



# The diversity and evolution of pollination systems in Annonaceae

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*Received 9 May 2011; Revised 6 July 2011; accepted for publication 4 November 2011*

The pollination biology of Annonaceae has received considerable attention, with data now available for > 45% of the genera (or genus-equivalent clades) included in recent molecular phylogenetic analyses. This provides a basis for understanding evolutionary shifts in the pollination system within the family. The present study focuses on subfamilies Anaxagoreoideae, Ambavioideae and Annonoideae, for which robust, well-resolved phylogenetic trees are available. Information is summarized on the pollination biology of individual clades and the evolutionary adaptations favouring different pollinator guilds evaluated. Although the majority of species of Annonaceae are pollinated by small beetles, five other pollinator groups are known: large beetles, thrips, flies, bees and cockroaches. Small-beetle pollination is inferred as the ancestral pollination system, with all other systems being derived. Evolutionary shifts to pollination by large beetles, thrips and flies are unlikely to have been significantly constrained by previous adaptations favouring pollination by small beetles, as many of the adaptations to these different pollinator guilds are similar (including protogyny, partially enclosed floral chambers and olfactory cues). In contrast, however, the evolutionary shift to bee pollination has presumably been constrained by both protogyny (as pollen-collecting bees are unlikely to visit pistillate-phase flowers) and the presence of floral chambers. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2012, **169**, 222–244.

ADDITIONAL KEYWORDS: cantharophily – pollination ecology – reproductive biology.

## INTRODUCTION

Pollination systems in Annonaceae have received considerable attention, particularly in the Neotropics. Published reports on the pollination biology of the family suggest that the majority of species are beetle pollinated, with distinct small- and large-beetle pollination systems (e.g. Gottsberger, 1999; Silberbauer-Gottsberger, Gottsberger & Webber, 2003). Despite the prevalence of beetle pollination in the family, a diverse array of other insect guilds also act as pollinators, including thrips (Gottsberger, 1970; Webber & Gottsberger, 1995; K uchmeister *et al.*, 1998; Momose, Nagamitsu & Inoue, 1998a; Momose *et al.*, 1998b; Silberbauer-Gottsberger *et al.*, 2003), flies (Gottsberger, 1985; Morawetz, 1988; Norman, Rice & Cochran, 1992; Su *et al.*, 2005), bees (Olesen, 1992; Carvalho & Webber, 2000; Silberbauer-Gottsberger *et al.*, 2003; Teichert, 2007; Teichert *et al.*, 2009) and

cockroaches (Nagamitsu & Inoue, 1997). There is therefore convincing evidence that many pollination systems in Annonaceae are specialized at the pollinator guild level.

Recently published molecular phylogenetic analyses of Annonaceae provide an ideal basis for investigating the evolution of pollination systems and associated floral morphology. The most taxonomically comprehensive of these analyses is that of Couvreur *et al.* (2011), who adopted a supermatrix approach, concatenating data from seven plastid markers (*atpB-rbcL*, *matK*, *ndhF*, *psbA-trnH*, *rbcL*, *trnS-trnG* and *trnL-trnF*); this analysis included 93 of the 112 currently recognized genera (83%). Four main groups are consistently evident in published molecular phylogenetic analyses of the family, including that of Couvreur *et al.* (2011): the subfamily Anaxagoreoideae (*sensu* Chatrou *et al.*, 2012), consisting solely of the genus *Anaxagorea* St.Hil., sister to all other Annonaceae; subfamily Ambavioideae (the ‘ambavioid’ clade, consisting of nine genera: *Ambavia* Le Thomas,

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*Cananga* (DC.) Hook.f. & Thomson, *Cleistopholis* Pierre ex Engl., *Cyathocalyx* Champ. ex Hook.f. & Thomson, *Drepananthus* Maingay ex Hook.f., *Lettowianthus* Diels, *Meiocarpidium* Engl. & Diels, *Mezzettia* Becc. and *Tetrameranthus* R.E.Fr.); and two large sister clades, namely subfamily Annonoideae (formerly known as the 'long-branch clade') and subfamily Malmeoideae (formerly the 'short-branch clade').

Subfamily Malmeoideae are comparatively poorly resolved, with numerous polytomies and weakly supported clades. Any attempt at interpreting evolutionary changes in reproductive characters in this clade is unlikely to be reliable and, for this reason, the present study focuses on subfamilies Anaxagoreoideae, Ambavioideae and Annonoideae. The large genera *Annona* L. (c. 200 species, including *Rollinia* A.St.-Hil.: Rainer, 2007) and *Uvaria* L. (c. 210 species, including *Anomianthus* Zoll., *Balanga* Le Thomas, *Cyathostemma* Griff., *Dasoclema* J.Sinclair, *Ellipeia* Hook.f. & Thomson, *Ellipeiopsis* R.E.Fr. and *Rauwenhoffia* Scheff.: Zhou, Su & Saunders, 2009, Zhou *et al.*, 2010) show a diversity of floral structures and pollination systems. This variation has been accommodated in the present study by interpolating topologies from species-level phylogenetic studies of *Annona* (H. Rainer, unpubl. data) and *Uvaria* (Zhou *et al.*, 2009, 2010, 2012) into the phylogenetic analyses published by Couvreur *et al.* (2011). The various pollinator guilds observed in each clade (Table 1) were mapped as an unordered character on the combined topology (Fig. 1) using Mesquite ver. 2.73 (Maddison & Maddison, 2010). *Eupomatia* R.Br. (Eupomatiaceae) was included as an outgroup for comparative purposes as it has repeatedly been shown to be sister to Annonaceae (e.g. Qiu *et al.*, 2005).

## POLLINATION SYSTEMS IN INDIVIDUAL CLADES

### OUTGROUP: *EUPOMATIA* (EUPOMATIACEAE)

The pollination biology of *Eupomatia laurina* Hook. has been reported by Hamilton (1897), Endress (1984) and Armstrong & Irvine (1990). The flowers are hermaphroditic and are markedly protogynous, with a 12- to 24-h separation between the pistillate and staminate phases. The flowers lack any perianth; the androecium consists of numerous, spirally arranged stamens towards the outside of the flower, and numerous petaloid sterile staminodes towards the centre. The staminodes perform several functions, including the emission of scent from osmophores, and as a food reward in the form of the soft staminode apex and sticky exudate (Endress, 1984; Armstrong & Irvine, 1990). The staminodes also form a loose pollination chamber that shelters the

pollinators. The only floral visitors observed were small weevils (Curculionidae), which were observed copulating in the flowers and laying eggs amongst the staminodes.

### CLADE 1: *ANAXAGOREA*

*Anaxagorea* flowers are bisexual and consist of two whorls of valvate petals, which are generally fleshy. The inner petals are almost equal or slightly shorter than the outer petals and are apically connivent over the reproductive organs during the reproductively active phases, forming a pollination chamber.

The reproductive biology of the genus is comparatively well investigated, with studies of six species (*A. brevipes* Benth., *A. crassipetala* Hemsl., *A. dolichocarpa* Sandwith & Sandwith, *A. manausensis* Timmerman, *A. phaeocarpa* Mart., and *A. prinoides* St.Hil. & A.DC.: Bawa *et al.*, 1985; Maas-van de Kamer, 1993; Armstrong & Marsh, 1997; K uchmeister *et al.*, 1998; J urgens, Webber & Gottsberger, 2000; Webber, 2002; Teichert, 2007; Braun, 2010; Teichert, D otterl & Gottsberger, 2011). Flowers of all these species are visited by small diurnal beetles (Nitidulidae and, to a lesser extent, Staphylinidae). The flowers are protogynous, with a 2-day diurnal rhythm (i.e. the pistillate and then staminate phases cover a 2-day period); in several species, there is evidence that the pistillate and staminate phases are temporally separated overnight to prevent autogamy (Armstrong & Marsh, 1997; J urgens *et al.*, 2000). There is evidence of heterodichogamy in *A. prinoides*, with the occurrence of pistillate-phase and staminate-phase flowers synchronized between individuals, thereby promoting xenogamy (Teichert *et al.*, 2011); this was not observed, however, in *A. dolichocarpa* (Braun, 2010). Sterile staminodes act as a physical barrier to the transfer of pollen in several species, by elongating and essentially covering the stigmas towards the end of the pistillate phase (*A. brevipes*: Webber, 2002; *A. dolichocarpa*: Maas-van de Kamer, 1993; Braun, 2010; *A. javanica* Blume: Corner, 1988).

The flowers emit a fruity odour at anthesis (correlated with the pistillate and staminate reproductive phases) and are thermogenic (c. 1.5–5.5 °C above ambient levels, depending on species: K uchmeister *et al.*, 1998; J urgens *et al.*, 2000; Braun, 2010). The beetles appear to be rewarded by copious stigmatic exudate during the pistillate phase (Maas-van de Kamer, 1993; Armstrong & Marsh, 1997) and pollen during the staminate phase (Braun, 2010), although there is no evidence that the flowers act as a brood site for the beetles (Armstrong & Marsh, 1997; Braun, 2010). *Anaxagorea* does not appear to possess a biochemical self-incompatibility mechanism (Bawa *et al.*, 1985; Armstrong & Marsh, 1997; Braun, 2010).

**Table 1.** Presence (•) and absence (◦) of different pollinator guilds in Annonaceae subfamilies Anaxagoreoideae, Ambavioideae and Annonoideae. “?” indicates data unknown. Numbered clades are discussed in the text and shown in Figure 1

	Small beetles	Large beetles	Thrips	Flies	Bees	Cockroaches
Outgroup						
<i>Eupomatia</i>	•	◦	◦	◦	◦	◦
Clade 1						
<i>Anaxagorea</i>	•	◦	◦	◦	◦	◦
Clade 2						
<i>Meiocarpidium</i>	?	?	?	?	?	?
Clade 3						
<i>Cyathocalyx</i>	?	?	?	?	?	?
<i>Drepananthus</i>	•	◦	◦	◦	◦	◦
<i>Cananga</i>	•	◦	◦	◦	◦	◦
<i>Lettowianthus</i>	?	?	?	?	?	?
Clade 4						
<i>Tetrameranthus</i>	•	◦	◦	◦	◦	◦
<i>Cleistopholis</i>	?	?	?	?	?	?
<i>Mezzettia</i>	•	◦	◦	◦	◦	◦
<i>Ambavia</i>	?	?	?	?	?	?
Clade 5						
<i>Mkilua</i>	?	?	?	?	?	?
<i>Cymbopetalum</i>	◦	•	◦	◦	◦	◦
<i>Porcelia</i>	◦	•	◦	◦	◦	◦
<i>Trigynaea</i>	?	?	?	?	?	?
<i>Hornschuchia</i>	?	?	?	?	?	?
Clade 6						
<i>Xylopia</i>	•	◦	•	◦	◦	◦
<i>Artabotrys</i>	•	◦	◦	◦	◦	◦
Clade 7						
<i>Duguetia</i>	•	•	•	◦	◦	◦
<i>Fusaea</i>	?	?	?	?	?	?
<i>Letestudoxa</i>	?	?	?	?	?	?
<i>Pseudartabotrys</i>	?	?	?	?	?	?
Clade 8						
<i>Guatteria</i>	•	◦	◦	◦	◦	◦
Clade 9						
<i>Anonidium</i>	?	?	?	?	?	?
<i>Neostenanthera</i>	?	?	?	?	?	?
Clade 10						
<i>Goniothalamus</i>	•	◦	◦	◦	◦	◦
Clade 11						
<i>Asimina</i>	•	•	◦	•	◦	◦
<i>Disepalum</i>	?	?	?	?	?	?
Clade 12						
<i>Annona</i> 1	•	◦	◦	◦	◦	◦
<i>Annona</i> 2	◦	•	◦	◦	◦	◦
<i>Annona</i> 3	•	◦	◦	◦	◦	◦
<i>Annona</i> 4	•	◦	◦	◦	◦	◦
<i>Annona</i> 5	•	◦	◦	◦	◦	◦
<i>Annona</i> 6	◦	•	◦	◦	◦	◦
Clade 13						
<i>Monodora</i>	◦	◦	◦	•	◦	◦
<i>Isolona</i>	•	◦	◦	◦	◦	◦
<i>Asteranthe</i>	?	?	?	?	?	?
<i>Hexalobus</i>	?	?	?	?	?	?
<i>Uvariastrum</i>	?	?	?	?	?	?

Table 1. Continued

	Small beetles	Large beetles	Thrips	Flies	Bees	Cockroaches
Clade 14						
<i>Mischogyne</i>	?	?	?	?	?	?
<i>Uvari dendron</i>	○	●	○	○	○	○
<i>Monocyclanthus</i>	?	?	?	?	?	?
<i>Uvariopsis</i>	○	○	○	●	○	○
Clade 15						
<i>Sanrafaelia</i>	?	?	?	?	?	?
<i>Ophrypetalum</i>	?	?	?	?	?	?
Clade 16						
<i>Dielsiothamnus</i>	?	?	?	?	?	?
Clade 17						
<i>Fissistigma</i>	●	○	○	○	○	○
<i>Mitrella</i>	?	?	?	?	?	?
Clade 18						
<i>Uvaria</i> 1	●	○	○	○	○	○
<i>Uvaria</i> 2	●	○	○	○	○	○
<i>Uvaria</i> 3	●	○	○	○	○	○
<i>Uvaria</i> 4	●	○	○	○	●	●
Clade 19						
<i>Melodorum</i>	●	○	○	○	○	○
<i>Sphaerocoryne</i>	?	?	?	?	?	?
<i>Toussaintia</i>	?	?	?	?	?	?
Clade 20						
<i>Monanthotaxis</i>	?	?	?	?	?	?
<i>Dasymaschalon</i>	●	○	○	○	○	○
<i>Desmos</i>	●	○	○	○	○	○
<i>Friesodielsia</i>	●	○	○	○	○	○
Subfamily Malmeoideae	●	●	●	●	●	○

CLADE 2: *MEIOCARPIDIUM*

There are no published data on the reproductive biology of *Meiocarpidium lepidotum* Engl. & Diels, the sole representative of the genus. The flowers are hermaphroditic with cream-coloured petals that form a loose chamber around the reproductive organs (van Heusden, 1992); these features are typical of other Annonaceae that are pollinated by small beetles.

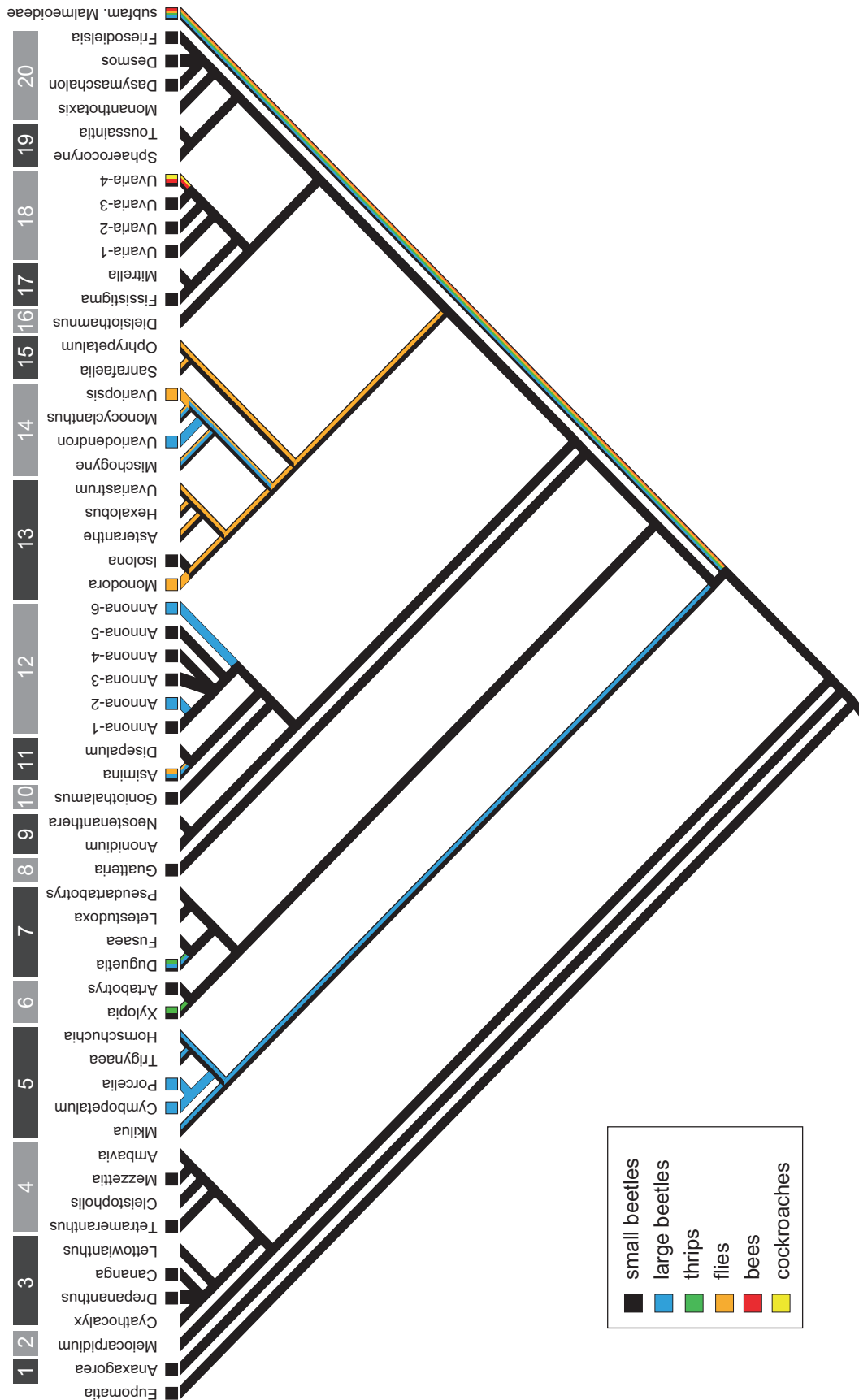
CLADE 3: *CANANGA*, *CYATHOCALYX*, *DREPANANTHUS* AND *LETTOWIANTHUS*

Despite the considerable economic importance of *Cananga* as the source of ylang-ylang for the perfume industry, little is known of its reproductive biology. The flowers are bisexual, with valvate inner and outer petals that are subequal in length. The inner petals are connivent over the reproductive organs during the receptive phases, forming a pollination chamber.

One of the few published studies of the reproductive biology of *Cananga* was based on cultivated *C. odorata* (Lam.) Hook.f. & Thomson trees in the Ivory Coast, West Africa (Deroin, 1988a, b). The flowers were visited by small nitidulid and chry-

somelid beetles; despite the fact that the trees were not indigenous to the study site, it seems probable that similar beetles act as pollinators in natural populations. The flowers are protogynous, although it is unclear whether there is a non-receptive interim period between the pistillate and staminate phases. A strong odour is reported to develop in the early evening as the flower enters its pistillate phase, and apparently does not dissipate overnight or the following day. According to Deroin (1988b), the stamens dehisce in the early evening of the second day at the same time that the other floral organs abscise (with the exception of the sepals, which are persistent). Although the reproductive cycle is therefore conducted over 2 days, organ abscission appears earlier than in most species with a 2-day rhythm; it seems likely that anther dehiscence slightly precedes organ abscission, and therefore the entire reproductive cycle is completed within 24 h. The beetles are presumably rewarded by stigmatic exudate and pollen as food.

There is no published information on the reproductive biology of either *Cyathocalyx* or *Drepananthus* (treated here as distinct genera, following proposals by



**Figure 1.** Cladogram showing Annonaceae subfamilies Anaxagoreoideae, Ambavioideae and Annonoideae, adapted from Couvreur *et al.* (2011). Clades 1–20 are discussed in the text. Pollinator guilds (small beetles, large beetles, thrips, flies, bees and cockroaches; data given in Table 1) mapped as an unordered character using parsimony reconstruction in Mesquite ver. 2.73 (Maddison & Maddison, 2010).

Surveswaran *et al.*, 2010), other than a casual observation by Corner (1988: 136) that the flowers of some *Drepananthus* spp. (cited under the generic name *Cyathocalyx*) are visited by beetles. The inner and outer petals of both genera are subequal in length, with the inner petals connivent over the reproductive organs, forming a tightly constricted pollination chamber; it can be inferred that the pollinating beetles are small, based on the size of the floral chamber.

No data are available on the reproductive biology of *Lettowianthus stellatus* Diels, the only species in the genus. The flowers are hermaphroditic and lack a pollination chamber (Saunders, 2010), superficially resembling flowers of *Uvaria*, which are pollinated by small beetles.

CLADE 4: *TETRAMERANTHUS*, *CLEISTOPHOLIS*,  
*MEZZETTIA* AND *AMBAVIA*

Unusually for Annonaceae, *Tetrameranthus* flowers possess eight petals, in two whorls of four. The petals do not form a pollination chamber over the reproductive organs. The reproductive biology of *T. duckei* R.E.Fr. was investigated by Webber (1981a) and subsequently discussed by Westra (1985). The flowers are primarily visited by small curculionid beetles, but also by opportunist meliponine bees. The flowers are protogynous and remain closed until shortly before the stigmas become receptive in the early evening. The beetles are attracted to the flower at this time by a strong musky odour, although data were not collected to indicate the possibility of thermogenesis. The staminate floral phase begins in the afternoon of the following day, with beetles observed crawling among the stamens, consuming pollen. The petals abscise later on the second day, although the beetles remain on the flower until the odour dissipates on the third day. It therefore appears that *T. duckei* flowers are protogynous over a 2-day period, without overlapping pistillate and staminate phases. Although the beetles were observed feeding on pollen, the petals are fleshy and possess a callus-like tissue that may be an adaptation for beetle consumption; Westra (1985), however, suggested that the callus-like tissue possibly acts as an osmophore.

*Mezzettia* flowers are bisexual, with the inner whorl of petals smaller than the outer whorl, and lacking any pollination chamber. Although detailed studies of the reproductive biology of the genus are lacking, Sakai *et al.* (1999) observed that *M. havilandii* Ridl. flowers were visited by beetles. The beetles were not identified or described, but the size of the flowers (van der Heijden & Kessler, 1990) suggests that the pollinators are likely to be small.

There are no published reports of the pollination biology or breeding systems of either *Cleistopholis* or

*Ambavia*. Both genera have small bisexual flowers, with enclosed pollination chambers [Cavaco & Keraudren, 1958 (*Ambavia* as '*Popowia*' Endl.); Le Thomas 1972; van Heusden 1992] and might therefore be inferred to be pollinated by small beetles.

CLADE 5: *CYMBOPETALUM*, *PORCELIA*, *MKILUA*,  
*TRIGYNAEA* AND *HORN SCHUCHIA*

The pollination biology of *Cymbopetalum* Benth. is comparatively well investigated, with seven species studied: *C. baillonii* R.E.Fr., *C. brasiliense* Benth., *C. costaricense* (Donn.Sm.) R.E.Fr., *C. euneurum* N.A.Murray, *C. lanugipetalum* Schery, *C. penduliflorum* Baill. and *C. torulosum* G.E.Schatz (Bawa, Perry & Beach, 1985; Bawa *et al.*, 1985; Schatz, 1985, 1990; Murray, 1993; Webber & Gottsberger, 1993; Braun, 2010). All these studies confirm that the flowers are pollinated by large scarab beetles (Scarabaeidae: Dynastinae). The flowers are correspondingly large, with petals that are essentially valvate. In several species, the inner petals are extremely thick, cymbiform (boat-shaped) and laterally convergent, thereby forming a loose pollination chamber around the reproductive organs (Murray, 1993). The flowers are bisexual and protogynous, with a 2-day reproductive cycle. In *C. baillonii*, abscission of stigmas at the end of the pistillate phase precedes anther dehiscence, thereby preventing autogamy; in other species, however, including *C. brasiliense* and *C. lanugipetalum*, anther dehiscence occurs slightly before the stigmas abscise (Murray, 1993; Braun, 2010). The pollination ecology of *C. baillonii* (Murray, 1993) is typical of the genus: the formation of the pollination chamber is associated with the onset of stigmatic receptivity and is followed by the emission of a fruity odour in the evening. The aggregate of stigmatic heads abscise the following morning, with anther dehiscence beginning in the afternoon of that day and continuing until the third day. Both the pistillate and staminate reproductive phases of the flower are associated with brief (c. 1 h) periods with elevated internal temperatures (5.7–6.3 °C above ambient levels), when a strong fruity odour is emitted. The beetles were observed to gnaw at the fleshy inner petals, indicating that food is clearly a major reward. Beetles were also observed copulating within the floral chamber, however, presumably benefiting from the raised internal temperatures. Bawa *et al.* (1985) found no evidence of a biochemical self-incompatibility system in an unidentified *Cymbopetalum* species. Braun (2010) conducted controlled pollination experiments on *C. brasiliense* and noted fruit set in the absence of pollinators and even in emasculated flowers that had been bagged to exclude pollinators. Braun suggested that this was probably

attributable to apomixis: significantly, *C. brasiliense* is polyploid (Morawetz, 1986), a feature typical of gametophytic apomicts (Bicknell & Koltunow, 2004).

The inner and outer petals of *Porcelia* Ruiz & Pav. are imbricate at anthesis, thereby forming a loose pollination chamber. Although some species possess cymbiform inner petals as in *Cymbopetalum*, others do not; the petals of *Porcelia* also differ as they are considerably less fleshy than those of *Cymbopetalum*. Murray (1993) studied the pollination biology of four species (*P. magnifructa* (Schery) R.E.Fr., *P. mediocris* N.A.Murray, *P. steinbachii* (Diels) R.E.Fr. and *P. venezuelensis* Pittier). All species examined are visited by large scarab beetles (Scarabaeidae: Dynastinae and Melolonthinae), with a strong fruity odour acting as an attractant. Although the petals in *Porcelia* are not as fleshy as those of many *Cymbopetalum* species, all species possess a strip of tissue that is consumed by the beetles (Murray, 1993). Other information on the pollination ecology and breeding system is lacking, although Schatz (1990) provides confirmation of scarab pollination.

There is no published information on the reproductive biology of the other three genera included in clade 5: *Trigyna* Schldl., *Hornschuchia* Nees and *Mkilua* Verdc. All three genera possess bisexual flowers, with pollination chambers observed in *Trigyna* and *Hornschuchia* (Johnson & Murray, 1995) but not *Mkilua* (Verdcourt, 1970).

#### CLADE 6: XYLOPIA AND ARTABOTRYS

*Xylopi* L. flowers are hermaphroditic, with a pollination chamber around the reproductive organs formed by the loosely convergent inner petals. The torus is distinctly concave, with the carpels protected within the toral rim.

The reproductive biology of representative Neotropical, African and Asian species have been studied: *X. amazonica* R.E.Fr. (Webber, 1996, 2002; Silberbauer-Gottsberger *et al.*, 2003); *X. aromatica* Baill. (Gottsberger, 1970, 1988; Silberbauer-Gottsberger *et al.*, 2003); *X. benthamii* R.E.Fr. (Webber, 2002); *X. bocatorena* Schery (Kress & Beach, 1994); *X. brasiliensis* Spreng. (Andrade, Oliveira-Filho & Soares, 1996); *X. championii* Hook.f. & Thomson (Ratnayake *et al.*, 2007); *X. crinita* R.E.Fr. (Küchmeister *et al.*, 1998); and *X. excellens* R.E.Fr. (Küchmeister *et al.*, 1998; Silberbauer-Gottsberger *et al.*, 2003). Flowers of most of the species studied were visited by small beetles, predominantly either Chrysomelidae (*X. brasiliensis*: Andrade *et al.*, 1996), Curculionidae (*X. championii*: Ratnayake *et al.*, 2007), Nitidulidae (*X. benthamii* and *X. excellens*: Küchmeister *et al.*, 1998; Webber, 2002; Silberbauer-Gottsberger *et al.*, 2003) or Staphylinidae (*X. crinita*: Küchmeister

*et al.*, 1998). Other species are reported to be wholly or predominantly visited by thrips (Thysanoptera): *X. amazonica* (Webber, 1996, 2002; Silberbauer-Gottsberger *et al.*, 2003) and *X. aromatica* (Gottsberger, 1970; Silberbauer-Gottsberger *et al.*, 2003).

Amongst the beetle-pollinated *Xylopi* spp., *X. championii* has been studied in the greatest detail (Ratnayake *et al.*, 2007). The flower buds open fully several days before the reproductive organs become receptive. The flower closes around midday, with the three inner petals forming a loose pollination chamber. The carpels subsequently become receptive by the early evening of the same day, with curculionid beetles arriving shortly afterwards. The beetles remain inside the floral chamber overnight, departing the following morning when the flower opens and stigmatic receptivity ceases. There is then an interim phase in which neither the stigmas nor the stamens are functional. By mid afternoon on the second day, however, the flower closes and the pollination chamber forms again; this coincides with anther dehiscence and the arrival of another cohort of beetles, which again remain inside the floral chamber overnight, before departing the following morning when the petals abscise. The flowers are therefore strongly protogynous, with a functionally inactive phase separating the pistillate and staminate phases, thereby preventing autogamy. A close correlation was observed between the onset of floral receptivity and both the emission of a fruity scent and an increase in temperatures within the floral chamber by up to 8.5 °C. Gas chromatography-mass spectrometry (GC-MS) analysis of the scent volatiles revealed the presence of compounds that are known to act as aggregation pheromones and others that are known to be present in fruits; Ratnayake *et al.* (2007) speculated that a synergistic reaction may exist between these compounds, further enhancing beetle attraction. Ratnayake *et al.* (2007) also investigated the breeding system operating in *X. championii*, using controlled pollination experiments. Results showed that *X. championii* was largely xenogamous, with low levels of geitonogamy.

The pollination ecology and breeding system of *X. championii* seems to be generally typical of all other beetle-pollinated species in the genus that have been studied. The timing of floral receptivity and beetle activity appears to differ between species: most species, including *X. benthamii*, *X. championii*, *X. crinita*, *X. emarginata* Mart. and *X. excellens*, show a crepuscular–nocturnal pattern (Küchmeister *et al.*, 1998; Webber, 2002; Silberbauer-Gottsberger *et al.*, 2003; Ratnayake *et al.*, 2007), whereas it is diurnal in *X. brasiliensis* (Andrade *et al.*, 1996).

Another pollination system appears to operate within *Xylopi*, however, as several species are

reported to be visited by thrips (Thysanoptera), including *X. amazonica* (Webber, 1996, 2002; Silberbauer-Gottsberger *et al.*, 2003) and *X. aromatica* (Gottsberger, 1970; Silberbauer-Gottsberger *et al.*, 2003). Flowers of both these species possess a small pollination chamber, with diurnal receptivity over a 2-day cycle. Unlike most of beetle-pollinated *Xylopia* spp., *X. aromatica* does not exhibit thermogenesis; corresponding data are not available for *X. amazonica*.

Despite *Artabotrys* being one of the largest genera of Annonaceae, virtually nothing is known of its reproductive biology. There are only two published studies: one shows that unidentified beetles (presumably small, as the floral pollination chamber is small) visited flowers of *A. venustus* King (Sakai *et al.*, 1999); the other shows that curculionid and phalacrid beetles visited flowers of *A. siamensis* Miq. (Kato *et al.*, 2008).

CLADE 7: *DUGUETIA*, *FUSAEA*, *LETETUDOXIA*  
AND *PSEUDARTABOTRYS*

*Duguetia* A.St.-Hil. flowers are hermaphroditic, with subequal outer and inner petals that are imbricate, forming a pollination chamber. The pollination ecology of several species has been studied, including *D. asterotricha* (Diels) R.E.Fr., *D. cadaverica* Huber, *D. eximia* Diels, *D. flagellaris* Huber, *D. furfuracea* (A.St.-Hil.) Saff., *D. lanceolata* A.St.-Hil., *D. riparia* Huber, *D. stelechantha* (Diels) R.E.Fr., *D. ulei* (Diels) R.E.Fr. and an unnamed species (Gottsberger, 1970, 1999; Maas-van de Kamer, 1993; Webber, 1996; K uchmeister *et al.*, 1998; J urgens *et al.*, 2000; Silberbauer-Gottsberger *et al.*, 2001, 2003; Teichert, 2007, 2008). There appear to be several distinct pollination systems within the genus, including small beetle, large beetle and thrips pollination.

Small beetles are the most widely reported pollinators of *Duguetia* (*D. asterotricha*: J urgens *et al.*, 2000; *D. eximia*: Teichert, 2007; *D. furfuracea* and an unnamed species: Gottsberger, 1970, 1999; Silberbauer-Gottsberger *et al.*, 2003; *D. lanceolata*: Silberbauer-Gottsberger *et al.*, 2003; and *D. stelechantha*: Webber, 1996). In all these species, the floral visitors were mainly nitidulid beetles, although Curculionidae (and rarely Dermestidae) were reported visiting both *D. furfuracea* and the unnamed species. The flowers are markedly protogynous, with 1-day (*D. asterotricha*: J urgens *et al.*, 2000) or 2-day (*D. furfuracea*: Silberbauer-Gottsberger *et al.*, 2003) reproductive cycles (although detailed observations are lacking, and this apparent difference may reflect different definitions of cycle length). All reports confirm that floral receptivity and pollinator activities

were diurnal, and primarily occur in the afternoon. The pollinator attractants include strong fruity floral scents, although thermogenesis was not observed in any of the species studied. A similar nitidulid pollination system occurs in *D. cadaverica* (Maas-van de Kamer, 1993; Teichert, 2007), although pollination is by mycetophagous nitidulid beetles that are known to feed on mushrooms. This species possesses flowers at ground level, from ‘runners’ that extend from the base of the trunk. The flowers are red to white, and emit an offensive sulphurous smell reminiscent of ‘sweaty cheese’.

K uchmeister *et al.* (1998) reported a similar pollination system in *D. flagellaris*, although the flowers were visited by a combination of thrips (Thysanoptera) and small beetles (Nitidulidae and Staphylinidae). As with all the previously studied *Duguetia* spp., the flowers were protogynous, with a 2-day reproductive cycle. Evidence for floral thermogenesis was rather equivocal, with internal floral chamber temperatures c. 1.3  C above ambient levels.

Pollination by large scarab beetles (Scarabaeidae: Dynastinae) has been reported in *D. riparia* and *D. ulei* (K uchmeister *et al.*, 1998; Silberbauer-Gottsberger *et al.*, 2001; Silberbauer-Gottsberger *et al.*, 2003). The flowers of these species are correspondingly large, with thick, fleshy petals which are consumed as food by the beetles. Flowers of both species are strongly protogynous, with a non-receptive period between the pistillate and staminate phases, and show nocturnal receptivity over a 2-day period. The beetles are attracted to the flowers by a pungent scent which is coincident with thermogenesis, c. 2.1–2.7  C above ambient levels. The beetles are rewarded by food in the form of petal tissue (and also pollen during the staminate phase) and a direct heat reward.

Information is not available on the pollination ecology or breeding systems of *Fusaea* Saff., *Letestudoxia* Pellegr. or *Pseudartabotrys* Pellegr., although interpretation of floral structure would suggest pollination by small beetles. The inner petals of the flowers of *Fusaea* fold against each other to form a pollination chamber, and there is some evidence that staminodes are occasionally gnawed, suggesting that they may act as a pollinator food reward (Chatrou & He, 1999).

CLADE 8: *GUATTERIA*

The reproductive biology of *Guatteria* Ruiz & Pav. is relatively well documented with detailed studies of eight species: Webber (1996; Gottsberger, 1999; Silberbauer-Gottsberger *et al.*, 2003) studied *G. foliosa* Benth. and *G. megalophylla* Diels; and Gottsberger (1970, 1977) studied *G. curvinervia* R.E.Fr., *G. ne-*



*glecta* R.E.Fr., *G. parvifolia* R.E.Fr., *G. hilariana* Schltld. and two unnamed species. Other, less detailed, reports exist on *G. modesta* Diels (van Dulmen, 2001), *G. aeruginosa* Standl. and '*G. inuncta*' R.E.Fr. (Bawa *et al.*, 1985; the last species being equivalent to *G. diospyroides* Baill., *vide* Kress & Beach, 1994).

*Gutteria* flowers are bisexual, with outer and inner petals that are either subequal, or with inner petals that are slightly longer than the outer petals. The inner petals turn yellowish and become loosely constricted over the reproductive organs during sexually receptive phases, forming a pollination chamber (Gottsberger, 1970; Silberbauer-Gottsberger *et al.*, 2003). The flowers show a diurnal, 2-day rhythm, with marked protogyny. In *G. foliosa* (Silberbauer-Gottsberger *et al.*, 2003), for example, the pistillate phase begins in the early morning of the first day, with an exudate becoming apparent on the stigmas (indicative of stigmatic receptivity), together with the emission of a slight fruity odour; the petals become reddish-brown later that day. In the morning of the second day, the stigmas abscise and the thecae dehisce.

The species studied are visited by small chrysomelid, curculionid, nitidulid and staphylinid beetles (Gottsberger, 1970, 1977, 1999; Webber, 1996; Silberbauer-Gottsberger *et al.*, 2003). The beetles are attracted by the fruity floral odours that may mimic the fruits that they normally feed on and they are rewarded by food in the form of fleshy petals and stamens (Gottsberger, 1970, 1977). The beetles also use the flowers as brood sites, copulating and laying eggs (Gottsberger, 1970, 1977), although there is no evidence of thermogenesis in either *G. foliosa* or *G. megalophylla* (Webber, 1996; Silberbauer-Gottsberger *et al.*, 2003).

#### CLADE 9: *ANONIDIUM* AND *NEOSTENANTHERA*

Little is known of the reproductive biology of *Anonidium* Engl. & Diels and *Neostenanthera* Exell. *Anonidium* spp. are androdioecious and the flowers lack any pollination chamber (van Heusden, 1992). In contrast, *Neostenanthera* flowers are hermaphroditic and the inner petals (which are markedly shorter than the outer petals) are apically connivent over the reproductive organs, as in *Goniothalamus* (Blume) Hook.f. & Thomson (Le Thomas, 1969; van Heusden, 1992). Interpretation of the floral anatomy of *Neostenanthera* would suggest that it shares a similar pollination system to that observed in *Goniothalamus*.

#### CLADE 10: *GONIOTHALAMUS*

Despite its large size, the pollination ecology and breeding systems of *Goniothalamus* spp. have been poorly studied: limited studies have been published

on only five species, namely *G. australis* Jessup (Silberbauer-Gottsberger *et al.*, 2003), *G. wightii* (Devy & Davidar, 2003: online supplemental data), and '*G. uvarioides*' King, *G. velutinus* Airy Shaw and an unnamed species (Momose *et al.*, 1998; Momose, 2005; Roubik, Sakai & Karim, 2005). In addition, I have undertaken a study of the pollination ecology of *G. gardneri* Hook.f. & Thomson and have made more casual observations of floral visitors to *G. thwaitesii* Hook.f. & Thomson (R. M. K. Saunders, unpubl. data).

*Goniothalamus* flowers are hermaphroditic, with two whorls of three petals. The outer petals are generally larger than the inner (rarely subequal) and the inner petals are apically connivent to form a mitri-form dome over the reproductive organs. Small basal apertures between the inner petals allow the entry of pollinators, although access is controlled by the movements of the outer petals that block the apertures most of the time. This led to erroneous assumptions of cleistogamy in the early literature (e.g. Burck, 1890, 1906).

Studies have revealed that *Goniothalamus* spp. are pollinated by small curculionid and/or nitidulid beetles. The flowers are markedly protogynous, with a 2-day floral rhythm: the flowers of *G. gardneri*, for example, emit a strong fruity scent late in the afternoon of the first day, coincident with the secretion of stigmatic exudate (indicative of stigmatic receptivity) (R. M. K. Saunders, unpubl. data). Movement of the outer petals during this phase enables the entry of pollinators, although the beetles are subsequently prevented from leaving because of further movement of the outer petals, closing the apertures between the inner petals. Stigmatic receptivity ceases the following morning, accompanied by a dissipation of the floral scent. Scent production begins again towards the end of the second day, as the apertures between the inner petals are again opened. The second cohort of beetles are again trapped within the flower, but are released on the morning of the third day, as the petals abscise. Theca dehiscence occurs prior to petal abscission, ensuring that the departing beetles are dusted with pollen. Although the floral phenology and pollinator activities indicate that *G. gardneri* is crepuscular/nocturnal, other reports suggest that some *Goniothalamus* species show diurnal activity (e.g. *G. australis*: Silberbauer-Gottsberger *et al.*, 2003).

The beetles are clearly attracted to the flowers by the fruity scent. Although there was no evidence of petal consumption, the beetles may feed on the stigmatic exudate. The beetles were observed copulating within the floral chambers of *G. gardneri*, although there was no evidence of elevated internal temperatures (R. M. K. Saunders, unpubl. data); thermogen-

esis was similarly absent from *G. australis* flowers (Silberbauer-Gottsberger *et al.*, 2003).

Some *Goniothalamus* spp. (e.g. *G. fasciculatus* Boerl. and *G. ridleyi* King) produce flowers that are restricted towards the base of the trunk, generally at soil level. Ridley (1910) reported that *G. ridleyi* has a close association with ants: the ants form nests and accumulate soil over the fascicles of flowers while the flowers are still in bud and later feed off the stigmatic exudate. The flowers subsequently develop into fruits despite the fact that the ants completely cover the flowers, preventing access by other potential pollinators. Ridley (1910) consequently concluded that the ants were acting as pollinators, although it has not been demonstrated whether fertilization is cleistogamous. Ants are generally inefficient pollinators (Jolivet, 1996: 57), however, and it is likely that fertilization is cleistogamous, autogamous or, at best, geitonogamous. The evolution of this form of cauliflory is more likely to be an adaptation to enhance seed dispersal by animals that inhabit the forest floor, rather than an adaptation to a specific pollinator. Significantly, Moog *et al.* (2003) dismissed the possibility of *G. ridleyi* being myrmecophilous in a detailed survey of myrmecophytes in Peninsular Malaysia.

#### CLADE 11: ASIMINA AND DISEPALUM

*Asimina* Adans. flowers are hermaphroditic, with larger outer and smaller inner petals that do not form an enclosed pollination chamber. There are two distinct floral forms within *Asimina*: one group (consisting of *A. parviflora* Dunal and *A. triloba* Dunal) possesses small maroon flowers that emit a foetid aroma; and the other group (consisting of all other species) possesses large, white, pink or yellow flowers that emit a more pleasant fragrance (Kral, 1960; Goodrich & Raguso, 2009). These differences clearly represent different pollination syndromes: observations of floral visitors confirm that the foetid-smelling species are visited by small flies and/or small beetles (Willson & Schemske, 1980; Norman *et al.*, 1992; Rogstad, 1993), whereas the fragrant species are typically visited by large beetles (Norman & Clayton, 1986; Norman *et al.*, 1992) or rarely by flies (Uphof, 1933; Norman *et al.*, 1992).

All *Asimina* spp. examined are protogynous, although unlike most protogynous Annonaceae the floral rhythm is much longer, ranging from 3 to 12 days depending on species (Kral, 1960; Willson & Schemske, 1980; Norman & Clayton, 1986; Norman *et al.*, 1992; Rogstad, 1993). The degree to which the pistillate and staminate phases are temporally separated or overlap appears to vary both within and between species. In *A. obovata* Nash, for example, some flowers were observed to undergo a 1-day non-

receptive interim phase between the end of the pistillate phase and the start of the staminate phase, whereas other flowers showed some overlap (Norman & Clayton, 1986). The pistillate and staminate phases were similarly observed to overlap occasionally in *A. parviflora* (Norman *et al.*, 1992).

The fragrant-scented species have received less attention than the foetid-smelling species. Norman & Clayton (1986) investigated the reproductive biology of two fragrant species, *A. obovata* and *A. pygmaea* Dunal. The inner petals of these species have a grooved, saccate region adaxially with corrugations; this was referred to as a 'nectary' by Kral (1960), although Norman & Clayton (1986) observed that the large beetles that visit the flowers consume this tissue as well as pollen. The petal food tissue was shown to be high in carbohydrates, with moderate levels of lipids and proteins (Norman & Clayton, 1986). The beetles (belonging to Scarabaeidae and Cerambycidae) were diurnal and the flowers were correspondingly sexually receptive during the day. There was no evidence of the beetles copulating in the flowers, nor of the flowers being used as brood sites. Similar results have also been undertaken with *A. angustifolia* A.Gray, showing pollination by large scarab beetles and, to a lesser extent, small nitidulid beetles (Winnett-Murray, 1980). Controlled pollination experiments (Norman & Clayton, 1986) showed that *A. obovata* and *A. pygmaea* possess a xenogamous breeding system, with 4% and 0% fruit set, respectively, after artificial self-pollination.

The foetid-smelling species have received greater attention, with detailed studies of *A. triloba* (Willson & Schemske, 1980; Rogstad, 1993) and *A. parviflora* (Norman *et al.*, 1992). The latter study showed that the main floral visitors were *Drosophila* spp. (Diptera), although pollen was never observed adhering to their bodies; in contrast, pollen was observed attached to calliphorid flies and nitidulid beetles, despite these being less frequent visitors. The floral odour was described as 'yeasty'. Recent analyses of the floral odour (Goodrich *et al.*, 2006; Goodrich & Raguso, 2009) have identified various fermentation volatiles that the authors believe may act as beetle and fly attractants.

Although *Deeringothamnus* Small was not included in the phylogenetic analysis by Couvreur *et al.* (2011), it is recognized as being closely allied to *Asimina* (Kral, 1960); *Deeringothamnus* spp. are furthermore known to hybridize with *Asimina* (Norman, 2003). *Deeringothamnus* flowers are hermaphroditic and lack an enclosed pollination chamber (Kral, 1960). There is no evidence of specialized petal tissue for feeding floral visitors. Both species are protogynous over several days, although generally with an overlap between the pistillate and staminate phases

(Norman, 2003). Floral visitors were scarce, but included flies, tumbling beetles and thrips (Norman, 2003). The breeding system in *Deeringothamnus* appears to be facultatively xenogamous with a capacity for autogamy attributable to incomplete protogyny.

*Disepalum* flowers are hermaphroditic and are often large. In the larger-flowered species, the petals are free and imbricate, whereas in the smaller-flowered species, the petals are partially connate; in all cases, an enclosed pollination chamber is absent (Johnson, 1989). There is no published information on reproductive biology.

#### CLADE 12: *ANNONA*

*Annona* is very diverse and, as would be expected for a genus that includes so many species of commercial importance, a considerable body of knowledge on pollination ecology and breeding systems has accumulated. A distinction is made here between six main clades within the genus (labelled 1–6 in Fig. 1) for which data on reproductive biology are available.

Data on reproductive biology are only available for one species in the 'Annona 1' clade (Webber, 1981b). *Annona sericea* Dunal flowers are protogynous with a temporal separation between the shedding of the stigmas at the end of the pistillate phase and the initiation of anther dehiscence at the start of the staminate phase. These phases are nocturnal and correlated with thermogenesis of up to 6 °C above ambient levels. The flowers are visited by small chrysomelid beetles, which feed on the internal parts of the perianth and mate inside the flowers, although sciarid flies were also reported as secondary pollinators.

'Annona 2' is represented by *A. cornifolia* A.St.-Hil., for which information on reproductive biology is available (Gottsberger & Silberbauer-Gottsberger, 1988; Gottsberger, 1989a, b, 1999). The inner petals are apically connivent to form a pollination chamber and the flowers are protogynous over 2–3 days (Gottsberger, 1989a) with nocturnal receptivity. The floral visitors are large nocturnal scarab beetles (Scarabaeidae), which are attracted to the flowers by a fruity scent and rewarded by food in the form of petal tissue and pollen (and possibly also stigmatic exudate). Floral thermogenesis was evident and the beetles were observed mating within the floral chamber, although it is unclear whether they use the flowers as a brood site.

The 'Annona 3' clade includes species that were formerly classified in the genus *Rollinia*, which has recently been shown to be nested in *Annona* (Rainer, 2007). The species within this clade have long been recognized as specialized derivatives of larger-

flowered *Annona* spp. (e.g. Gottsberger, 1989b), differing in the possession of extended outer petal 'wings'. The flowers are hermaphroditic, with connivent inner and outer petals, forming a pollination chamber. The reproductive biologies of several species have been investigated, including *A. exsucca* Dunal (Webber, 1981a, 1992, as *R. exsucca* A.DC.), *A. neoinsignis* (Jürgens *et al.*, 2000, as *R. insignis* R.E.Fr.), and *A. mucosa* Jacq. (Falcão *et al.*, 1981; Webber, 1981a, 1992; Murray & Johnson, 1987; Gottsberger, 1989b; as *R. mucosa* Jacq. and *R. jimenezii* Saff.). All these species are reported to be protogynous, with a 2-day receptive cycle. The stigmas are shed before anther dehiscence in *A. mucosa* to prevent autogamy (Falcão *et al.*, 1981; Webber, 1981a, 1992), whereas in *A. exsucca* there appears to be some overlap between the pistillate and staminate phases (Webber, 1981a, 1992). The possibility of geitonogamy is reduced by synchronous dichogamy in *A. mucosa* (Murray & Johnson, 1987), in which only a small proportion of trees in a population bear pistillate- and staminate-phase flowers concurrently. All species studied are visited by small diurnal or crepuscular beetles in Chrysomelidae, Nitidulidae and/or Staphylinidae (Falcão *et al.*, 1981; Webber, 1981a, 1992; Murray & Johnson, 1987; Jürgens *et al.*, 2000). The beetles are attracted to the flowers by a yeasty or (alcoholic) fruity scent and are rewarded with pollen as food. The beetles were never observed mating within the pollination chamber. Tests for floral thermogenesis were only conducted with *A. neoinsignis* (Jürgens *et al.*, 2000), with negative results.

'Annona 4' is represented by the commercially important species, *A. cherimola* Miller and *A. squamosa* L. Information is available on the reproductive biology of both species and the interspecific hybrid (e.g. Venkataratnam, 1959; Gazit, Galon & Podoler, 1982; George *et al.*, 1989; Nagel, Peña & Habeck, 1989; Nadel & Peña, 1994; Blanche & Cunningham, 2005), although based on cultivated orchards outside the natural range of the species. The flowers of both species are protogynous, with a 2-day diurnal rhythm. The floral visitors were predominantly small nitidulid beetles; although the plants were cultivated as exotics, it seems likely that similar beetles pollinate natural populations.

The 'Annona 5' clade comprises two species, *A. glabra* L and *A. senegalensis* Pers.; aspects of the reproductive biology of both these species have been studied (Venkataratnam, 1959; Derooin, 1988a, 1989; Gottsberger, 1989b, 1999). The flowers have apically convergent inner petals, forming a pollination chamber. The floral visitors were small diurnal chrysomelid and curculionid beetles and the flowers show a corresponding diurnal pattern of receptivity. The flowers are protogynous over a 2-day cycle, although

*A. glabra* is capable of autogamous self-pollination (Gottsberger, 1989b) and the pistillate and staminate phases therefore presumably overlap in at least some flowers. The beetles are attracted to the flowers by strong fruity scents, and in *A. senegalensis* at least are rewarded by pollen as food (Deroin, 1988a, 1989). Beetles were also observed mating within the pollination chambers of *A. senegalensis*, although there was no evidence that the flower is used as a brood site.

The 'Annona 6' clade is interpreted here as including the following species for which data on reproductive biology are available: *A. aurantiaca* Barb.Rodr., *A. coriacea* Mart., *A. crassiflora* Mart., *A. montana* Macfad. & R.E.Fr., *A. muricata* L. and *A. warmingiana* Mello-Silva & Pirani (= *A. pygmaea* W.Bartram) (Venkataratnam, 1959; Gottsberger, 1970, 1989a, b, 1999; Webber, 1981a; Bawa *et al.*, 1985; Deroin, 1988a; Gottsberger & Silberbauer-Gottsberger, 1988; Maas-van de Kamer, 1993; Silberbauer-Gottsberger, Gottsberger & Gottsberger, 1997). All these species possess relatively large flowers with a pollination chamber formed by the imbricate petals and are visited by large scarab beetles (Scarabaeidae). The flowers are protogynous, with apparent temporal separation between the end of the pistillate phase and the start of the staminate phase (Gottsberger, 1989a), although information is unclear for some species. The floral phenological cycle typically extends over 2 days (Webber, 1981a; Deroin, 1988a; Gottsberger & Silberbauer-Gottsberger, 1988; Gottsberger, 1989a; Silberbauer-Gottsberger *et al.*, 1997), although occasionally completed within 1 day in some hybrids (Silberbauer-Gottsberger *et al.*, 1997). Reproductive activity of the flowers and the activities of the beetles is consistently nocturnal. The beetles are attracted by a strong aroma of rotten fruit and feed off the petals, stigmatic exudate and pollen. The flowers are strongly thermogenic, with temperatures peaking, for example, at c. 34 °C (c. 14 °C above ambient levels) in *A. coriacea* (Gottsberger & Silberbauer-Gottsberger, 1988; Gottsberger, 1989a). Beetles have been observed copulating within the flowers, although there is again no evidence that they use the flowers as brood sites.

CLADE 13: *MONODORA*, *ISOLONA*, *ASTERANTHE*,  
*HEXALOBUS* AND *UVARIASTRUM*

*Monodora* Dunal is remarkable for its large, showy flowers. The outer petals are generally reddish, up to 9 cm long in some species, with a convoluted margin (Couvreur, 2009). The inner petals are generally white with red or brown spots; they are slightly smaller than the outer ones and are apically connivent, forming a large enclosed pollination chamber

with three lateral apertures at the base of the mitri-form dome. The base of the petals is slightly translucent and appears to act as a 'light window' (Gottsberger, Meinke & Porembski, 2011). As with most Annonaceae, the flowers are hermaphroditic.

The reproductive biology of only two species, *M. myristica* Dunal (Lamoureux, 1975) and *M. tenuifolia* Benth. (Gottsberger *et al.*, 2011), have been studied in detail. Although *M. myristica* is indigenous to tropical Africa, Lamoureux's study was conducted in the Bogor Botanical Garden (Kebun Raya), Indonesia; the study therefore focused on aspects of floral structure, development and phenology, and did not involve any assessment of pollination ecology. Gottsberger (1985; unpubl. data, cited in Keßler, 1993) has reported, however, that *M. myristica* is sapromyophilous. Lamoureux (1975) showed that *M. myristica* is strongly protogynous, with the receptive phases occurring over an extended period: the pistillate phase lasts for 7–8 days, with stigmatic abscission before the staminate phase (4–5 days) begins. Attempts by Lamoureux (1975) to cross-pollinate trees artificially in Kebun Raya were unsuccessful, although this is probably because the trees were part of a single clone; this suggests that a self-incompatibility mechanism operates.

*Monodora tenuifolia* was also revealed to be protogynous, but with a much shorter receptive period, with the pistillate and staminate phases extending over only 2 days and 1 day, respectively (Gottsberger *et al.*, 2011). The flowers emitted a strong scent, which although sweet also exhibited 'musty/mouldy' and 'cabbage-like' elements. Although effective pollinators were not identified unequivocally, the flowers were observed to be visited during the day by small and medium-sized flies. There was no evidence of thermogenesis.

*Isolona* Engl. flowers are hermaphroditic and are unusual as all six petals are basally connate, forming a single whorl; although an enclosed pollination chamber does not form, the petals are inwardly curved to form a loose chamber (Couvreur, 2009). The petals are yellowish or reddish and are often darker towards the inside of the flower. Relatively little is known of the reproductive biology, although the flowers of *I. campanulata* Engl. & Diels have been shown to be protogynous, with the reproductive phases extending over a 2-day (or possibly 3-day) period, with diurnal receptivity (Deroin, 1988a; Gottsberger *et al.*, 2011). The flowers emit a fruit-like, slightly fermented odour, and are visited by small unidentified beetles (Gottsberger *et al.*, 2011).

There are no published reports on the reproductive biology of *Asteranthe* Engl. & Diels, *Hexalobus* A.DC. or *Uvariastrum* Engl. & Diels. The flowers of *Asteranthe* and *Hexalobus* are hermaphroditic and

have a corolla that is basally connate (van Heusden, 1992; Botermans *et al.*, 2011); in contrast, those of *Uvariastrum* are either hermaphroditic or unisexual and have free petals (van Heusden, 1992).

CLADE 14: *UVARIODENDRON*, *UVARIOPSIS*,  
*MISCHOGYNE* AND *MONOCYCLANTHUS*

*Uvariadendron* (Engl. & Diels) R.E.Fr. flowers are robust, with a loose floral chamber formed by the inwardly curving inner petals (Verdcourt, 1969) or sometimes, as in *U. calophyllum* R.E.Fr., apically connivent inner petals (Gottsberger *et al.*, 2011). The pollination ecology of two species, *U. connivens* (Benth.) R.E.Fr. and *U. calophyllum*, have been investigated in West Africa (Gottsberger *et al.*, 2011). Both species are hermaphroditic and are markedly protogynous over a 2-day period, with the carpels receptive from late afternoon on day 1 until the following morning, and stamens dehiscing from the afternoon of day 2 until the morning of day 3. These receptive periods were associated with the emission of a strong fruity scent, reported to be slightly unpleasant in *U. connivens* but sweet in *U. calophyllum*. Several different species of floral visitors were recorded, although the most effective pollinators of both *Uvariastrum* spp. were determined to be large scarab beetles, which fed on petals, pollen and stigmatic exudate and were often observed mating. Smaller curculionid, staphylinid and nitidulid beetles were also observed to visit the flowers, feeding on petals and pollen, but were regarded as secondary pollinators as pollen did not adhere to their bodies as effectively.

*Uvariopsis* Engl. ex Engl. & Diels flowers (including *Dennettia* Baker f.) are unusual in having a single whorl of petals resulting from compression of separate ancestral whorls (Kenfack *et al.*, 2003; Saunders, 2010). The flowers are unisexual and are typically cauliflorous, with the pistillate flowers borne lower on the trunk than the staminate flowers (Kenfack *et al.*, 2003); a similar separation of pistillate and staminate flowers is observed in *Stelechocarpus* Hook.f. & Thomson in subfamily Malmeoideae (van Heusden, 1995). The pollination ecology of two species of *Uvariopsis*, *U. bakeriana* (Hutch. & Dalziel) Robyns & Ghesq. and *U. congolana* (De Wild.) R.E.Fr., have been studied in West Africa (Gottsberger *et al.*, 2011). The petals of *U. bakeriana* are elongated, violet-brown and highly tuberculate on the adaxial surface, although the base of the corolla forms a translucent 'light window'; in contrast, the petals of *U. congolana* are considerably shorter, but are also adaxially tuberculate. The flowers of both sexes are receptive for approximately 4 days in both species. *Uvariopsis bakeriana* flowers emit a faint, slightly spicy or nutmeg-

like scent, whereas those of *U. congolana* are more pungent, with a mouldy or musty smell, becoming putrid in older flowers. Both species were predominantly visited by flies: visitors to *U. bakeriana* flowers included medium-sized flies, small gnats (Nematocera) and, rarely, drosophilid-like flies, whereas visitors to *U. congolana* included drosophilid-like and sarcophagid flies and some beetles. There was no evidence of thermogenesis in *U. congolana*.

There are no published reports on the reproductive biology of either *Mischogyne* Exell or *Monocyclanthus* Keay. Both genera have small hermaphroditic flowers with free petals (yellow, 14–16 mm long in *Monocyclanthus*, and white, 7–25 mm long in *Mischogyne*) that do not form a pollination chamber (Exell, 1932; Keay, 1952); these characteristics appear typical of small-beetle pollination. The flowers of *Mischogyne michelioides* Exell are unusual as the carpels are borne on a long gynophore (Exell, 1932), although the function of this is unclear.

CLADE 15: *SANRAFAELIA* AND *OPHRYPETALUM*

Information is lacking on the reproductive biology of the two monotypic genera *Sanrafaelia* Verdc. and *Ophrypetalum* Diels. Both taxa possess hermaphroditic flowers. The corolla of *Sanrafaelia ruffonammari* Verdc. is cup-shaped, with petals that are basally fused to form a short tube, c. 3 mm long (Verdcourt, 1996). *Ophrypetalum odoratum* Diels has free petals with a dense brush of 'hair-like appendages' (Verdcourt, 1960); these hairs are in contact with the stamens and presumably perform a role in pollination, although the precise function is unknown.

CLADE 16: *DIELSIOTHAMNUS*

There is no information available on the reproductive biology of the monotypic genus *Dielsiothamnus* R.E.Fr. The flowers are small, with free brownish-yellow petals (up to 12 mm long) forming an open flower (Robson, 1960); these features are characteristic of small-beetle pollinated flowers.

CLADE 17: *FISSISTIGMA* AND *MITRELLA*

*Fissistigma* Griff. flowers are hermaphroditic, with yellowish or purplish-pink petals. One of the most important taxonomic differences between *Fissistigma* and its close ally *Mitrella* Miq. is that the flowers of the latter genus have inner petals that are apically convergent, forming a mitriform dome (van Heusden, 1992). Although this feature is generally absent from *Fissistigma*, it is apparent in some species (van Heusden, 1992).

Reports of floral visitors exist for three *Fissistigma* species, *F. kingii* (Boerl.) Burkill, *F. latifolium* Merr. and *F. paniculatum* Merr. (Momose *et al.*, 1998; Sakai *et al.*, 1999; Momose, 2005; Roubik *et al.*, 2005): all these species are visited by small beetles, which in the case of *F. paniculatum*, were identified as belonging to Curculionidae. The most detailed studies of pollination ecology are those of *F. paniculatum* (Momose *et al.*, 1998; Momose, 2005; Roubik *et al.*, 2005), although the great taxonomic breadth of these studies inevitably limited the depth of the research. This species possesses a pollination chamber and was shown to be protogynous, although the length of the reproductive cycle was not reported. The curculionid visitors were observed to feed by licking the stigmatic exudate.

*Mitrella* has hermaphroditic flowers and, as noted above, the inner petals are apically convergent, forming a mitriform dome; the flowers are considerably smaller than those of *Fissistigma*, and the mitriform dome correspondingly smaller. There are no published studies of the pollination ecology or breeding system, although interpretation of floral structure would suggest pollination by small beetles.

#### CLADE 18: *UVARIA*

The generic delimitation of *Uvaria* has been significantly expanded in recent years as a result of molecular phylogenetic research, and the genus now includes species formerly classified in *Anomianthus*, *Balonga*, *Cyathostemma*, *Dasoclema*, *Ellipeia*, *Ellipeiopsis*, *Rauwenhoffia* and at least the Australian species of *Melodorum* Lour. (Zhou *et al.*, 2009, 2010). These genera were previously distinguished based on floral differences such as receptacle shape, petal shape, the formation of floral chambers and the presence of glandular tissue on the petals; these features are now regarded as little more than specialized forms (often autapomorphic) nested within *Uvaria*.

*Uvaria* flowers are variable in size but are often relatively large. The petals are imbricate and either open fully at maturity or remain partially closed to form an incomplete pollination chamber, depending on species: those formerly classified in *Cyathostemma*, for example, have a bowl-shaped corolla (Type V chamber, *sensu* Saunders, 2010), whereas others such as *Uvaria semecarpifolia* Hook.f. & Thomson have apically imbricate inner petals (Type VI chamber, *sensu* Saunders, 2010). Petal colour is variable, with some correlation with geographical origin: species from Africa typically have cream or yellow petals, whereas those from Asia often have pink, red or purple petals (van Heusden, 1992).

Three different pollination systems (small beetle, cockroach and bee pollination) have been identified in

*Uvaria*. This diversity is accommodated in the present study by distinguishing between four clades within *Uvaria* (labelled 1–4 in Fig. 1) for which data on reproductive biology are available. Small-beetle pollination is the ancestral and most widespread pollination system in the genus, occurring in all four of the main clades indicated in Figure 1; in contrast, cockroach and bee pollination are restricted to the ‘*Uvaria* 4’ clade.

Examples of small-beetle pollination in *Uvaria* are relatively uniform throughout the four clades. The ‘*Uvaria* 1’ clade consists of African and Madagascan species, for which the reproductive biology is comparatively poorly known. The only species studied is *U. ovata* A.DC., which has protogynous flowers with a 3-day reproductive cycle (Deroin, 1988a); although pollinators were not observed, the floral morphology suggests that they are likely to be small beetles. Momose (2005; Roubik *et al.*, 2005) similarly reported that an undescribed new species of ‘*Anomianthus*’ (i.e. related to *Uvaria dulcis* Dunal, a member of the ‘*Uvaria* 2’ clade) was protogynous and was visited by small curculionid beetles.

More detailed studies of small-beetle pollination exist for species in the ‘*Uvaria* 3’ clade, including *U. semecarpifolia* (Attanayake, 2010) and an unidentified Australian species of ‘*Melodorum*’ (Silberbauer-Gottsberger *et al.*, 2003), which presumably represents a species of *Uvaria* (Zhou *et al.*, 2010). The flowers of *U. semecarpifolia* are protogynous over a 3-day period, with a non-receptive interim phase separating the pistillate and staminate phases (Attanayake, 2010). The pollinators were diurnally active nitidulid beetles, and there was evidence of fruit and/or beetle pheromone mimicry in the floral scents, with sugary stigmatic exudate and pollen as food rewards. The flowers of the ‘*Melodorum*’ species were protogynous over a 2-day period, and were visited by small diurnal curculionid beetles that were attracted to the flowers by an ‘acetone-like’ scent (Silberbauer-Gottsberger *et al.*, 2003); the beetles were observed to mate within the floral chamber. Tests for floral thermogenesis were negative.

Species in the ‘*Uvaria* 4’ clade show a broader range of pollination systems. Some, such as *U. cordata* Wall. (C. C. Pang & R. M. K. Saunders, unpubl. data), are protogynous and pollinated by crepuscular and nocturnal nitidulid beetles, and are therefore similar to the other species described above. The ‘*Uvaria* 4’ clade also includes species that were formerly classified under the generic name *Cyathostemma*, which have flowers that are much smaller than other members of the genus, with inwardly curving petals that do not expand or reflex at maturity (Utteridge, 2000). Studies of *U. aff. clementis* (Merr.) Attanayake *et al.* (Momose *et al.*, 1998; Momose, 2005; Roubik *et al.*,

2005; as '*Cyathostemma* aff. *hookeri* King') have shown that the flowers were visited by small curculionid beetles, which were observed feeding off stigmatic exudate. Momose *et al.* (1998) noted that the flowers were protogynous, although no information was given on the duration of receptivity. There is some doubt about the identity of the species studied by Momose *et al.* (1998) as they described the flowers as purple, whereas Utteridge (2000) described '*Cyathostemma hookeri*' flowers as yellow.

The '*Uvaria* 4' clade also includes a species that was reported by Nagamitsu & Inoue (1997; see also Roubik *et al.*, 2005) to be pollinated by cockroaches (Blattellidae). The species was identified as *U. elmeri* Merr. by Nagamitsu & Inoue (1997), but as '*U. aff. elmeri*' by Roubik *et al.* (2005). The flowers were shown to be protogynous over a 3-day period, with nocturnal receptivity, during which period the flowers emitted a scent of rotting wood and mushrooms. This scent attracted cockroaches, which fed off stigmatic exudate and pollen. Nagamitsu & Inoue (1997) also observed pollination by drosophilid flies, although it was estimated that cockroaches were 8.9 times more effective at pollen transfer.

Bee pollination has been observed in *U. concava* from the '*Uvaria* 4' clade (Silberbauer-Gottsberger *et al.*, 2003). The flowers were bright red, and were also protogynous over a 3-day period, although apparently with some overlap between stigmatic receptivity and anther dehiscence. The bee pollinators (belonging to Meliponinae) collected pollen and stigmatic exudate.

#### CLADE 19: *SPHAEROCORYNE* AND *TOUSSAINTIA*

There is no published information on the reproductive biology of either *Sphaerocoryne* Scheff. ex Ridl. or *Toussaintia* Boutique. *Sphaerocoryne* flowers are cream-coloured or yellow, with six free petals in two whorls, with the outer whorl longer than the inner (van Heusden, 1992). *Toussaintia* flowers are white (sometimes red towards the base of the adaxial surface of the petals), with six to 12 free petals forming an open flower (van Heusden, 1992; Deroin & Luke, 2005). An unusual feature of *Toussaintia* flowers is the formation of an elongated androgynophore (Deroin & Luke, 2005).

#### CLADE 20: *DESMOS*, *DASYMASCHALON*, *FRIESODIELSIA* AND *MONANTHOTAXIS*

*Desmos* Lour. flowers are hermaphroditic, with generally yellowish petals that are basally tightly constricted around the reproductive organs. A study of *D. chinensis* Lour. (C. C. Pang & R. M. K. Saunders, unpubl. data) has revealed that the flowers are pro-

togynous over a 2-day period, with the pistillate phase (c. 18 h) beginning at dawn, followed by a non-receptive interim phase (c. 6 h) prior to the onset of the staminate phase (c. 3 h) in the early morning of the following day. Floral receptivity is associated with the emission of a strong fruity scent, although there was no evidence of floral thermogenesis. The flowers were visited by small nitidulid beetles. There was evidence of inter- and intra-individual synchrony of flowering, with flowering individuals generally bearing either pistillate-phase or staminate-phase flowers, but not both concurrently, and with two cohorts in the population with flowers in opposing receptive stages. Controlled pollination experiments revealed that *D. chinensis* is predominantly xenogamous, with autogamy avoided by protogyny and geitonogamy largely prevented by floral synchrony. Kojima & Morimoto (1995) have furthermore reported that a small curculionid beetle was associated with flowers of an unidentified *Desmos* species from Borneo.

*Dasymaschalon* Dalla Torre & Harms is unusual in possessing only three petals per flower; these petals, which are homologous to the outer petals of other Annonaceae, are apically connivent to form a pollination chamber (Wang, Chalermglin & Saunders, 2009; Saunders, 2010). Many species superficially appear to be cleistogamous, leading some authors (e.g. Keßler, 1993) to assume that they are autogamous. A study of *D. trichophorum* Merr. (C. C. Pang & R. M. K. Saunders, unpubl. data) has demonstrated protogyny, with the pistillate phase (c. 8 h) extending from dawn until noon, followed by a non-receptive phase (c. 5 h), and with anther dehiscence beginning at approximately 17:00 h. The staminate phase continues overnight until dawn on the second day, although the pollinators are trapped inside the flower by the closure before nightfall of the apertures between the petals. The flowers are pollinated by small curculionid beetles, which were observed copulating within the floral chambers and laying eggs in holes drilled into the fleshy petals with their mouthparts. Inter- and intra-individual floral synchrony was observed, similar to that described above for *Desmos chinensis*.

*Friesodielsia* Steenis is not monophyletic (e.g. Wang, 2009; Couvreur *et al.*, 2011), although all constituent clades are included in clade 20. The flowers are hermaphroditic, with a pollination chamber formed in some species by the apically convergent inner petals. The pollination ecologies of two species from Borneo, *F. glauca* (Hook.f. & Thomson) Steenis and *F. filipes* (Hook.f. & Thomson) Steenis, have been studied (Momose *et al.*, 1998; Momose, 2005; Roubik *et al.*, 2005). The flowers of both species are yellow, and are visited by small curculionid and nitidulid beetles that were observed to consume stigmatic

exudate. The flowers are protogynous, although the length of the receptive period was not recorded.

There are no published reports on the reproductive biology of any species of *Monanthotaxis* Baill. The inner and outer petals are subequal in size; in *M. whytei* (Stapf) Verdc., at least, the inner petals are apically convergent to form a loose pollination chamber (Ronse Decraene & Smets, 1990, erroneously as '*Popowia whitei*'). According to van Heusden (1992), some species bear hermaphroditic flowers, whereas others bear pistillate flowers (although it is unclear whether such species are dioecious or gynodioecious).

#### GENERA IN SUBFAMILY MALMEOIDEAE

Resolution of phylogenetic relationships within subfamily Malmeoideae is inadequate for interpreting changes in reproductive biology characters. Flowers of most of the genera studied are visited exclusively or predominantly by small beetles, although other pollinator guilds are also important, including large beetles (*Malmea* R.E.Fr.: Gottsberger, 1999; *Mosannonna* Chatrou: Schatz, 1987, 1990; Murray, 1993; Chatrou & Listabarth, 1998), thrips (*Bocageopsis* R.E.Fr.: Webber & Gottsberger, 1995; Silberbauer-Gottsberger *et al.*, 2003; *Oxandra* A.Rich.: Webber & Gottsberger, 1995; *Popowia* A.Rich.: Momose *et al.*, 1998a, b; Roubik *et al.*, 2005), bees (*Sapranthus* Seem.: Olesen, 1992; *Unonopsis* R.E.Fr.: Carvalho & Webber, 2000; Silberbauer-Gottsberger *et al.*, 2003; Teichert, 2007; Teichert *et al.*, 2009) and flies (*Pseuduvaria* Miq.: Morawetz, 1988; Silberbauer-Gottsberger *et al.*, 2003; Su *et al.*, 2005; Su & Saunders, 2006).

#### EVIDENCE FOR DISTINCT POLLINATION SYNDROMES

Annonaceae flowers are visited by a taxonomically diverse range of insects: predominantly beetles (Coleoptera), but also thrips (Thysanoptera), flies (Diptera) and, rarely, bees (Hymenoptera) and cockroaches (Dictyoptera). Species are typically pollinated by only one of these groups, although there are several examples of species that are pollinated by more than one group: *Duguetia flagellaris* Huber (Küchmeister *et al.*, 1998), *Oxandra euneura* Diels (Webber & Gottsberger, 1995) and *Xylopia aromatica* Baill. (Gottsberger, 1970; Silberbauer-Gottsberger *et al.*, 2003), for example, are visited by thrips and small beetles; *Asimina parviflora* (Norman *et al.*, 1992), *A. pygmaea* (Uphof, 1933; Norman & Clayton, 1986; Norman *et al.*, 1992) and *A. triloba* (Willson & Schemske, 1980; Johnson & Willson, cited in Norman *et al.*, 1992) are visited by flies and beetles; and *Sapranthus palanga* R.E.Fr. (Olesen, 1992) and

*Unonopsis guatterioides* (A.DC.) R.E.Fr. (Carvalho & Webber, 2000) are visited by bees and small beetles. The rarity of these examples, however, provides convincing evidence that the Annonaceae exhibit specialized pollination syndromes, in which a specific range of floral attributes co-occur repeatedly in phylogenetically distinct lineages. It should be noted, however, that few studies on Annonaceae pollination prove that the floral visitors actually result in cross-pollination: in order to demonstrate this unequivocally it is necessary to show that the floral visitors carry pollen, and to observe their movement between receptive staminate-phase and pistillate-phase flowers (e.g. Ratnayake *et al.*, 2006a). It is also significant that few studies provide corroborating evidence of xenogamy by using either field-based controlled pollination experiments or laboratory-based genetic analyses (e.g. Ratnayake *et al.*, 2006b). Few studies are furthermore based on multiple populations that are temporally and/or geographically separated, and it is therefore possible that different groups of floral visitors may result in pollination at different times or in different locations (Herrera, 2005).

Despite these caveats, the available data strongly suggest that distinct pollination syndromes occur in Annonaceae. There is only a limited level of specificity between the plant species and the pollinator, however. Almost all studies have shown that species of Annonaceae are pollinated by more than one species within a pollinator guild (often belonging to phylogenetically distant families), even if only one species is observed at any one time. It is also common for a single pollinating species to visit more than one species of Annonaceae: *Carpophilus plagiaticornis* (Coleoptera: Nitidulidae), the primary pollinator of *Polyalthia coffeoides* (Thwaites) Hook.f. & Thomson (Ratnayake *et al.*, 2006a), for example, is also the primary pollinator of *Goniothalamus gardneri* Hook.f. & Thomson (R. M. K. Saunders, pers. observ.). There is no evidence of co-evolution: evolutionary changes in floral structure are unlikely to have been mirrored by adaptations in the beetle pollinators.

#### POLLINATOR GUILDS AND ASSOCIATED POLLINATION SYNDROMES

##### BETLES (COLEOPTERA)

The small beetle pollinators of Annonaceae belong to the families Curculionidae, Nitidulidae and Staphylinidae (and, to a lesser extent, smaller members of the Chrysomelidae). Almost all Curculionidae (weevils) are associated with woody plants, feeding on a broad range of plant organs, including flowers, fruits and seeds. Nitidulidae (sap beetles) are also phytophagous, feeding on decaying plant material,



overripe fruit, sap and pollen. These two families are considered significant pests of crops and stored grain. Staphylinidae are diverse and occupy a correspondingly diverse range of habitats. Phytophagy is relatively less common than other feeding habits, although it is known from several subfamilies (Thayer, 2005). Although feeding on fruits and petals is reported, most phytophagous staphylinids consume pollen.

The large beetle pollinators of Annonaceae primarily belong to subfamilies Melolonthinae and Dynastinae of Scarabaeidae. Although the larvae feed on roots and tubers, the adults of some species (clearly including those implicated in pollination) feed on flowers (Scholtz & Grebennikov, 2005). The large size of the beetles necessitates large and robust flowers, with thick, fleshy petals that provide a food source.

Beetles typically depend on olfactory rather than visual cues for locating flowers. Floral scents in Annonaceae are often described as fruit-like and it is probable that they mimic the natural food of the beetles. In some species, the floral scents have also been shown to contain volatiles that mimic beetle sex pheromones, with possible synergism between the fruit-mimicking and pheromone-mimicking scents (e.g. Ratnayake *et al.*, 2007).

It is also possible that the beetles are attracted by infrared radiation (heat) generated within the flower. Recent research has shown that some beetles (including Curculionidae: Hausmann, Samietz & Dorn, 2004) have infrared (IR) sensors known as IR sensilla or IR pit organs, which can detect infrared radiation (Schmitz, Bleckmann & Murtz, 1997; Hammer *et al.*, 2001). Another possible role of floral thermogenesis is as a heat reward (Seymour, White & Gibernau, 2003). By providing beetles with this energy reward, the flower allows them to conserve considerable levels of energy required for feeding, mating and initiating flight. The temperatures maintained by thermogenic flowers are typically in the range favoured by active beetles (Seymour & Schultze-Motel, 1997); the flowers therefore assist with the maintenance of the body temperature of the beetles and stimulate their reproductive behaviour, feeding and digestion (Thien, Azuma & Kawano, 2000). Beetles also significantly require high thoracic temperatures (often > 30 °C) to initiate flight (Seymour & Schultze-Motel, 1997; Seymour *et al.*, 2003). It can also be speculated that floral thermogenesis is associated with increased volatilization of scent compounds, although there is no empirical support for this suggestion.

Beetle-pollinated flowers of Annonaceae typically possess a partially enclosed pollination chamber (Saunders, 2010); the beetles gain access to the floral chamber through an apical aperture or three lateral apertures (depending on the structure of the peri-

anth). The flowers of some of the species that are pollinated by small beetles open fully during the reproductively inactive phase between the pistillate and staminate phases (e.g. *Polyalthia* spp.: Ratnayake *et al.*, 2006a; *Xylopia* spp.: Ratnayake *et al.*, 2007). This encourages the departure of the beetles that had arrived at the start of the pistillate phase. Although the advantage of such a strategy is unproven, it may be that the beetles are less likely to move to other flowers after mating, and that a new cohort of unmated floral visitors would therefore be more effective in dispersing pollen.

#### THRIPS (THYSANOPTERA)

Thrips are small phytophagous insects that preferentially inhabit flowers and fruits, often causing serious damage to crops (Daly, Doyen & Purcell, 1998). Species which feed in flowers either suck the contents of pollen grains or, in larger species, ingest the pollen grain entire. The small size of individual thrips (and hence the limited number of pollen grains that could potentially be carried between flowers) is compensated for by the vast number of thrips that aggregate together.

Thrips pollination is considerably rarer in Annonaceae than beetle pollination and has only been observed in five genera: *Bocageopsis* (Webber & Gottsberger, 1995; Silberbauer-Gottsberger *et al.*, 2003), *Duguetia* (Küchmeister *et al.*, 1998), *Oxandra* (Webber & Gottsberger, 1995), *Popowia* (Momose *et al.*, 1998a, b; Roubik *et al.*, 2005) and *Xylopia* (Gottsberger, 1970; Webber, 1996, 2002; Silberbauer-Gottsberger *et al.*, 2003). Flowers that are exclusively pollinated by thrips typically have a small pollination chamber with small apertures and produce tiny pollen. Other morphological features typical of thrips-pollinated flowers are also observed in beetle-pollinated flowers, including pale coloration (white to yellow) and the presence of a pollination chamber.

#### FLIES (DIPTERA)

Despite the vast diversity of dipterans and their evident importance in pollination, there are few reports of fly pollination in Annonaceae: flower visits by flies have only been reported for *Annona* (Webber, 1981b; as secondary floral visitors only), *Asimina* (Norman *et al.*, 1992), *Monodora* (Gottsberger, 1985; Gottsberger *et al.*, 2011), *Pseuduvaria* (Morawetz, 1988; Silberbauer-Gottsberger *et al.*, 2003; Su *et al.*, 2005) and *Uvariopsis* (Gottsberger *et al.*, 2011). It should be noted, however, that Norman *et al.* (1992) did not observe any pollen attached to the common drosophilid flies that visited *Asimina* flowers (pollination resulted from visits by nitidulid beetles and rarer

calliphorid flies), and that pollen transfer between flowers was not demonstrated in any of the other studies. Discussion of fly pollination in Annonaceae is also constrained by the failure to determine which groups of flies are involved: the only exceptions to this are the studies by Webber (1981b), Nagamitsu & Inoue (1997) and Norman *et al.* (1992).

As solitary insects, flies typically undertake different activities (such as mating, oviposition and foraging for food) over the same time period (Fægri & van der Pijl, 1979). To avoid confusion of stimuli, Calliphoridae (blowflies), which lay eggs in dung and carrion, favour yellow colours in the presence of sweet scents, but brown–purple colours in the presence of foetid scents (Kugler, 1956). The latter pollination system is observed in *Asimina parviflora* (Norman *et al.*, 1992) and operates by deceit as the flies visit the flowers in order to lay eggs. Sapromyophilous flowers, furthermore, often have partially enclosed pollination chambers that require the flies to crawl in through narrow openings (Fægri & van der Pijl, 1979).

#### BEES (HYMENOPTERA)

Hymenoptera are another major group of pollinators that are under-represented in Annonaceae. Bee pollination has only been described unequivocally in two genera, *Unonopsis* (Carvalho & Webber, 2000; Silberbauer-Gottsberger *et al.*, 2003) and *Uvaria* (Silberbauer-Gottsberger *et al.*, 2003), although opportunist visits by bees have also been recorded by Olesen (1992) in *Sapranthus* and Gottsberger *et al.* (2011) in *Uvariadendron*. It is unlikely that opportunist visits by bees will successfully pollinate flowers of Annonaceae because of protogyny.

Both the bee-pollinated species recorded, *Unonopsis guatterioides* and *Uvaria concava*, lack a pollination chamber. Two main types of bees have been reported as floral visitors: both plant species were visited by meliponine bees (Apidae subfamily Meliponinae); and *U. guatterioides* was also visited by euglossine bees (Apidae subfamily Bombinae tribe Euglossini). The meliponine bees are small, stingless and highly social bees that collect pollen (Michener, 2000). They are relatively unlikely candidates as pollinators in Annonaceae because the flowers are protogynous: the bees would be unlikely to visit pistillate-phase flowers because of the absence of pollen. Significantly, however, Silberbauer-Gottsberger *et al.* (2003) observed that meliponine bees collected stigmatic exudate from flowers of *U. concava* and that there was overlap between the pistillate and staminate phases. The euglossine bees that were highlighted as the main pollinator of *U. guatterioides* are large, solitary, communal or primitively social bees. They feed on nectar, although the male bees additionally collect

fragrant compounds from the flowers using brushes of hairs on their forelegs and subsequently deposit the scent at sites to attract females (Williams, 1982).

#### COCKROACHES (DICTYOPTERA)

There is only one case of cockroach pollination recorded in Annonaceae (*Uvaria elmeri*: Nagamitsu & Inoue, 1997; Roubik *et al.*, 2005). This unusual form of pollination has already been discussed in detail in the treatment of the pollination system in clade 18. Most cockroaches are scavengers or detritus feeders, although some have been reported to use floral resources (see references cited by Nagamitsu & Inoue, 1997).

#### EVOLUTIONARY SHIFTS IN POLLINATION SYSTEM

Mapping the occurrence of different pollinator guilds (Table 1) onto a molecular phylogenetic tree (Fig. 1) enables insight into the evolution of pollination systems. Small beetles are the most common pollinators in Annonaceae and are observed in almost all main clades. This pollination system is particularly prevalent in the basal grade, in which no other system has been observed (although observations are lacking for several genera), and also occurs in the outgroup, *Eupomatia*. Small-beetle pollination can therefore be inferred as the ancestral mechanism, with all other pollination systems being derived. Within subfamily Annonoideae, large-beetle pollination appears to have evolved independently in at least five separate lineages (clade 5: *Cymbopetalum* and *Porcelia*; clade 7: *Duguetia*; clade 11: *Asimina*; clade 12: *Annona*; and clade 14: *Uvariadendron*). Optimization of pollinator guilds onto the molecular tree furthermore suggests that large-beetle pollination may have evolved more than once within *Annona*; this contradicts earlier suggestions that dynastid scarab pollination was ancestral within the genus, with reversion to small-beetle pollination in *Rollinia* and small-flowered *Annona* spp. (Gottsberger, 1989b). Similar interpretation of the other pollinator guilds suggests that thrips pollination has evolved in two lineages within subfamily Annonoideae (clade 6: *Xylophia*; and clade 7: *Duguetia*). Fly pollination has possibly evolved in three lineages within subfamily Annonoideae (clade 11: *Asimina*; clade 13: *Monodora*; and clade 14: *Uvariopsis*), although the parsimony character mapping is ambiguous, and possibly supports a single origin of fly pollination in the ancestor of clades 13–15 (Fig. 1). Bee and cockroach pollination have only evolved once each within subfamily Annonoideae, both within *Uvaria* (clade 18).

Evolutionary shifts in pollination system are likely to be facilitated or constrained to varying degrees according to the suitability of previous adaptations to the ancestral pollination system. It is unlikely that adaptations favouring pollination by small beetles (including protogyny, partially enclosed floral chambers and olfactory cues) would significantly constrain evolutionary shifts to pollination by large beetles or thrips as these pollinator guilds all have similar requirements. This may provide a partial explanation for the frequency with which these changes appear to have occurred in Annonaceae, and the frequency with which primary pollinators are supplemented by rarer, more casual pollinators belonging to a different guild (e.g. 80% of recorded floral visitors to *Xylopia aromatica* were thrips, with 20% of visits by small beetles: Gottsberger, 1970). The evolutionary change from small- to large-beetle pollination involved an overall increase in flower size, with the formation of thick fleshy petals as a food source. In contrast, the evolutionary change from small-beetle pollination to thrips pollination is associated with a reduction in flower size (or floral chamber and/or apertures) and a reduction in the size of the pollen grains.

Sapromyophilous flowers are also typically protogynous and have floral chambers (e.g. *Monodora* and *Pseuduvaria*) and could therefore easily be derived from small-beetle pollinated ancestors. This evolutionary change is associated with a change in floral scent from fruit mimicry to foetid scents, and the occurrence of dark red pigmentation (often localized). Flies do not nurse their brood, but only take food for their own consumption, and they are therefore rather irregular and unreliable pollinators (Fægri & van der Pijl, 1979). Unlike beetles, which typically remain in the flower throughout the duration of the pistillate and/or staminate phase, flies will only visit briefly. It is presumably in response to low visitation rates that the flowers of fly-pollinated species of Annonaceae have typically evolved longer receptive periods (3–12 days in *Asimina*; 11–13 days in *Monodora*). This increase in floral longevity is not observed in *Pseuduvaria*, which is also fly-pollinated [*P. froggattii* (F.Muell.) Jessup flowers are only receptive for 1 day: Silberbauer-Gottsberger *et al.* 2003]; this is presumably because the flowers are unisexual.

In marked contrast, the shift in pollination system from small beetles to bees would be less easily achieved than that to large beetles, thrips or flies. Pollen-collecting bees are unlikely to be effective pollinators of protogynous flowers as there is no reward provided in pistillate-phase flowers. Significantly, the only two well-documented cases of bee pollination in Annonaceae involve either a partial breakdown in protogyny (i.e. overlap between the pistillate and staminate phases, as in *Uvaria concava*: Silberbauer-

Gottsberger *et al.*, 2003), or else involve pollination by bees that are attracted by scent or stigmatic exudate in addition to pollen. The foraging activities of bees furthermore favour flowers that lack pollination chambers and the inferred presence of such chambers in ancestral species of Annonaceae may have limited the chances of such a change in pollination system. It is significant that non-opportunist bee visits in Annonaceae have only been recorded in *Uvaria* and *Unonopsis*, which both lack pollination chambers.

#### ACKNOWLEDGEMENTS

I am grateful to Lars Chatrou and Heimo Rainer for allowing access to unpublished molecular phylogenies, and Achala Attanayake, Thierry Deroin, Gerhard Gottsberger, Ada Ng, Pang Chun Chiu and Sena Ratnayake for information on the reproductive biology of specific genera. I am also grateful to Scott Armbruster, Richard Corlett, Pang Chun Chiu, Sena Ratnayake, Yvonne Su, Daniel Thomas and Timo van der Niet for critically reading the manuscript.

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