A linear sequence to facilitate curation of herbarium specimens of Annonaceae

Lars W. Chatrou1, Ian M. Turner2,3, Bente B. Klitgaard4, Paul J. M. Maas5 & Timothy M. A. Utteridge4

Summary. This paper provides a linear sequence of four subfamilies, 15 tribes and 106 genera of the magnoliid family Annonaceae, based on state-of-the-art and stable phylogenetic relationships. The linear sequence facilitates the organisation of Annonaceae herbarium specimens.

Key Words. Annonaceae, classification, herbaria, phylogenetic hypotheses, systematics, taxonomy.

Introduction

Botany in the eighteenth and nineteenth century to a large extent involved the rejection of Linnaeus’ artificial system, replacing it with classifications that reflected supposed evolutionary relationships based on careful observations of plant characters. This endeavour was greatly facilitated by collections that arrived in Europe from all over the world and were kept in newly established flourishing herbaria. Up to that point, private ownership of plant collections had been common practice. In the mid-19th century, however, these collections were often sold to the burgeoning herbaria, with the specific goal of making the collections available for study by staff and visitors. Until then, classifications such as those by Linnaeus and de Jussieu (1789) had primarily been based on European temperate plants. The influx of samples representing the wide plant diversity in colonial territories challenged these classification systems, with many non-temperate plant groups such as Annonaceae that were largely unknown to European botanists. Proliferating collections and botanical studies resulted in natural classifications by, e.g., Bentham & Hooker (1862 – 1883) and Engler & Gilg (1924), which have been the basis for taxonomic literature and for the arrangement of herbaria and botanic gardens for a long time. Given the Herculean task of changing the classification system followed in any sizeable herbarium (e.g. Wearn et al. 2013; Le Bras et al. 2017), many herbaria are still organised to date on...
Over the past two decades or so, phylogenetic systematics has resulted in a notable transformation of the classification of plants, and of angiosperms in particular. Based on the results of phylogenetic analyses, initially the delineation of angiosperm orders and families was evaluated and changed if necessary to make plant families comply with the prime guiding criterion of monophyly (APG I 1998; APG II 2003; APG III 2009; APG IV 2016). Subsequently, working groups of systematists have applied the results of phylogenetic analyses to revise inframfamilial classifications (e.g. Schneider et al. 2014; Bone et al. 2015; Chacón et al. 2016; Claudel et al. 2017; De Faria et al. 2017; Simões & Staples 2017), an endeavour that is still ongoing. Systematists have spent great effort in revising the classification of angiosperms because of the awareness that phylogenetics has brought methodological rigour to systematics and predictivity to classifications, which enabled the treatment of phylogenetic relationships — and therefore of classifications — as testable hypotheses, rather than opinions of scientists, however scholarly they might be.

Recently, the herbarium of the Royal Botanic Gardens, Kew, was reorganised following the APG III system at the family level and taking phylogenetic classifications into account at the infrafamilial level. Linear sequences of plant taxa enable curators to curate herbarium collections in accordance with phylogenetic relationships among genera. Linear sequences reflect the order of names attached to the tips of a phylogenetic tree, after the branches in the tree have been ordered according to some projection method. Alternatively, herbarium collections may be organised alphabetically, and the choice between an arrangement based on alphabet or on classification has been cause for debate (Funk 2003; Burger 2004). Storing collections according to any organising system remains indispensable as herbaria have retained their historic functions, being the basis for plant systematics and taxonomy, floristics and identification, assessment of botanical diversity, and teaching. In addition, scientific developments have unlocked new applications of herbarium collections, such as the characterisation of phenological responses to climate change (Willis et al. 2017), the assessment of global rarity of plant species to guide conservation (bioquality; Marshall et al. 2016), the sequencing of near-complete plastomes (Bakker et al. 2016; Hoekstra et al. 2017) and the targeted enrichment of nuclear genes (Hart et al. 2016), both for phylogenetic and evolutionary studies.

In this paper, we present a linear sequence of genera of Annonaceae. Generally, the family is among the most species-rich and abundant families in tropical rain forest communities (e.g. Cardoso et al. 2017; Sosef et al. 2017; Turner in press) and is amply represented in major herbaria.

### Linear sequences

Haston et al. (2007, 2009) published a simple methodology for translating tree-like relationships into a linear sequence, and applied this to a phylogenetic tree of angiosperm families. Similarly, linear sequences have been produced for gymnosperms (Christenhusz et al. 2011a) and lycophytes and ferns (Christenhusz et al. 2011b). In order to extend the phylogenetic arrangement of collections to the level of genera, linear sequences that translate family phylogenies are indispensable. So far, linear sequences are available for Fabaceae (Lewis et al. 2013), and monocots excluding Poaceae and Orchidaceae (Trias-Blasi et al. 2015).

The assembly of the phylogenetic tree underpinning the linear sequence, and the translation of the tree into the sequence consisted of the following steps.

- a summary tree showing relationships of all genera of Annonaceae was assembled. Details are given below, in the section ‘Annonaceae classification’. Nodes that did not receive significant support (parsimony or maximum likelihood bootstrap percentages, Bayesian posterior probabilities) in any of the published studies were resolved according to the topology most frequently inferred in all used publications.
- we defined clade size in terms of number of species, and not number of higher taxa (e.g. number of genera to define the size of tribes) as the former estimate of clade size can be expected to be more stable than the latter, i.e. more robust to changing taxonomic concepts (Hawthorne & Hughes 2008).
- species numbers for all genera were taken from Annonbase (Rainer & Chatrou 2006).
- following Haston et al. (2007), nodes of the phylogenetic tree were rotated in such a way that clades with fewer species were placed before clades with more species. This clade size criterion was applied subsequently to all nodes in the tree, starting from the root node (Fig. 1). The names along the tips, reading down from the top, represent the linear sequence.

### Annonaceae classification

Historically, botanists have been reluctant to provide a classification for genera in the magnoliid family Annonaceae. Even though subfamilies and tribes were described by eminent botanists such as Rafinesque (1815), Endlicher (1839), Hooker & Thomson (1855) and Baillon (1868), these were hardly used by
Annonaceae workers at the end of the 20th century, just before the breakthrough of phylogenetic methods. The classification most frequently referred to was the one by Fries (1959), who identified informal groups of genera but was reluctant to solidify his arrangement into a formal classification. Based on phylogenetic analyses of almost all genera, Chatrou et al. (2012) revised the infrafamilial classification of the family, and divided the family into four subfamilies and 14 tribes. An addition to the classification by Chatrou et al. (2012) was published by Guo et al. (2017b) with the new tribe Phoenicantheae, necessary to achieve monophyly of infrafamilial taxa belonging to the grade of species-poor lineages basal to tribe Milluiseae. Further detailed phylogenetic studies of specific tribes and genera, or the discovery of new genera of Annonaceae, did not reveal any previously overlooked deeper lineages within the family, and changes in generic circumscription could be accommodated into existing tribes (Chaowasku et al. 2012; Chaowasku et al. 2013; Guo et al. 2014; Xue et al. 2014; Chaowasku et al. 2015; Couvreur et al. 2015; Tang et al. 2015; Thomas et al. 2015; Ortiz-Rodriguez et al. 2016; Ghogue et al. 2017; Guo et al. 2017a; Stulk et al. 2017; Pirie et al. 2018). Thus, we have arrived at a point where the classification of Annonaceae, principally based on plastid sequence data, can be considered stable, and can be used to arrange herbarium specimens. Annonaceae currently contain 2430 species (Rainer & Chatrou 2006, accessed 15th May 2018), classified into 106 genera.

A few decisions, which cannot be derived from the large-scale phylogenetic trees in Chatrou et al. (2012), Chaowasku et al. (2014) and Guo et al. (2017b), need to be justified:

- We consider the generic name Haplostichanthus a synonym of Polyalthia. Xue et al. (2012) reduced nine species of Haplostichanthus into synonymy of Polyalthia, but did not discuss the status of Haplostichanthus gamopetala (Boerl. ex Koord.) Heusden. Given the morphological similarities of this species with other former species of Haplostichanthus (van Heusden 1994a) we consider this species a synonym of Polyalthia gamopetala Boerl. ex Koord., thus removing the name Haplostichanthus from accepted names in Annonaceae taxonomy.

- Thomas et al. (2012) showed that species formerly included in Oncodostigma are nested in Meigyne, thus validating the classification of some species of Oncodostigma in the latter genus by van Heusden (1994b). The last remaining species of Oncodostigma have recently been sunk into synonymy of Meigyne (Turner & Utteridge 2015; Xue et al. 2017), making the further use of the name Oncodostigma unnecessary.

- We have not included the genus Melodorum. The type specimen of the type species Melodorum fruticosum Lou. cannot be distinguished from Uvaria siamensis (Scheff.) L. L. Zhou, Y. C. F. Su & R. M. K. Saunders. The problem has been that Melodorum fruticosum has widely been misapplied to Sphaerocoryne spp. Guo et al. (2017b) note this as the probable reason that the position of Melodorum was not resolved before.

- For the tribe Malmeeae we based the linear sequence on Chatrou et al. (2012) and Pirie et al. (2006) with one exception. Analysing an alignment of 66 plastid markers, Lopes et al. (2018) inferred the Malmea / Cremastosperma / Pseudoxandra clade as sister to the remaining Malmeeae, instead of the Onychopetalum / Bocageopsis / Unonopsis clade. As these relationships were maximally supported in Bayesian analyses we adopt the result of Lopes et al. (2018).

- the position of Dichinanona was clarified in Erkens et al. (2014), that of Wangia was taken from Guo et al. (2014).

- we consider the genus Winitia (Chaowasku et al. 2013) a synonym of Stelechocarpus (Turner 2016).

**Linear sequence of Annonaceae**

Accepted names are listed in bold and synonyms in italics. We listed Unona L.f. and Uva Kunze as synonyms of Xylopia and Uvaria respectively, as the type specimens of the former two genera have been put into synonymy of the latter two. Note, however, that species previously classified in Unona or Uva can now be found in dozens of genera of Annonaceae.

We considered it beyond the scope of this paper to include details on revisions and other taxonomic information, for which we refer to a recent overviews (e.g. Maas et al. 2011; Erkens et al. 2012) and continuously updated taxonomic data in Annonbase (Rainer & Chatrou 2006), and the website http://annonaceae.myspecies.info.

**ANAXAGOREOIDEAE CHATROU, PIRIE, ERKENS & COUVREUR**

*Anaxagorea A.St.-Hil.*

_Eburopetalum Becc., Pleuripetalum T. Durand, Rhopalocarpus Teijsm. & Binn. ex Miq._

**AMBAVIOIDEAE CHATROU, PIRIE, ERKENS & COUVREUR**

_Meiocarpidium Engll. & Diels_

_Tetrameranthus R. E. Fr._

_Cleistopholis Pierre ex Engl._

_Ambavia Le Thomas_

_Mezzettia Becc._

_Lonchomera Hook. f. & Thomson_

_Lettowianthus Diels_

_Cyathocalyx Champ. ex Hook. f. & Thomson_
Fig. 1. Summary tree underlying the linear sequence of Annonaceae genera (Fig. 1a: Anaxagoreoideae, Ambavioideae and Malmeoideae; Fig. 1b: Annonoideae). Nodes marked with an asterisk have not received significant support (parsimony or maximum likelihood bootstrap, Bayesian posterior probability) in any publication. The number of species for each genus is indicated. Inset pictures show flowers of Fenerivia capuronii (Cavaco & Keraudren) R. M. K. Saunders (Fig. 1a) and Guatteria aeruginosa Standl. (Fig. 1b). PHOTOS: L. W. CHATROU.
Cananga (Dunal) Hook. f. & Thomson
Canangium Baill. ex King, Fitzgeraldia F. Muell.
Drepananthus Maingay ex Hook. f.

Malmeoideae Chatrou, Pirie, Erkens & Couvreur
Piptostigmateae Chatrou & R. M. K. Saunders
Annickia Setten & Maas
Enantia Oliv.
Greenwayodendron Verdc.

Mwasumbia Couvreur & D. M. Johnson
Sirdavidia Couvreur & Sauquet
Brieya De Wild.
Polyceratocarpus Engl. & Diels
Alphonseopsis Baker f., Dielsina Kuntze
Piptostigma Oliv.

Malmeae Chatrou & R. M. K. Saunders
Malmea R. E. Fr.
Pseudoxandra R. E. Fr.
Cremastosperma R. E. Fr.
Onychopetalum R. E. Fr.
Bocageopsis R. E. Fr.
Unonopsis R. E. Fr.
Mosannona Chatrou
Ruizodendron R. E. Fr.
Ephedranthus S. Moore
Pseudomalmea Chatrou
Pseudephedranthus Aristeg.
Klarobelia Chatrou
Oxandra A. Rich.

Maasiaceae Chatrou & R. M. K. Saunders
Maasia Mols, Kessler & Rogstad

Feneriviaceae Chatrou & R. M. K. Saunders
Fenerivia Diels

Phoenicanthae X. Guo & R. M. K. Saunders
Phoenicanthus Alston

Dendrokingstonieae Chatrou & R. M. K. Saunders
Dendrokingstonia Rauschert
   Kingstownia Hook. f. & Thomson

Monocarpieae Chatrou & R. M. K. Saunders
Monocarpia Miq.

Miliisaceae Hook. f. & Thomson
Platymitra Boerl.
   Macanea Blanco
Alphonsea Hook. f. & Thomson
Mitrephora (Blume) Hook. f. & Thomson
   Kinginda Kuntze
Meiogyne Miq.
   Anciana F. Muell., Ararocarpus Scheff., Chieniodendron
   Tsiang & P. T. Li, Fitzalania F. Muell., Guamia
   Merr., Oncodostigma Diels, Polyvalax Backer
Wuodendron B. Xue, Y. H. Tan & Chaowasku
Tridimeris Baill.
Sapranthus Seeem.
Desmopsis Saff.
   Reedrollinsia J. W. Walker
Stenanona Standl.
Phaeanthus Hook. f. & Thomson
Stelechocarpus Hook. f. & Thomson
   Winitia Chaowasku
Sageraea Dalzell
Wangia X. Guo & R. M. K. Saunders

Neouvaria Airy Shaw
Monoon Miq.
   Cleistopetalum H. Okada, Enicosanthum Becc.,
   Griffithia Maingay ex King, Griffithianthus Merr.,
   Marcuccia Becc., Woodiella Merr., Woodiellantha
   Rauschert
Huberantha Chaowasku
   Hubera Chaowasku
Miliusa Lesch. ex A. DC.
   Hyalostemma Wall., Saccopetalum Benn.
Orophea Blume
   Mezzettiopsis Ridl.
Trivalvaria (Miq.) Miq.
Marsypopetalum Scheff.
Pseudovaria Miq.
   Craibella R. M. K. Saunders, Y. C. F. Su &
   Chalermglin, Oreomitra Diels, Petalolophus K. Schum.
Popowia Endl.
Polyalthia Blume
   Haplostichanthus F. Muell., Papualthia Diels,
   Sphaerothalamus Hook. f.

Phoenicantheae X. Guo & R. M. K. Saunders
Phoenicanthus Alston

Dendrokingstonieae Chatrou & R. M. K. Saunders
Dendrokingstonia Rauschert
   Kingstownia Hook. f. & Thomson

Monocarpieae Chatrou & R. M. K. Saunders
Monocarpia Miq.

Miliusaceae Hook. f. & Thomson
Platymitra Boerl.
   Macanea Blanco
Alphonsea Hook. f. & Thomson
Mitrephora (Blume) Hook. f. & Thomson
   Kinginda Kuntze
Meiogyne Miq.
   Anciana F. Muell., Ararocarpus Scheff., Chieniodendron
   Tsiang & P. T. Li, Fitzalania F. Muell., Guamia
   Merr., Oncodostigma Diels, Polyvalax Backer
Wuodendron B. Xue, Y. H. Tan & Chaowasku
Tridimeris Baill.
Sapranthus Seeem.
Desmopsis Saff.
   Reedrollinsia J. W. Walker
Stenanona Standl.
Phaeanthus Hook. f. & Thomson
Stelechocarpus Hook. f. & Thomson
   Winitia Chaowasku
Sageraea Dalzell
Wangia X. Guo & R. M. K. Saunders

Neouvaria Airy Shaw
Monoon Miq.
   Cleistopetalum H. Okada, Enicosanthum Becc.,
   Griffithia Maingay ex King, Griffithianthus Merr.,
   Marcuccia Becc., Woodiella Merr., Woodiellantha
   Rauschert
Huberantha Chaowasku
   Hubera Chaowasku
Miliusa Lesch. ex A. DC.
   Hyalostemma Wall., Saccopetalum Benn.
Orophea Blume
   Mezzettiopsis Ridl.
Trivalvaria (Miq.) Miq.
Marsypopetalum Scheff.
Pseudovaria Miq.
   Craibella R. M. K. Saunders, Y. C. F. Su &
   Chalermglin, Oreomitra Diels, Petalolophus K. Schum.
Popowia Endl.
Polyalthia Blume
   Haplostichanthus F. Muell., Papualthia Diels,
   Sphaerothalamus Hook. f.

ANNONOIDEAE RAF.
Bocageae Endl.
Milua Verdc.
Hornschuchia Nees
   Mosenodendron R. E. Fr.
Bocagea A. St.-Hil.
Trigynaeae Schldl.
Froesiodendron R. E. Fr.
Porcelia Ruiz & Pav.
Cardiopetalum Schldl.
   Stormia S. Moore
Cymbopetalum Benth.

Xylopieae Endl.
Artabotrys R. Br.
   Ropalopetalum Griff.
Xylopia L.
   Coeloclina A. DC., Habzelia A. DC., Krockeria Necker,
   Parabotrys Müll., Parartabotrys Miq., Patonia Wight,
   Pseudannona Saff., Unona L. f., Waria Aubl.,
   Xylopiastrum Roberthy, Xylopicron Adans., Xylopicrum
   P. Browne

Duguetieae Chatrou & R. M. K. Saunders
Pseudartabotrys Pellegr.
Letestudoxa Pellegr.
Duckeanthus R. E. Fr.
Fusaea (Baill.) Saff.
Duguetia A. St.-Hil.
   Aberemoa Aubl., Alcmene Urb., Geantheum (R. E.
   Fr.) Saff., Pachypodanthium Engl. & Diels
Guatteriaceae Hook. f. & Thomson
Guatteria Ruiz & Pav.
Guatteriella R. E. Fr., Guatteriopsis R. E. Fr., Heteropetalum Benth.

Annonaceae Endl.
Anonidium Engl. & Diels
Boutiquea Le Thomas
Neostenanthera Exell
Sienenanthera Engl. & Diels
Goniothalamus Hook. f. & Thomson
Atrutegia Bedd., Beccariodendron Warb., Richella A. Gray
Diclinanona Diels
Disepalum Hook. f.
Enicosanthisum Bân
Asimina Adans.
Deeringothamnus Small, Orchidocarpum Michx., Piyothanthus Small
Annona L.
Guanabanus Mill., Raimondia Saff., Rollinia A. St.-Hil., Rolliniosis Saff.

Monodorea Baill.
Ophrypetalum Diels
Sanrafaelia Verde.
Mischogyne Exell
Uvariodendron (Engl. & Diels) R. E. Fr.
Monocyclanthus Keay
Uvaropsis Engl.
Dennettia Baker f., Tetrastemma Diels, Thommera De Wild.
Asteranthe Engl. & Diels
Asteranthopsis Kuntze
Hexalobus A. DC.
Uvariastrum Engl.
Monodora Dunal
Isolona Engl.

Uvaricaceae Hook. f. & Thomson
Uvaria L.
Anomianthus Zoll., Armenteria Thouars ex Baill., Balonga Le Thomas, Gyathostemma Griff., Dasocala J. Sinclair, Ellipeia Hook. f. & Thomson, Ellipeiospis R. E. Fr., Mareuteria Thouars, Melodorum Lour., Narum Adans., Naruma Raf., Pyragma Noronha, Roswennhoffia Scheff., Tetrapetalum Miq., Uva Kuntze, Uvaria Ridi.
Dielsiothamnus R. E. Fr.
Pyramidanteria Miq.
Mitrella Miq.
Fissistigma Griff.
Afroguatteria Boutique

Toussaintia Boutique
Cleistochlamys Oliv.
Sphaerocorne (Boerl.) Scheff. ex Ridd.
Friesodielsia Steenis
Oxymitra (Blume) Hook. f. & Thomson, Schefferomitra Diels
Desmos Lour.
Dasymaschalon (Hook. f. & Thomson) Dalla Torre & Harms
Pelicalys Griff.
Monanthotaxis Baill.
Atopostema Boutique, Clathropermum Planch. ex Benth., Enneastemon Exell, Exellia Boutique, Gilbertiella Boutique

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