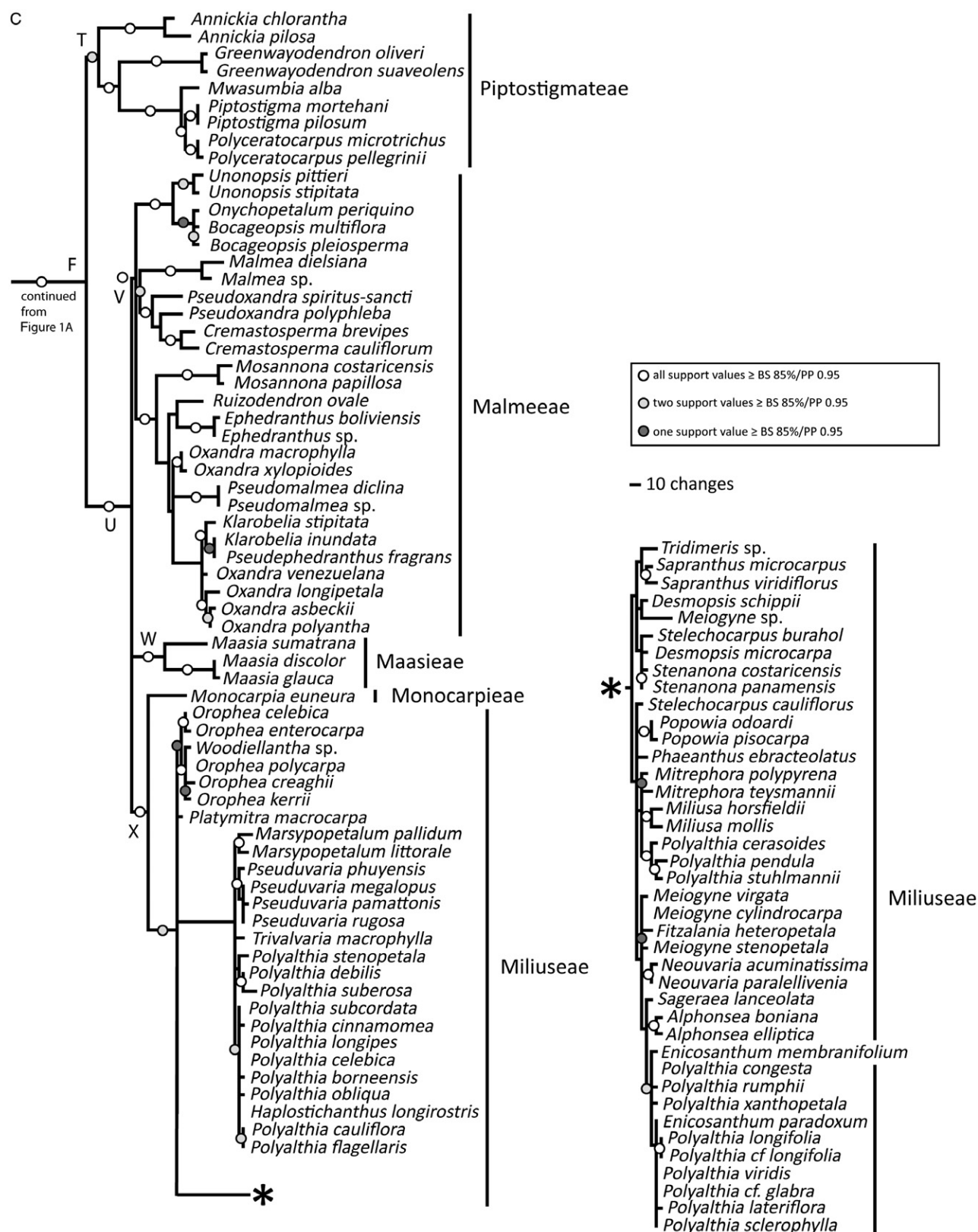


Figure 1. Continued



pared with BPs) reported here are a further attribute known to be associated particularly with matrices comprising a proportion of missing data (Wiens, 2006; Pirie *et al.*, 2008). We consider $PP \geq 0.95$ to be robust, even if BPs are considerably lower.

MORPHOLOGICAL CHARACTERS AND THE HISTORY OF ANNONACEAE CLASSIFICATION

'The family of Annonaceae is a very natural one'. With this statement, King (1893) was hardly exaggerating the perceived monophyly of the family, although he clearly would not have used that term. Apart from frequent inclusion of the monotypic Eupomatiaceae in the past (e.g. Baillon, 1868; Diels, 1912), delimitation of the Annonaceae has never been ambiguous, because of the presence of synapomorphies, such as simple vessel perforations, a 'cobweb-like' wood structure in cross-section (caused by broad and high multiseriate xylem rays with many narrow, tangential parenchyma bands perpendicular to the xylem rays; Koek-Noorman & Westra, 2012), alternate, distichous leaves, trimerous calyx and corolla, and perichalazal ovules (Sauquet *et al.*, 2003). On the other hand, ambiguity has governed the delimitation of groups within the family from the stance of their recognition. A number of attempts have been made to formally classify Annonaceae in tribes or subfamilies (e.g. Endlicher, 1839; Hutchinson, 1923) or to produce informal groupings of genera (e.g. Diels, 1932; Fries, 1959; Walker, 1971). Each of these classifications differs in the kinds of characters that were emphasized (a summary is provided in Table 4). Following the first treatment of the family by Dunal (1817), several authors used fruit characters for the main divisions of the family (Endlicher, 1839; Diels, 1932). Baillon (1868) and Prantl (1891) produced similar treatments, as the groups they proposed were based solely on floral characters. Fries (1959) produced a comprehensive treatment of the family, the size of which had greatly expanded because of his numerous revisionary works (e.g. Fries, 1930, 1931, 1934, 1937, 1939). Floral characters plus a single fruit character (free vs. fused carpels) formed the basis for the delimitation of informal groups of genera ('natürliche Gruppen') in tribes. The work of Fries (1959) is probably the most influential classification of Annonaceae to date, in particular having served as a guide for the planning of taxonomic studies in the family. It has, however, not gone without criticism, even before the application of molecular phylogenetic data. Le Thomas (1969), for example, expressed doubts as to the systematic value of sepal and petal aestivation, one of the key floral characters in the classification of Annonaceae, notably in the system by Fries (1959), but also by Hooker & Thomson (1855). In Le Thomas'

(1969) treatment of Annonaceae for the *Flore du Gabon*, the limited systematic value of petal aestivation was illustrated with reference to Uvarieae. This tribe featured genera with both apocarpous (e.g. *Uvaria*, *Cleistopholis* Pierre ex Engl.) and syncarpous [*Letestudoxa*, *Pachypodanthium* Engl. & Diels (now *Duguetia*)] fruits. In addition, substantial variation in the number of ovules and placentation type occurs within these seven genera. In effect, Uvarieae was considered to be related only because of imbricate petals and occasional stellate hairs. In this article, we will limit ourselves to a few examples, such as that of Uvarieae given here. Almost any past classification can be justified to some extent, in that the responsible author hypothesized a close relationship between particular genera, which, with hindsight, appears to have been correct. However, in each case, there are also as many (if not more) problems to be pointed out. We consider that there is little point in evaluating in detail these various classification schemes, as the common methodological ground and explicit justification that are necessary to clarify or test the reasons for differences between them are missing. They are all highly intuitive and therefore irrefutable.

Students of Annonaceae in the 19th and most of the 20th century assembled impressive numbers of collections, observations and taxonomic papers, but simply lacked the rigour of using any formal methodology to establish a classification. In reviewing those leading up to that of Fries (1959), it does, however, become apparent that a limited number of key characters have consistently been used for infrafamilial classification. These can be summarized as those concerning phyllotaxy, indument, inflorescence position, sepal and petal aestivation, petal fusion, shape and form, anther connective form, carpel fusion and placentation.

Subsequent to Fries (1959), Annonaceae systematics has focused on a wider range of differing sources of data and has generally involved a variety of more or less formal methodologies. Walker (1971) used pollen and, to a lesser extent, floral morphology and phytogeography. Following this pioneering work, Le Thomas (1980, 1981), Le Thomas & Lugardon (1976) and Walker (1971, 1972) assembled a comprehensive overview of palynological characters of Annonaceae. Although these data were largely novel, the analytical approach was similar to that of several preceding studies: observed similarities between Annonaceae, on the one hand, and presumed primitive angiosperms, extant and fossil, on the other, together with assumed transformation series, were taken as a primary guide to hypothesize relationships. In addition, Le Thomas (1980, 1981) based several decisions on ancestral and derived pollen characters on presumed evolutionary trends ('series'), for instance from

Table 4. Overview of previous infrafamilial classifications of Annonaceae. Informal names given in inverted commas. Lists of genera included in infrafamilial taxa are not comprehensive, and are restricted to major genera and generally to names currently recognized

Publication	Taxa	Diagnostic characters (and key genera included)
Rafinesque (1815)	Subfamily Anonoideae Raf. Subfamily Uvarioideae Raf. Subfamily Xylopioideae Raf.	Monocarps fused (<i>Annona</i>) Monocarps free, indehiscent (<i>Guatteria</i> , <i>Melodorum</i> , <i>Porcelia</i> and <i>Uvaria</i>) Monocarps free, dehiscent (<i>Xylopia</i>)
Kosteletsky (1836)	Subfamily Anonoideae Raf. Subfamily Monodorioidae Kostel. Subfamily Uvarioideae Raf.	Monocarps many, fused (<i>Annona</i>) Monocarps single, possibly fused (<i>Monodora</i>) Monocarps many, free (<i>Artabotrys</i> , <i>Polyalthia</i> , <i>Uvaria</i> and <i>Xylopia</i>)
Reichenbach (1837)	'Anonariae' 'Uvarieae' (subgroup) 'Bocageae' (subgroup) 'Anoneae genuinae' (subgroup) 'Cardiopetaleae' 'Guatterieae'	Petals free; monocarps free or fused Stamens many; monocarps free (<i>Asimina</i> , <i>Porcelia</i> and <i>Xylopia</i>) Stamens 6, opposite the petals (<i>Bocagea</i>) Stamens many; monocarps fused (<i>Annona</i> and <i>Monodora</i>) Petals basally fused (<i>Hexalobus</i> , <i>Miliusa</i> and <i>Orophea</i>) Petals connivent or patent; monocarps single-seeded (<i>Anaxagorea</i> , <i>Artabotrys</i> , <i>Duguetia</i> , <i>Guatteria</i> and <i>Polyalthia</i>)
Endlicher (1839)	Tribe Anoneae Endl. Tribe Bocageae Endl. Tribe Xylopieae Endl.	Stamens many; ovules basal (<i>Anaxagorea</i> , <i>Annona</i> , <i>Artabotrys</i> , <i>Duguetia</i> and <i>Guatteria</i>) Stamens few; ovules ventral (<i>Bocagea</i> , <i>Miliusa</i> , <i>Orophea</i> and <i>Popowia</i>) Stamens many; ovules ventral (<i>Hexalobus</i> , <i>Polyalthia</i> , <i>Uvaria</i> and <i>Xylopia</i>)
Hooker & Thomson (1855)*	Tribe Anoneae Endl. Tribe Guatterieae Hook.f. & Thomson Tribe Miliuseae Hook.f. & Thomson† Tribe Mitrephoreae Hook.f. & Thomson Tribe Uvarieae Hook.f. & Thomson Tribe Xylopieae Endl.	Monocarps fused (<i>Annona</i>) Petals flat or basally slightly curved (<i>Anaxagorea</i> , <i>Artabotrys</i> , <i>Cananga</i> , <i>Cyathocalyx</i> , <i>Guatteria</i> , <i>Phaeanthus</i> and <i>Polyalthia</i>) Stamens loosely imbricate (<i>Miliusa</i> and <i>Orophea</i>) Inner petals clawed (<i>Goniothalamus</i> , <i>Mitrephora</i> , <i>Orophea</i> and <i>Popowia</i>) Petal aestivation imbricate (<i>Sageraea</i> , <i>Stelechocarpus</i> and <i>Uvaria</i>) Inner petals thick, 3-angled (<i>Melodorum</i> and <i>Xylopia</i>)
Bentham (1863)‡	Tribe Miliuseae Hook.f. & Thomson Tribe Mitrephoreae Hook.f. & Thomson Subtribe Eumitrephoreae Benth. & Hook.f. Subtribe Phaeantheae Benth. & Hook.f. Tribe Unoneae Benth. & Hook.f. Tribe Uvarieae Hook.f. & Thomson Tribe Xylopieae Endl.	Petals diverse; stamens loosely imbricate, connective dorsally conspicuously or not enlarged (<i>Alphonsea</i> , <i>Bocagea</i> , <i>Miliusa</i> and <i>Orophea</i>) Petals valvate, outer apert, inner connivent or connate Inner petals shorter than outer or subequal, often basally clawed (<i>Goniothalamus</i> , <i>Mitrephora</i> and <i>Monodora</i>) Inner petals much larger than outer, erect (<i>Cymbopetalum</i> and <i>Phaeanthus</i>) Petals flat, slightly unequal or inner smaller than outer, generally apert (<i>Anaxagorea</i> , <i>Artabotrys</i> , <i>Asimina</i> , <i>Cananga</i> , <i>Cyathocalyx</i> , <i>Disepalum</i> , <i>Polyalthia</i> , <i>Popowia</i> , <i>Hexalobus</i> and 'Unona') Petals flat, spreading, at least inner imbricate; stamens densely crowded, connective apex enlarged (<i>Duguetia</i> , <i>Guatteria</i> , <i>Porcelia</i> , <i>Sageraea</i> , <i>Stelechocarpus</i> and <i>Uvaria</i>) Outer petals thick, connivent or slightly apert; inner petals enclosed, small or absent (<i>Annona</i> , <i>Melodorum</i> and <i>Xylopia</i>)
Baillon (1868)§	Tribe Anoneae Endl. Subtribe Oxymitreae Baill. Subtribe Rollinieae Baill. Subtribe Unoneae Baill. Subtribe Uvarieae Baill. Subtribe Xylopieae Baill. Tribe Eupomatieae Baill.¶ Tribe Miliuseae Hook.f. & Thomson Tribe Monodoreae Baill.	(<i>Cymbopetalum</i> , <i>Mitrephora</i> , <i>Orophea</i> and 'Oxymitra') (<i>Artabotrys</i> , <i>Cyathocalyx</i> , <i>Hexalobus</i> and 'Rollinia') (<i>Anaxagorea</i> , <i>Bocagea</i> , <i>Disepalum</i> , <i>Popowia</i> and 'Unona') (<i>Cananga</i> , <i>Oxandra</i> , <i>Sageraea</i> and <i>Uvaria</i>) (<i>Annona</i> and <i>Xylopia</i>) (<i>Eupomatia</i>) (<i>Miliusa</i> and <i>Phaeanthus</i>) (<i>Monodora</i>)
Prantl (1891)	Tribe Eupomatieae Baill.¶ Tribe Melodoreae Prantl Tribe Miliuseae Hook.f. & Thomson Tribe Mitrephoreae Hook.f. & Thomson	Perianth absent; perigynous (<i>Eupomatia</i>) All or only inner petals erect, petals touching; stamens numerous; apocarpous; hairs simple (<i>Melodorum</i> , <i>Phaeanthus</i> and <i>Piptostigma</i>) Stamens connective apex not expanded over anthers; stamens few; apocarpous; hairs simple (<i>Alphonsea</i> , <i>Bocagea</i> , <i>Mezzettia</i> , <i>Miliusa</i> , <i>Oxandra</i> and <i>Sageraea</i>) Inner petals usually clawed, apically connivent; stamens sometimes few; apocarpous; flowers small (<i>Mitrephora</i> , <i>Orophea</i> and <i>Popowia</i>)

Table 4. *Continued*

Publication	Taxa	Diagnostic characters (and key genera included)
Hutchinson (1923, 1964)	Tribe Monodoreae Baill.	Syncarpous, unilocular with parietal placentation; petals more or less fused at base; valvate (<i>Monodora</i>)
	Tribe Unoneae Benth. & Hook.f.	Petals subequal, spreading or slightly converging; stamens numerous; hairs simple (<i>Anaxagorea</i> , <i>Cananga</i> , <i>Cymbopetalum</i> , <i>Disepalum</i> , <i>Polyalthia</i> and <i>Unona</i>)
	Tribe Uvarieae Hook.f. & Thomson	At least outer petals imbricate, spreading or slightly erect; stamens numerous (<i>Asimina</i> , <i>Duguetia</i> , <i>Guatteria</i> , <i>Porcelia</i> , <i>Stelechocarpus</i> and <i>Uvaria</i>)
	Tribe Xylopieae Endl.	Petals spoon-shaped at base, more or less constricted above and then spreading or laterally compressed (<i>Annona</i> , <i>Artabotrys</i> , <i>Cyathocalyx</i> , <i>Hexalobus</i> and <i>Xylopia</i>)
	Subfamily Annonoideae Raf.	Carpels free or fused into multilocular syncarp; stigmas erect (rarely radiating)
	Tribe Miliuseae Hook.f. & Thomson	Petals in one or two whorls, valvate; outer petals smaller than inner (<i>Cymbopetalum</i> , <i>Marsypopetalum</i> , <i>Miliusa</i> , <i>Orophea</i> , <i>Phaeanthus</i> , <i>Piptostigma</i> and <i>Trivalvaria</i>)
	Tribe Unoneae Benth. & Hook.f.	Petals in one or two whorls, valvate; outer petals subequal or larger than inner
	Subtribe Annonineae Hutch.	Carpels fused (<i>Annona</i>)
	Subtribe Xylopiineae Hutch.	Carpels free or only slightly fused (<i>Alphonsea</i> , <i>Anaxagorea</i> , <i>Artabotrys</i> , <i>Asimina</i> , <i>Cyathocalyx</i> , <i>Dasymaschalon</i> , <i>Desmopsis</i> , <i>Desmos</i> , <i>Disepalum</i> , <i>Drepananthus</i> , <i>Goniothalamus</i> , <i>Haplostichanthus</i> , <i>Hexalobus</i> , <i>Hornschuchia</i> , <i>Meiogyne</i> , <i>Melodorum</i> , <i>Mezzettia</i> , <i>Mitrephora</i> , <i>Monanthotaxis</i> , <i>Monocarpia</i> , <i>Orophea</i> , <i>Platymitra</i> , <i>Polyalthia</i> , <i>Popowia</i> , <i>Unonopsis</i> , <i>Uvariastrum</i> , <i>Uvariopsis</i> and <i>Xylopia</i>)
	Tribe Uvarieae Hook.f. & Thomson	Petals in two whorls, both or inner imbricate; leaf indument stellate or lepidote (<i>Duguetia</i> , <i>Enicosanthum</i> , <i>Ephedranthus</i> , <i>Fusaea</i> , <i>Guatteria</i> , <i>Malmea</i> , <i>Oxandra</i> , <i>Porcelia</i> , <i>Sageraea</i> , <i>Sapranthus</i> , <i>Stelechocarpus</i> and <i>Uvaria</i>)
	Subfamily Monodoroideae Kostel.	Carpels fused into unilocular ovary, placentation parietal; stigmas radiating (<i>Isolona</i> and <i>Monodora</i>)
Fries (1959)	Subfamily Annonoideae Raf.	Carpels spirally arranged (sometimes few in a whorl); apocarpous, rarely syncarpous (forming multilocular syncarp)
	Tribe Tetrameranthae R.E.Fr.	Petals in whorls of four, imbricate; stigma 3-lobed, appressed to ovary; leaves spirally arranged (<i>Tetrameranthus</i>)
	Tribe Unoneae Benth. & Hook.f.	Petals (at least outer) valvate (imbricate in <i>Porcelia</i>); leaves distichous (<i>Alphonsea</i> , <i>Anaxagorea</i> , <i>Annona</i> , <i>Anonidium</i> , <i>Artabotrys</i> , <i>Cananga</i> , <i>Cyathocalyx</i> , <i>Cymbopetalum</i> , <i>Dasymaschalon</i> , <i>Desmos</i> , <i>Disepalum</i> , <i>Drepananthus</i> , <i>Fissistigma</i> , <i>Goniothalamus</i> , <i>Marsypopetalum</i> , <i>Meiocarpidium</i> , <i>Meiogyne</i> , <i>Mezzettia</i> , <i>Miliusa</i> , <i>Mitrephora</i> , <i>Monanthotaxis</i> , <i>Monocarpia</i> , <i>Neostenanthera</i> , <i>Onychopetalum</i> , <i>Orophea</i> , <i>Phaeanthus</i> , <i>Piptostigma</i> , <i>Polyalthia</i> , <i>Polyceratocarpus</i> , <i>Popowia</i> , <i>Porcelia</i> , <i>Pseuduvaria</i> , <i>Sphaerocoryne</i> , <i>Trigynaea</i> , <i>Trivalvaria</i> , <i>Unonopsis</i> , <i>Uvariastrum</i> , <i>Uvariadendron</i> , <i>Uvariopsis</i> and <i>Xylopia</i>)
	Tribe Uvarieae Hook.f. & Thomson	Petals imbricate; leaves distichous (<i>Asimina</i> , <i>Cleistopholis</i> , <i>Crematosperma</i> , <i>Desmopsis</i> , <i>Duguetia</i> , <i>Enicosanthum</i> , <i>Ephedranthus</i> , <i>Fusaea</i> , <i>Guatteria</i> , <i>Hexalobus</i> , <i>Malmea</i> , <i>Oxandra</i> , <i>Pseudoxandra</i> , <i>Sageraea</i> , <i>Sapranthus</i> , <i>Stelechocarpus</i> , <i>Stenanona</i> and <i>Uvaria</i>)
	Subfamily Monodoroideae Kostel.	Carpels whorled, fused in unilocular ovary, placentation parietal (<i>Isolona</i> and <i>Monodora</i>)

*Partial study, geographically focused on taxa from 'British India'.

†Listed as tribe 'Saccopetaleae' (Hooker & Thomson, 1855: pp. 91, 92).

‡Similar infrafamilial classification adopted by Hooker & Thomson (1872), although without recognition of subtribes within tribe Mitrephoreae.

§Descriptions not provided for tribes and subtribes, although with extensive descriptions of genera included.

¶Now excluded from Annonaceae as Eupomatiaceae.

simple to complex characters or from free to fused parts, and on an analogy between morphological series in pollen characters and macromorphological characters. Although Le Thomas (1980, 1981) mentioned the concepts of homology and convergent evolution, she lacked the analytical tools to demonstrate the significant levels of homoplasy that have since been demonstrated (Doyle & Le Thomas, 2012). Noteworthy contributions to the classification of Annonaceae (van Heusden, 1992; van Setten & Koek-Noorman, 1992) appeared immediately before the first cladistic papers (Doyle & Le Thomas, 1994, 1995), allowing the last two publications to benefit from the comprehensive overviews of floral morphology (van Heusden, 1992) and fruit and seed morphology (van Setten & Koek-Noorman, 1992). Observations that led to intuitive groupings of genera in each of these publications separately were combined and used for a phenetic analysis (Koek-Noorman, van Setten & van Zuilen, 1997). Koek-Noorman *et al.* (1997) used a neighbor-joining tree derived from these data to produce an informal classification ('grouping') that was similar to that of van Setten & Koek-Noorman (1992). In a few cases, particular results from the neighbor-joining tree were disregarded in the classification, for example, in the case of *Porcelia* Ruiz & Pav.: established opinion based on inflorescence type, anther septation and pollen size was that the genus was allied to the other genera in Bocageae (Fig. 1B), but, in the analysis of Koek-Noorman *et al.* (1997), it was clustered distant from its putative close relatives, possibly as a result of the absence of a seed appendage, either an aril or a caruncle (Johnson & Murray, 1995), that is otherwise present in all species of Bocageae.

The first formal cladistic analyses based on morphological, anatomical and palynological characters revealed rampant homoplasy. The consistency index of 79 characters scored for 42 genera of Annonaceae was as low as 0.27 in Doyle & Le Thomas (1996). The retention index was not reported, but, as autapomorphies were absent and the number of symplesiomorphies was low, the proportion of similarity in their tree to be interpreted as synapomorphies is also likely to have been low. There are several reasons for this high level of homoplasy, one of which is the difficulty of homology assessment, as acknowledged by Doyle & Le Thomas (1996), in cases in which observations on living material were absent and characters were scored on the basis of observations of herbarium material (e.g. petal connivence, fruit wall thickness). Moreover, some characters were included that have been shown to be derived via different developmental pathways. Because of the lack of similarity in anatomy and development, it comes as no surprise that these characters were demonstrated by Doyle &

Le Thomas (1996) to be homoplasious. An example of such a character is syncarpous fruits, as opposed to those consisting of free monocarps. Several papers have demonstrated that syncarpy can better be interpreted as different, nonhomologous, suites of characters related to fusion or coherence between carpels, fusion or coherence between carpels and receptacle, and syncarpy in flowering stage (Briechle-Mäck, 1994; Chatrou & He, 1999; Chatrou *et al.*, 2000; Couvreur *et al.*, 2008). Finally, part of the homoplasy as found by Doyle & Le Thomas (1996) can be explained by patterns apparent in their family-wide analysis. In many cases, homoplasy was not distributed evenly across the tree. This can be illustrated by the fact that similar characters, when used in phylogenetic analyses of morphological characters of clades within Annonaceae (Johnson & Murray, 1995; Chatrou *et al.*, 2000), showed little to no homoplasy. Examples are the occurrence of different trichome types, lianescent habit and presence vs. absence of styles in the clade comprising *Duguetia* and related genera (Chatrou *et al.*, 2000), and the occurrence of bilobed arils and different shapes of the floral receptacle in Bocageae (Johnson & Murray, 1995). These characters do not exhibit homoplasy in these relatively small, more exclusive clades, but have all evolved in parallel multiple times in Annonaceae as a whole.

A NEW INFRAFAMILIAL CLASSIFICATION OF ANNONACEAE

Because classifications are important for communication and information retrieval, stability and universal applicability should be their main features. Previous classifications of Annonaceae, to a large extent, fail to meet both criteria.

We assign the rank of subfamily to four clades: *Anaxagorea* (Anaxagoreoideae); clade C (Ambavioideae), corresponding to the clade previously referred to informally as the ambavoids (e.g. Doyle & Le Thomas, 1994, 1995, 1996; Doyle *et al.*, 2000; Sauquet *et al.*, 2003); clade E (Annonoideae), the LBC or inaperturate clade (e.g. Richardson *et al.*, 2004; Erkens *et al.*, 2007; Couvreur *et al.*, 2008; Zhou *et al.*, 2009); and clade F (Malmeoideae), the SBC or malmeoid/piptostigmoid/miliusoid clade (e.g. Richardson *et al.*, 2004; Pirie *et al.*, 2006). These four clades include all the genera sampled for these analyses (i.e. 90% of all accepted genera).

Clade E, which includes the genus *Annona*, must be assigned the name Annonoideae Raf. (McNeill *et al.*, 2006; art. 19.4). All other previously described subfamilies of Annonaceae are based on names of genera that belong to Annonoideae, namely Bocageoideae Pfeiff., Monodoroideae Kostel., Uvarioideae Raf. and

Xylopioideae Raf., and are therefore all superfluous. The somewhat curious bias towards subfamilies based exclusively on annonoid genera can be explained by their greater morphological variability (particularly in fruit characters). In the absence of further available subfamilial names, Anaxagoreoideae, Ambavioideae and Malmeoideae are newly described here.

As with all recent classificatory endeavours in angiosperms (e.g. APG III, 2009), strongly supported monophyly is the foremost principle, at any taxonomic level. For our classification of Annonaceae, this is also true. Monophyly is the only characteristic that these subfamilies have in common, however: they are not otherwise equivalent in terms of age, geographical distribution or any other biological attributes (and should not be expected to be so). Following monophyly, morphological diagnosability is an important subsidiary criterion for the classification of groups, which, in this case, is challenging. As stated above, clear morphological synapomorphies have yet to be identified for most clades of Annonaceae. However, we do not believe that this should prevent us from recognizing infrafamilial taxa, especially because the use of different terms for the same clades, as mentioned above, is likely to cause misunderstanding (APG I, 1998). The plethora of informally named groups resulting from the classifications proposed to date demonstrates the need for named units within the family. Furthermore, there are many characters awaiting evaluation for their diagnostic value; two recently published examples of characters that have a good, although not perfect, fit onto the phylogenetic tree for Annonaceae are phyllotaxis (Johnson, 2003) and orbicules (Huysmans *et al.*, 2010).

The need to identify clades and to name them extends beyond the level of subfamilies. A comprehensive classification of Annonaceae recognizes further taxa at lower, namely tribal, ranks. Characters that are diagnostic for these less inclusive clades are more straightforward to identify than for the four subfamilies. Nevertheless, extensive homoplasy still makes the diagnosis of tribes only possible by the enumeration of a suite of characters that individually are found in several clades (i.e. that are individually homoplasious). Some useful characters include phyllotaxis (distichous phyllotaxis is shared by members of clade L), habit (a climbing habit is common to species of clade Q, although with exceptions, e.g. in most species of *Dasymaschalon* (Hook.f. & Thomson) Dalla Torre & Harms; Wang, Chalermglin & Saunders, 2009) and pollen characters (clade R is characterized by cryptoaperturate/disulcate pollen grains; T. Chaowasku *et al.*, unpubl. data). The phylogenetic tree presented here includes some poorly resolved clades, but the lack of resolution does not prevent

formal classification at the tribal level. The composition of taxa at lower ranks, such as tribes, has frequently changed, and they have rarely been used in formal classifications. Fries (1959) named only three tribes in his classification of the family: Uvarieae, Unoneae and Tetramerantheae. Of these, Tetramerantheae included the ambavioid genus *Tetrameranthus* R.E.Fr. only. Uvarieae and Unoneae, by contrast, included genera dispersed across Annonoideae, Malmeoideae and Ambavioideae as circumscribed here. A more recent revision and recircumscription of Saccopetaleae (Keßler, 1988) also resulted in a non-monophyletic group of genera (this study; T. Chaowasku *et al.*, unpubl. data). As many clades are well supported, it makes sense to recognize them formally, and thus, in addition to the naming of subfamilies, we provide a set of tribes in order to avoid adding further disorder to the classification of Annonaceae.

Eupomatia R.Br., containing three species, has previously been included in Annonaceae (Bentham, 1863; Baillon, 1868; Prantl, 1891; Diels, 1912), usually in its own tribe: Eupomatiaceae Baill. Subsequent pre-cladistic classifications (e.g. Hutchinson, 1973; Cronquist, 1988; Takhtajan, 1997) always considered Eupomatiaceae to be a separate family from Annonaceae. Given this classificatory history and the fact we are presenting a new classification of Annonaceae, the classification of *Eupomatia* needs to be addressed here. *Eupomatia* has been shown to be sister to Annonaceae in several phylogenetic analyses of angiosperms (e.g. Qiu *et al.*, 2005) and Magnoliales (Sauquet *et al.*, 2003). Therefore, both recognition and rejection of familial status for *Eupomatia* would be in agreement with the principle of monophyly. Despite the 'annonaceous appearance' of *Eupomatia*, there are hardly any characters that are synapomorphic for Annonaceae and *Eupomatia* combined. Sauquet *et al.* (2003) only listed fibrous mesotesta as a possible synapomorphy. The similarities between Annonaceae and *Eupomatia* are often symplesiomorphies as they are shared with the sister clade of Annonaceae/*Eupomatia*, consisting of Himantandraceae and Degeneriaceae. These characters include adaxial prophylls, a flat-concave floral receptacle, apical extension of the connective and testal ruminations (Doyle & Le Thomas, 1997; Endress & Doyle, 2009; Endress & Armstrong, 2011). Furthermore, the clearest synapomorphies of Annonaceae (that is, characters showing no or hardly any homoplasy) are not shared with *Eupomatia*. Despite considerable variation in floral morphology (Xu & Ronse De Craene, 2010), the floral *bauplan* of Annonaceae is uniform (Saunders, 2010) and provides several synapomorphies (Endress & Armstrong, 2011), such as a whorled floral phyllotaxis (vs. spiral in Eupomatiaceae), plicate carpels (vs. ascidiate carpels) and trimerous

perianth (vs. many tepals). The broad and high multiseriate xylem rays with many narrow, tangential parenchyma bands perpendicular to the xylem rays is a typical wood anatomical feature characterizing every species of Annonaceae investigated so far (Koek-Noorman & Westra, 2012). This wood structure is absent in *Eupomatia* (L. Y. T. Westra & L. W. Chatrou, pers. observ.; <http://insidewood.lib.ncsu.edu>). Given the character distribution described here, we do not favour the inclusion of *Eupomatia* in Annonaceae and leave it out of the classification presented here.

Because subfamily Anaxagoreoideae consists of *Anaxagorea* only, we feel that it would be taxonomically redundant to also recognize this clade at the tribal level. Subfamily Ambavioideae comprises nine genera and just over 50 species. To split this subfamily further into tribes would involve the recognition of three tribes, consisting of *Meiocarpidium*, the clade containing *Cananga* (DC.) Hook.f. & Thomson, and the clade containing *Ambavia* Le Thomas, respectively. Apart from creating undesirably species-poor tribes, this alternative would focus on differences between the three groups, such as the basic chromosome number $x = 7$ for the *Cananga* clade and $x = 8$ for the *Ambavia* clade. In order to avoid insoluble debates about the level of morphological difference required for a clade to be recognized as a classificatory unit, not just in Ambavioideae but in other subfamilies as well, we focus on synapomorphies recognizing clades that are as inclusive as possible. In the case of Ambavioideae, these are the presence of a middle integument (Christmann, 1989) and some palynological synapomorphies (Doyle & Le Thomas, 2012).

Parts of the tree for Annonaceae that require additional sampling of taxa and character include the relationships among species-rich clades in Annonoideae (clades I, J, K and L). We argue that these species-rich clades can be given tribal status without their interrelationships being fully resolved. The clades are morphologically distinct and, to a large extent, they have been recognized in the past as groups of related genera. An exception is the clade comprising *Artabotrys* and *Xylopia*, for which clear synapomorphies have yet to be identified.

The clade that would require much better resolution before any classificatory conclusion can be drawn is clade X, containing most Asian and Central American endemic genera in Malmeoideae. Sequence divergence is low among species in this clade and, as a result, support is low in general. So far, our knowledge of phylogenetic relationships is based on only one-eighth of the species in clade X. An advantageous strategy would seem to be to increase taxon sampling, as this would provide a more accurate estimation of phylogenetic model parameters (Heath, Hedtke &

Hillis, 2008). In the light of this, we recircumscribe tribe Miliuseae (clade X excluding *Monocarpia*) and envisage that its classification be revisited once relationships are better resolved. The inclusion of the genus *Monocarpia* in Miliuseae would have been possible from the perspective of monophyly; we prefer, however, to erect a new tribe for *Monocarpia* alone as this genus has never previously been included in Miliuseae (Mols & Keßler, 2003; Mols *et al.*, 2004). *Monocarpia* furthermore lacks cryptoaperturate/disulculate pollen, which is synapomorphic for Miliuseae as circumscribed here (Chaowasku, Keßler & van der Ham, 2012). Relationships among clades V, W and X are unresolved. We apply a similar reasoning here as for clades I, J, K and L in Annonoideae: the lack of interclade resolution does not hinder the recognition of tribes, which are morphologically distinct. Saunders *et al.* (2011) demonstrated that the Malagasy genus *Fenerivia* Diels, unsampled in this study, is part of this polytomy. Hence, clades V, W, X and *Fenerivia* are given tribal status. Furthermore, we classify the genus *Dendrokingstonia* Rauschert in tribe Dendrokingstonieae, in accordance with results of phylogenetic analyses (Chaowasku *et al.*, 2012). In doing so, we assign all genera of Annonaceae without exception to a tribe.

Considering the nomenclature of tribes, the principle has been adopted that published names of tribes, based on a generic name, are assigned to clades containing that genus. To a large extent, we could use tribal names that have been published before, using the oldest names that apply to clades in our tree. Names that have become superfluous are Tetrameranthae R.E.Fr., Melodoreae Prantl, Mitrephoreae Hook.f. & Thomson and Unoneae Benth. & Hook.f. Six new tribes need to be described as none of the existing names could be applied.

The macromorphological characters most frequently emphasized in classifications of Annonaceae concern the form of the fruit, inflorescence position, and shape and aestivation of the sepals and petals. Some are demonstrably nonhomologous, such as syncarpous fruits (as discussed above). The primary homology of further historically important characters, such as numbers of carpels, numbers of ovules per carpel, fusion of petals, and shape and insertion of petals, can best be tested in the light of our tree. We have not attempted a formal character analysis here. It is, however, clear from the phylogenetic relationships presented here that historically important characters do not consistently characterize major clades. Indeed, it is not obvious which, if any, individual traits might be interpreted as unequivocal diagnostic characters for more inclusive clades. In our description of subfamilies and tribes, we document what we see as suites of characters most useful for broadly defining clades.

These characters have been taken from our own observations and those of Maas & Westra (1984), Westra (1985), Morawetz & Le Thomas (1988), van Heusden (1992), van Setten & Koek-Noorman (1992), Johnson & Murray (1995), Doyle & Le Thomas (1996), Svoma (1998), Johnson (2003), Maas, Westra & Chatrou (2003), Tsou & Johnson (2003), Scharaschkin & Doyle (2005, 2006), Su & Saunders (2006), Maas, Westra & Vermeer (2007), Couvreur (2009), Huysmans *et al.* (2010), Surveswaran *et al.* (2010) and Weerasooriya & Saunders (2010).

Anaxagoreoideae Chatrou, Pirie, Erkens & Couvreur, *subfam. nov.*—**TYPE:**

Anaxagorea A.St.-Hil.

Trees with distichous phyllotaxis; hermaphroditic; carpels free in flower and fruit; stamen apex pointed or rounded; connective extension anthers nonseptate; inner staminodes present; orbicules present; ovules two (basal); monocarp abscission at base of stipe; monocarps ventrally dehiscent; seeds not arillate, asymmetrical; middle seed integument absent; basic chromosome number $x = 8$.

Included genus: *Anaxagorea*.

Ambavioideae Chatrou, Pirie, Erkens & Couvreur, *subfam. nov.*—**TYPE:** *Ambavia* Le Thomas

Trees with spiral or distichous phyllotaxis; hermaphroditic; carpels free in flower and fruit; apical connective prolongation tongue-shaped, peltate-apiculate or peltate-truncate; anthers nonseptate; staminodes absent; ovules two—numerous (lateral); orbicules present; monocarp abscission at apex or base of stipe; monocarps indehiscent; seeds sometimes arillate, symmetrical; middle seed integument usually present; endosperm ruminations irregular; basic chromosome number $x = 7$ or 8 .

Included genera: *Ambavia*, *Cananga*, *Cleistopholis*, *Cyathocalyx* Champ. ex Hook.f. & Thomson, *Drepananthus* Maingay ex Hook.f., *Lettowianthus* Diels, *Meiocarpidium*, *Mezzettia* Becc., *Tetrameranthus*.

A synapomorphy for this clade is a middle integument (Christmann, 1989; Svoma, 1998; Lucas *et al.*, 2012).

Annonoideae Raf., *Anal. Nat.* 175., Apr–Jul 1815 ('*Annonidia*'), *descr. emend.*—**TYPE:** *Annona* L.

Trees or lianas with spiral or distichous phyllotaxis; hermaphroditic, sometimes (andro)dioecious, rarely (andro)monoecious; carpels free or fused in flower and fruit; ovules one (basal, rarely apical) to numerous (lateral); apical connective prolongation peltate-truncate, peltate-apiculate, rarely tongue-shaped or absent; anthers septate or nonseptate; outer staminodes rarely present; orbicules usually absent; monocarps indehiscent or dehiscent (adaxially or

abaxially); seeds sometimes arillate, symmetrical; middle seed integument absent (only present in *Artabotrys*); endosperm ruminations usually lamelliform, sometimes irregular; basic chromosome number $x = 7$, 8 or 9 .

Although *Bocagea* A.St.-Hil., *Cardiopetalum* Schltld. and *Froesiodendron* R.E.Fr. have not been sampled for our phylogenetic analyses, we believe their inclusion in Annonoideae is warranted. Together with *Cymbopetalum* Benth., *Mkilua* Verdc., *Porcelia* and *Trigynaea* Schltld., these genera belong to Bocageae, which are clearly set apart from other Annonaceae by a combination of inflorescence, pollen and seed characters (Johnson & Murray, 1995). The inflorescence is an internodal pedicel that is articulated at the base (Murray, 1993; Johnson & Murray, 1995). The lack of bracts, below and above the articulation, precludes sympodial growth of the inflorescence and, as a consequence, the flowers are solitary. Like solitary flowers, columellar polyads (Johnson & Murray, 1995; Tsou & Fu, 2007; Doyle & Le Thomas, 2012) only occur in this clade of Annonaceae, and therefore are clear synapomorphies. Bilobed arils (Murray, 1993; Johnson & Murray, 1995) are an additional feature characteristic of the genera in clade G, even though these are also present in *Asimina*, *Xylopia* and *Cananga*. Given that these three characters occur in the three unsampled genera, they are included here.

The unsampled genus *Afroguatteria* Boutique is also included in Annonoideae. This genus of two species has not been included in any molecular phylogenetic analysis. However, in a morphological cladistic analysis by Doyle & Le Thomas (1996), it was found to be in a clade of climbers that corresponds to clade O in our analyses. Species of *Afroguatteria* are climbers, which, on its own, merits inclusion in Annonoideae. The many-seeded apocarpous fruits, valvate sepals and imbricate petals could indicate a close relationship between *Afroguatteria* and *Uvaria*. A climbing habit also supports the addition of two monotypic African genera, *Exellia* Boutique and *Gilbertiella* Boutique, to Annonoideae. These two genera have habitually been treated as *Monanthotaxis* s.l., based on pollen and flower morphology (Le Thomas, 1969; Le Thomas & Doyle, 1996). Bygrave (2000) included *Exellia scamnopenetala* (Exell) Boutique in his phylogenetic analysis of *rbcL* sequences of Annonaceae, which placed it in an unresolved position in a clade of climbing taxa, compatible with our clade O. We were, however, unable to obtain that *rbcL* sequence.

Cleistochlamys Oliv. is a third monotypic genus that has been associated with *Monanthotaxis* (in this case, *Popowia* Endl.; Verdcourt, 1971). Its facultative climbing habit and association with *Hexalobus* A.DC.

and other annonoid genera based on pollen characters (Walker, 1971) underpin its incorporation in Annonoideae.

Despite its absence in our phylogenetic analyses, the monotypic African genus *Boutiquea* Le Thomas is placed in Annonoideae, based on palynological characters. *Boutiquea* has pollen tetrads, with a granular infratectum similar to *Neostenanthera* (Le Thomas, 1980; Doyle & Le Thomas, 2012). Pollen characters are also among the characters to support inclusion of *Duckeanthus* R.E.Fr. in Annonoideae. Pollen of this relatively poorly known monotypic genus bears strong resemblance to that of *Fusaea* in having large tetrads with a minutely granular exine structure (Walker, 1971; Le Thomas, Lugardon & Doyle, 1994; Doyle & Le Thomas, 2012). Moreover, *Fusaea* and *Duckeanthus* share characters of inflorescences, stamen anatomy and aril structure, which made them appear as sister genera in a morphological cladistic analysis (Chatrou *et al.*, 2000). The only genus we include in our classification without reference to published data is *Schefferomitra* Diels. Just before submitting this paper, sequence data became available (PhD project of S. Meinke), showing affiliation of this monotypic genus with clade R in our analyses.

The genus *Diclinanona* Diels was shown to belong to Malmeoideae (Erkens *et al.*, 2009). Because of suspicion of a mixed origin of the available sequence data of *Diclinanona*, T. Chaowasku *et al.* (unpubl. data) extracted and sequenced *Diclinanona* again, and showed it to belong to Annonoideae, confirming the phylogenetic position found by Richardson *et al.* (2004), and congruent with the absence of orbicules (Huysmans *et al.*, 2010).

CIRCUMSCRIPTION OF TRIBES IN ANNONOIDEAE

Bocageae Endl., *Gen. Pl.*: 830, Jun 1839—**TYPE**: *Bocagea* A.St.-Hil.

Trees with spiral phyllotaxis; indument of simple hairs; bracts absent; flowers solitary, terminal, bisexual; carpels free in flower and fruit; placentation lateral, uni- or biseriate; monocarp abscission at base of stipe; aril bilobed, rarely absent; ruminations lamelliform; pollen inaperturate.

Included genera: *Bocagea*, *Cardiopetalum*, *Cymbopetalum*, *Froesiodendron*, *Hornschuchia*, *Mkilua*, *Porcelia*, *Trigyna*.

This tribe is equivalent to clade G (Fig. 1B).

Xylopieae Endl., *Gen. Pl.*: 831, Jun 1839—**TYPE**: *Xylopia* L.

Trees or lianas with spiral phyllotaxis; indument of simple hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual; carpels free in flower and fruit; placentation basal or lateral and

uniseriate; monocarp abscission at base of stipe; aril absent, rudimentary or bilobed; ruminations spiniform to lamelliform; pollen inaperturate or sulcate.

Included genera: *Artabotrys*, *Xylopia*.

This tribe is equivalent to clade I (Fig. 1B).

Duguetieae Chatrou & R.M.K.Saunders, **tribus nov.**—**TYPE**: *Duguetia* A.St.-Hil.

Trees, sometimes lianas, with spiral phyllotaxis; indument of lepidote, stellate and/or simple hairs; bracts present; inflorescences rhipidiate, terminal; flowers bisexual; carpels free in flower, in fruit usually fused; placentation basal; stipe absent; aril rudimentary, rarely absent; ruminations lamelliform; pollen inaperturate, sometimes sulcate.

Included genera: *Duckeanthus*, *Duguetia*, *Fusaea*, *Letestudoxa*, *Pseudartabotrys*.

This tribe is equivalent to clade J (Fig. 1B).

Guatterieae Hook.f. & Thomson, *Fl. Ind.* 1: 92, 126, Jul 1855—**TYPE**: *Guatteria* Ruiz & Pav.

Trees, phyllotaxis unknown; indument of simple hairs; bracts present; inflorescences rhipidiate, axillary, rarely terminal; flowers bisexual; carpels free in flower and fruit; placentation basal; monocarp abscission at base of stipe; aril absent or rudimentary; ruminations spiniform to lamelliform; pollen sulcate.

Included genus: *Guatteria*.

This tribe is equivalent to clade K (Fig. 1B).

Annoneae Endl., *Gen. Pl.*: 833, Jun 1839—**TYPE**: *Annona* R.E.Fr.

Trees with distichous phyllotaxis; indument of simple hairs, rarely stellate hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual, sometimes (andro)dioecious; carpels free in flower, free or fused in fruit; placentation basal or lateral and uni- or biseriate; monocarp abscission at base of stipe, sometimes at apex, or stipe absent; aril bilobed, rudimentary or absent; ruminations spiniform, irregular pegs or lamelliform; pollen inaperturate.

Included genera: *Annona*, *Anonidium*, *Asimina*, *Boutiquea*, *Diclinanona*, *Disepalum*, *Goniothalamus*, *Neostenanthera*.

This tribe is equivalent to clade M (Fig. 1B).

Monodoreae Baill., *Hist. Pl.* 1: 263, 288. Aug–Dec 1868—**TYPE**: *Monodora* Dunal.

Trees with distichous phyllotaxis; indument of simple hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual, sometimes dioecious; carpels free or fused in flower, free or fused in fruit; placentation parietal, or lateral and uni- or biseri-

ate; monocarp abscission at base of stipe, or stipe absent; aril absent; ruminations lamelliform; pollen inaperturate.

Included genera: *Asteranthe* Engl. & Diels, *Hexalobus*, *Isolona* Engl., *Mischogyne* Exell, *Monocyclanthus* Keay, *Monodora* Dunal, *Ophrypetalum*, *Sanrafaelia*, *Uvariastrum* Engl., *Uvariadendron* (Engl. & Diels) R.E.Fr., *Uvariopsis* Engl.

This tribe is equivalent to clade O plus clade P (Fig. 1B).

Uvarieae Hook.f. & Thomson, *Fl. Ind.* 1: 91, 92.

1–19 Jul 1855—**TYPE:** *Uvaria* L.

Lianas, rarely trees, with distichous phyllotaxis; indument of stellate, sometimes simple hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual; carpels free in flower and fruit; placentation basal, or lateral and uni- or biseriate; monocarp abscission at base of stipe; aril rudimentary or absent; ruminations lamelliform; pollen inaperturate; sometimes sulcate.

Included genera: *Afroguatteria*, *Cleistochlamys*, *Dasydaschalon*, *Desmos* Lour., *Dielsiothamnus* R.E.Fr., *Exellia*, *Fissistigma* Griff., *Friesodielsia*, *Gilbertiella*, *Melodorum* Lour., *Monanthotaxis*, *Pyramidanthe* Miq., *Schefferomitra*, *Sphaerocoryne* (Boerl.) Scheff. ex Ridl., *Toussaintia*, *Uvaria*.

This tribe is equivalent to clade Q (Fig. 1B).

Malmeeideae Chatrou, Pirie, Erkens & Couvreur, **subfam. nov.**—**TYPE:** *Malmea* R.E.Fr.

Trees with spiral phyllotaxis; hermaphroditic, sometimes (andro)dioecious, rarely (andro)monoecious; carpels free in flower and fruit; apical connective prolongation peltate-truncate, peltate-apiculate, tongue-shaped or absent; anthers nonseptate; outer staminodes rarely present; ovules one to numerous (basal or lateral, rarely apical); orbicules usually present; monocarps indehiscent; seeds not arillate, symmetrical; middle seed integument absent; endosperm ruminations usually spiniform, sometimes lamelliform or irregular; basic chromosome number $x = 8$ or 9.

Dendrokingstonia Rauschert is placed in Malmeeideae even though we did not include it in our analyses. Analyses by Chaowasku *et al.* (2012) put it in this subfamily, in a moderately supported position sister to clade X (Fig. 1C). The genus *Fenerivia* is absent from our analyses. Ten species that were until recently included in *Polyalthia* have been transferred to *Fenerivia* by Saunders *et al.* (2011). *Oncodostigma* Diels is included in Malmeeideae, but it may not be worthy of recognition: van Heusden (1994) brought the then recognized *Oncodostigma* spp. into synonymy under *Meiogyne* Miq., but treated the type species *O. leptoneura* Diels as a ‘dubious name’ as the holotype

appeared to be of mixed origin; the generic name was therefore never formally reduced to synonymy with *Meiogyne*. Okada (1996) subsequently described *Oncodostigma microflorum* H.Okada, in effect revitalizing the generic name. The taxonomy of *Oncodostigma* needs further clarification and, for now, we list the name in our classification. *Fitzalania* F.Muell. has been accommodated here even though a proposal has been published to give priority to the name *Meiogyne* (Chaowasku, Zijlstra & Chatrou, 2011).

CIRCUMSCRIPTION OF TRIBES IN MALMEOIDEAE

Piptostigmatheae Chatrou & R.M.K.Saunders, **tribus nov.**—**TYPE:** *Piptostigma* Oliv.

Trees; indument of simple hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual or androdioecious; carpels free in flower and fruit; placentation basal or lateral and uni- or biseriate; monocarp abscission at base or apex of stipe; aril absent; ruminations spiniform, sometimes irregular pegs; endosperm glass-like; pollen monosulcate.

Included genera: *Annickia* Setten & Maas, *Greenwayodendron* Verdc., *Mwasumbia* Couvreur & D.M.Johnson, *Piptostigma*, *Polyceratocarpus* Engl. & Diels.

This tribe is equivalent to clade T (Fig. 1C).

Malmeeae Chatrou & R.M.K.Saunders, **tribus nov.**—**TYPE:** *Malmea* R.E.Fr.

Trees; indument of simple hairs; bracts present; inflorescences rhipidiate, terminal or axillary; flowers bisexual or androdioecious; carpels free in flower and fruit; placentation basal, rarely lateral; monocarp abscission at base of stipe; aril absent; ruminations spiniform, irregular pegs or lamelliform; endosperm glass-like or soft; pollen monosulcate.

Included genera: *Bocageopsis* R.E.Fr., *Crematosperma* R.E.Fr., *Ephedranthus* S.Moore, *Klarobelia* Chatrou, *Malmea*, *Mosannona* Chatrou, *Onychopetalum* R.E.Fr., *Oxandra* A.Rich., *Pseudephedranthus* Aristeg., *Pseudomalmea* Chatrou, *Pseudoxandra* R.E.Fr., *Ruizodendron* R.E.Fr., *Unonopsis* R.E.Fr.

This tribe is equivalent to clade V (Fig. 1C).

Maasieae Chatrou & R.M.K.Saunders, **tribus nov.**—**TYPE:** *Maasia* Mols, Keßler & Rogstad

Trees; indument of simple hairs; bracts present; inflorescences rhipidiate, axillary; flowers bisexual; carpels free in flower and fruit; placentation basal, rarely ventral; monocarp abscission at base of stipe; aril absent; ruminations spiniform; endosperm glass-like; pollen monosulcate.

Included genus: *Maasia*.

This tribe is equivalent to clade W (Fig. 1C).

Fenerivieae* Chatrou & R.M.K.Saunders, *tribus nov.—**TYPE:** *Fenerivia* Diels.

Trees; indument of simple hairs; bracts present; flowers solitary, axillary, bisexual; carpels free in flower and fruit; placentation basal; monocarp abscission at base of stipe; aril absent; ruminations spiniform; endosperm glass-like; pollen monosulcate.

Included genus: *Fenerivia*.

This tribe is not represented in our analyses. Monophyly of *Fenerivia* has been demonstrated by Saunders *et al.* (2011), who also found a polytomy comprising the tribes Malmeeae, Maasieae, Monocarpieae together with Miliuseae, and Fenerivieae. This result is confirmed by T. Chaowasku *et al.* (unpubl. data).

Dendrokingstonieae* Chatrou & R.M.K.Saunders, *tribus nov.—**TYPE:** *Dendrokingstonia* Rauschert.

Trees; indument of simple, rarely stellate, hairs; bracts present; inflorescences rhipidiate, axillary, or flowers solitary; flowers bisexual; carpels free in flower and fruit; placentation lateral, uni- or biseriate; monocarp abscission at base of stipe; aril absent; ruminations lamelliform; endosperm soft; pollen monosulcate.

Included genus: *Dendrokingstonia*.

Monocarpieae* Chatrou & R.M.K.Saunders, *tribus nov.—**TYPE:** *Monocarpia* Miq.

Trees; indument of simple hairs; bracts present; inflorescences rhipidiate, terminal; flowers bisexual; carpels free in flower and fruit; placentation lateral; monocarp abscission at base of stipe; aril absent; ruminations spiniform; endosperm glass-like; pollen monosulcate.

Included genus: *Monocarpia*.

Miliuseae* Hook.f. & Thomson, *Fl. Ind. 1: 147. 1–19 Jul 1855—**TYPE:** *Miliusa* Lesch. ex A.DC.

Trees; indument of simple hairs, rarely T-shaped hairs; bracts present; inflorescences rhipidiate, terminal or axillary, flowers rarely solitary; flowers bisexual or (andro)dioecious, rarely monoecious; carpels free in flower and fruit; placentation basal or lateral; monocarp abscission at base of stipe; aril absent; ruminations spiniform, irregular pegs or lamelliform; endosperm soft or glass-like; pollen cryptoaperturate/disulcate.

Included genera: *Alphonsea* Hook.f. & Thomson, *Desmopsis*, *Enicosanthum* Becc., *Fitzalania*, *Haplostichanthus* F.Muell., *Marsypopetalum* Scheff., *Meiogyne*, *Miliusa*, *Mitrephora* (Blume) Hook.f. & Thomson, *Neo-uvaria* Airy Shaw, *Oncodostigma*, *Orophea* Blume, *Phaeanthus* Hook.f. & Thomson, *Phoenicanthus* Alston, *Platymitra* Boerl., *Polyalthia*, *Popowia*, *Pseuduvaria* Miq., *Sageraea* Dalzell,

Sapranthus, *Stelechocarpus* (Blume) Hook.f. & Thomson, *Stenanona*, *Tridimeris*, *Trivalvaria* (Miq.) Miq., *Woodiellantha* Rauschert.

This tribe is equivalent to clade X excluding *Monocarpia* (Fig. 1C).

CONCLUSIONS

The phylogenetic tree presented here represents a significant improvement in both the generic representation and resolution when compared with previous work on Annonaceae. Previous informal classifications failed to find general acceptance and were unstable with the addition of new data or the application of different methods of analysis. The knowledge of the phylogenetics of Annonaceae has now reached the point at which it is possible to define a formal classification, with the four subfamilies and 14 tribes treated here, which is likely to be stable in the face of new data. Such a classification is warranted as an aid to communication in this important and widely distributed tropical plant family.

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