Generalist and specialist pollination in basal angiosperms (ANITA grade, basal monocots, magnoliids, Chloranthaceae and Ceratophyllaceae): what we know now*

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With 3 figures and 2 tables

Abstract

An updated description of the pollination and reproductive biology of basal angiosperms is given to show their principal associations with pollinating agents. The review considers members of the ANITA grade, as well as some basal monocots, the magnoliids, Chloranthaceae and Ceratophyllaceae. Morphological, physiological and behavioral characteristics of flowers and their pollinating insects are evaluated. Based on current evidence, early-divergent angiosperms were and are pollination generalists, even so there has been early specialization for either flies, beetles, thrips or bees. Although there are many tendencies for development from generalist flowers to specialist ones, there are also reversals with the development from specialist flowers to generalist ones. The earliest specialization seems to be fly pollination. Adaptations to more recently evolved insect groups, such as scarab beetles or perfume-collecting euglossine bees, demonstrate that several basal angiosperm lines were flexible enough to radiate into modern ecological niches.

Introduction

Phylogenetic studies of angiosperms resulted in the recognition of 413 families by the Angiosperm Phylogeny Group (Bremer et al. 2009, APG III). Early-divergent members of flowering plants, commonly referred to as the "basal angiosperms", are treated in the APG III classification as comprising 28 families, wherein the most basal grade, called ANITA, consists of the three clades *Amborella* (Amborellales), Nymphaeales and Austrobaileyales, and the further clade magnoliids, consisting of the orders Canellales, Piperales, Laurales and Magnoliales. Another order, Chloranthales, is thought to be sister to the magnoliids. According to estimates by taxonomic authors in Kubitzki et al. (1993), the basal angiosperms recognized by APG III total about 10,000 to perhaps 11,000 extant species. Several of the families have only one (Amborellaceae, Austrobaileyaceae, Lactoridaceae, Gomortegaceae) or two (Degeneriaceae, Himantandraceae, Atherospermataceae), probably relictual species,

while others have three to twenty species (Eupomatiaceae, Hydatellaceae, Cabombaceae, Trimeniaceae, Canellaceae, Hydnoraceae, Saururaceae, Calycanthaceae), and still others have more than twenty but less than hundred species, namely Nymphaeaceae, Schisandraceae, Chloranthaceae, Winteraceae and Hernandiaceae. The families Aristolochiaceae, Siparunaceae, Monimiaceae, Magnoliaceae and Myristicaceae comprise between one hundred to several hundreds of species. The three largest families of the basal angiosperms are the Annonaceae (2300–2500 spp.), Lauraceae (2500–3500 spp.) and Piperaceae (ca. 3000–3600 spp.).

In recent years, work aimed at resolving deep angiosperm phylogeny has progressed, and it is currently estimated that after the origin of angiosperms (viz., the origin of the first representatives of the ANITA group), the following divergence of Mesangiospermae probably began several Mry later (e.g. Smith et al. 2010, Zeng et al. 2014, Beaulieu et al. 2015). According to recent hypotheses, the first mesangiosperm group to diverge were the monocots, followed by the magnoliids, then the Chloranthaceae and Ceratophyllaceae, and after this the eudicots diverged (Zeng et al. 2014). Thus, all groups treated in the present paper had probably diverged before the rapid diversification of the eudicots in the later Cretaceous. The monocots are a very large entity (about 20% of angiosperm species) and much diversified group, and cannot be treated here in its entirety. Only some data of three families of the early-divergent monocot orders Acorales and Alismatales are presented, mainly to show some developments which apparently occurred in parallel in the basal monocots as well as in the ANITA grade and the magnoliids. Thus, in addition to the 28 families mentioned above, data on representatives of a further four families, namely the Ceratophyllaceae and the monocot families Acoraceae, Alismataceae and Araceae are included in this review.

Basal angiosperms pollination and reproductive biology, continues to be a fascinating field of investigation. With respect to pollination biology, extant basal angiosperms exhibit both abiotic (rare) and biotic pollination; the most remarkable diversity is found among the latter wherein flies, thrips, beetles, moths, cockroaches and even bees have been found to act as pollen vectors (for reviews see e.g. Gottsberger 1974, 1977, 1988, 2012, Gottsberger et al. 1980, Thien 1980, Thien et al. 1985, 2000, 2009, Bernhardt & Thien 1987, Endress 1990, 1994, 2010, Bernhardt 2000). Abiotic pollination is rare among basal angiosperms and several members are wind-pollinated or wind is an additional vehicle complementary to insects.

In this paper, pollination examples are drawn from the literature to nourish a discussion of the principal associations of extant basal angiosperms to pollination agents, as well as to show likely evolutionary shifts and adaptations. Another goal is to highlight those groups exhibiting generalist pollination and those having developed specialist pollination, e.g. by either flies, beetles, thrips or bees, and to evaluate morphological, physiological and behavioral characteristics of flowers and their pollinating insects associated with the respective phenomena.

In general, pollination mode and pollinator type correspond to flower morphology. Such characters as color, odor, and the amount of floral resources (commonly called rewards) probably partly evolved as adaptations to the senses, behavior, and needs of the pollinating animals. If these floral characters function like a lock and a key, or nearly so, with respect to the pollinating animal, the floral biology of the plant species

is considered to be specialized; in the most extreme cases of specialization, flowers are pollinated by a single animal species or a single vector (wind or water). Alternately, there are plant species that have evolved floral characters which permit pollination by several animal orders. Such species may be pollinated by flies, bees, butterflies and beetles jointly. They are therefore called generalist or generalized with respect to their pollination mode. One has to be aware that the above-mentioned two possibilities are only the extremes of a continuum between broader and more narrow interrelationships of pollinators and their respective flowers. One fruitful way to look at it is that plant species "explore" different niches with respect to pollination. In "generalists" a broader proportion of the fauna can act as pollinators than in the "specialists", which are pollinated only by a few often closely related species of animals or even only by a single one. For morphological and functional aspects of generalized flowers see Frame (2003a) and Weberling (2007).

One important point to be made is that flower/insect associations, especially in generalist flowers, but also in specialist ones, may have changed over time, and that former partners of flowers have been likely substituted by new ones. "What we observe on a morphologically generalist flower now as a principal pollinator is not a dependable indicator of which insect was the principal pollinator a million or less years ago" (Frame 2003a). It is also relevant to keep in mind that any flower visitor spectrum, again particularly in generalist flowers, depends on local abundance and presence of potential pollinators and competition from other flowers.

Pollination in the ANITA grade

Analyses of molecular data (e.g. Qiu et al. 1999) and of molecular data combined with morphological data (e.g. Endress & Doyle 2009) indicated that the ANITA grade (**A**mborella, **N**ymphaeales, **I**llicium, **T**rimeniaceae, **A**ustrobaileyaceae) contains the first divergent angiosperm lineages.

Amborellaceae (Amborellales) with the single species *Amborella trichopoda*, is considered the sister group to all other angiosperms (APG III 2009), followed by Nymphaeales (Hydatellaceae, Cabombaceae, Nymphaeaceae) and Austrobaileyales (Austrobaileyaceae, Schisandraceae, Trimeniaceae). *Amborella*, and especially members of Nymphaeales and Austrobaileyales are thus key for reconstructing ancestral character states and transitions that occurred during the earliest radiation of angiosperms (for informations on flower characters, floral biology and pollination of this and all other groups mentioned in this review see Tables 1 and 2).

Amborella trichopoda (Amborellaceae, Amborellales)

This woody species from New Caledonia has attracted wide attention as it is thought to be the sole living representative of a lineage that seems to have emerged at the base of the flowering plants. The flowers of this dioecious species are far from what decades of botanists have postulated and expected to be characteristic of a most basal angiosperm representative. Its flowers with several cream-colored tepals are borne in inflorescences and are small, 4–5 mm in diameter in staminate and 3–4 mm in diameter in pistillate flowers. Floral phyllotaxis is spiral and also appears partly whorled (Buzgo et al. 2004).

Table 1. Flower characters of basal angiosperms

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
ANITA									
Amborellales									
AMBORELLACEAE									
Amborella trichopoda	di	nr	0.3–0.5	spir whorl	cream	3–5	t 6–15	st 11–21	4–7
Nymphaeales									
HYDATELLACEAE									
Trithuria spp.	bi uni mo di	protogyn	0.1–0.2		greenish			st 1	up to 19
CABOMBACEAE									
Cabomba caroliniana	bi	protogyn	c. 2.5	whorl	white yellow pink	2	t 3+3	st 3–6	1–4
Brasenia schreberi	bi	protogyn	c. 2	whorl	purple-red	2	t 3+3	st 18–36	4–18
NYMPHAEACEAE									
Nuphar spp.	bi	protogyn	2.5–4	spir-whorl	yellow	c. 5	ou t 5–14 in t many	st many	5–23
Euryale ferox	bi	protogyn	1–3	spir-whorl	blue violet	2–3	ou t 4 in t 20–35	st 78–92	8–16
Barclaya spp.	bi	protogyn	3–6	spir-whorl	pink red		ou t 4–5 in t 8–20	st many	8–14

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Nymphaea ondinea (former *Ondinea*)	bi	protogyn	c. 4	spir-whorl	purple	3	ou t 4 in t 0–4	st many	5–23
Nymphaea subgen. *Nymphaea, Brachyceras, Anecphya*	bi	protogyn	up to 14	spir-whorl	white yellow pink red blue	2–4	ou t 3–5 in t 8–40	st many	8–35
N. subgen. *Hydrocallis, Lotos*	bi	protogyn	up to 20	spir-whorl	white	2–5	ou t and in t 16–30	st many	up to 40
Victoria	bi	protogyn	25–30	spir-whorl	white	2	out t 4 in t 50–70	st 150–200 ou sto 20 in sto 25	30–40
Austrobaileyales AUSTROBAILEYACEAE									
Austrobaileya scandens	bi	protogyn	5–6	spir	yellow brown green		t 19–24	st 7–11 in sto 9–16	10–13
SCHISANDRACEAE									
Schisandra glabra	uni mo	nr	1.3	spir	green yellow crimson		t 8–13	st 4–7	25–30
S. henyi	uni di	nr	1–2	spir	yellow orange	2.5–4.5	t 6–10	st 14–40	50–60
S. sphenanthera	uni di	nr	1.6–1.7	spir	yellow red	up to 4	t 6–7		

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Kadsura longipedunculata	uni mo	nr	1.5–2.6	spir	red yellow	1–2.6	t c. 10	st c. 36	20–60
Illicium floridanum	bi	protogyn	3	spir	red purple	12–14	t 24–28	st 30–39	c. 13
I. dunnianum	bi	protogyn	c. 1			3–4		st 12–29	8
I. tsangii	bi	protogyn	0.8			2		st 7–10	
TRIMENIACEAE									
Trimenia moorei	andmo	protogyn	1.3	spir	cream	2–5	t 2–38	st 7–25	1–2
BASAL MONOCOTS									
Acorales									
ACORACEAE									
Acorus spp.	bi	protogyn	c. 0.2	whorl	greenish	3–5	t 3+3	st 3+3	2–3
Alismatales									
ALISMATACEAE spp.	bi uni mo di poly	protogyn homo protand	1–3	whorl-spir	white pink purple	1–2	s 3 p 3	st 3-many	3-many
ARACEAE spp.	bi uni	protogyn	0.1–0.3	whorl	white yellow green purple	1–4	t 3+3 2+2–9	st 3+3 2+2–8	3–1

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
MAGNOLIIDS									
Canellales									
CANELLACEAE spp.	bi	protogyn							
WINTERACEAE									
Takhtajania perrieri	bi	protogyn							
Tasmannia piperita	di bi				white	10–12			
Drimys brasiliensis	bi	protogyn	c. 2	spir-whorl	white	7–11	s 2 p 8–20	st 20–50	3–13
Pseudowintera colorata	bi	protogyn	1–1.3	spir-whorl	greenish-white	13–20	p 4–9	st 7–23	1–4
Zygogynum crassifolium, Z. pancheri, Z. pauciflorum	bi	protogyn	5–6	spir-whorl	pale-yellow white	4–5	p c. 15	st c. 20	6–7
Z. baillonii, Z. pomiferum, Z. stipitatum	bi	protogyn	3–5.5	spir-whorl	yellow orange green white	2	p 4–12	st 20–25	4–6
Piperales									
ARISTOLOCHIACEAE									
Saruma henryi	bi	protogyn		whorl	yellow		s 3 p 3	st 12	6
Asarum europaeum	bi	protogyn	c. 1	whorl	dark-purple	8–20	t 3	st 12	6

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Asarum caudatum and other spp.	bi	protogyn	8–12	whorl	dark-maroon-red	7–10	t 3	st 12	6
Aristolochia spp.	bi	protogyn	1–100	whorl	brown yellow purple green	2–9	t 3	st 6	6
LACTORIDACEAE									
Lactoris fernandeziana	gynmo	protogyn	0.35	whorl	green	1–2	t 3	st 6	3
HYDNORACEAE									
Hydnora spp.	bi	protogyn	5.5–11	whorl	pink red purple	2–5-more	t 2–5	staminal structure 3–5	3–5
Prosopanche americana and spp.	bi	protogyn		whorl			t 3		3
PIPERACEAE									
Piper spp., *Pothomorphe* spp. and *Peperomia* spp.	bi uni di mo gynmo andmo	protogyn (protand)	0.1	whorl	green cream yellow white	6 -more	0	st 2–6	1–4
SAURURACEAE									
Saururus cernuus	bi	protogyn	c. 2.5	whorl	white		0	st 6	4

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Laurales									
CALYCANTHACEAE									
Idiospermum australe	bi uni andmo	protogyn	c. 3.5	spir	cream white to dull-purple	3–4	t 32–52	st 10–20 in sto 8–10	1–5
Chimonanthus praecox	bi	protogyn	2.5–3	spir	cream yellow dull-purple	3–7	t 15–25	st 5–10	5–15
Calycanthus occidentalis and *C. floridus*	bi	protogyn	4–8	spir	red-brown marroon	1–2	t 15–30	st 10–20 in sto 10–25	15–35
Calycanthus chinensis	bi	protogyn	4–7	spir	whitish pale-yellow		t 21–34	st 18–19 sto 11–12	11–12
SIPARUNACEAE									
Siparuna spp.	uni mo di	nr	0.3–1	whorl-spir	cream yellow orange	9–24 (1–30)	t 3–6	st 5–9 (1–100)	3–35
GOMORTEGACEAE									
Gormortega keule	bi	protogyn	0.4–0.5	spir-whorl	white		t 7–10	st 7–13	2–5
ATHEROSPERMATACEAE spp.	bi	protogyn							

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
HERNANDIACEAE									
Hernandia nymphaeifolia	uni mo	heterodi-chogamie	c. 1.5	whorl	white	1	t 6–8	st 3	1
Sparattanthelium botocudorum	bi		c. 0.5	whorl	cream	1	t 4–5	st 4–5	1
MONIMIACEAE									
Mollinedia spp.	uni di	nr	0.4–0.5	whorl-spir	green yellow	up to 14	t 4	st many	many
Wilkiea huegeliana	uni mo	nr	0.4	whorl-spir	green yellow	2–17	t 4	st 5–11	23–64
Tambourissa spp. group 1 and group 2	uni mo di	nr	0.5–7.5		green brown pink orange red purple	7–20	t c. 10	st c. 30–1800	c. 35–2000
LAURACEAE spp.	bi uni mo di	protogyn	0.2–2	whorl	green yellow white red	1–2	t 6	st 9 sto 3	1

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Magnoliales									
MYRISTICACEAE									
Myristica spp.	uni di mo	nr	0.4–0.6	whorl	white yellow pink red green	1–3.5	t 2–5	st 2–40	1
DEGENERIACEAE									
Degeneria spp.	bi	protogyn	6–7	whorl-spir	cream yellow magenta pink	1–2	s 3 p 12–25	st many in sto many	1
HIMANTANDRACEAE									
Galbulimima spp.	bi	protogyn?	2–4	spir	cream		0	st 13–130 ou sto 3–23 in sto 13–20	7–28
MAGNOLIACEAE									
Magnolia ovata and Magnolia spp. Neotropics	bi	protogyn	up to 16	whorl-spir	yellow cream-white	2	s 3, p 6–9	st many	many
Magnolia spp. Liriodendron spp. Temp. Zones	bi	protogyn	up to 20	whorl- spir	white cream yellow purple	2–4	t 6 or more	st many	many

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
EUPOMATIACEAE									
Eupomatia spp.	bi	protogyn	3–4	spir	cream yellow	1–2	0	st 20–100 in sto 40–80	13–70
ANNONACEAE									
Anaxagorea spp.	bi	protogyn	2–2.5	whorl-spir	cream yellow	2	s 3 p 6	st many in sto 15–20	8–22
Guatteria spp. and other genera (small flowers)	bi	protogyn	3–8	whorl-spir	yellow brown	2	s 3 p 6	st many	many
Annona spp. and other genera (large flowers)	bi	protogyn	up to 8	whorl-spir	white cream yellow brown	2	s 3 p 6	st many	many
Bocageopsis spp. and other genera	bi	protogyn	up to 1.5	whorl-spir	green cream white	2	s 3 p 6	st many	many
Pseuduvaria spp. and other genera	uni	nr	c. 1.5	whorl-spir	cream purple	2	s 3 p 6	st many	many
Uvaria elmeri	bi	protogyn	3–4	whorl-spir	cream white brown	2	s 3 p 6	st many	many
Unonopsis spp.	bi	protogyn	up to 1.5	whorl-spir	cream	2	s 3 p 6	st many	many

Taxa	Sex expression	Dicho/ Homogamy	Size (diam, cm)	Phyllotaxis	Color	Duration (days)	Perianth number	No. Stamens Staminodes	No. Carpels
Chloranthales									
CHLORANTHACEAE									
Chloranthus fortunei	bi	protogyn	1		white	5–6	0	st 3	1
C. serratus	bi	protogyn	0.3		white	8	0	st 3	1
C. spicatus	bi	protogyn	small		yellow	c. 20	0	st 3	1
Sarcandra chloranthoides	bi	protogyn	0.7		yellow red	c. 20	0	st 1	1
S. glabra	bi	protogyn	0.6		green	c. 20	0	st 1	1
Ascarina rubricaulis	uni di	nr	very small		st red		0	st 1	1
Hedyosmum mexicanum	uni di	nr	0.3		green		t 0–3	st 1	1
Ceratophyllales									
CERATOPHYLLACEAE									
Ceratophyllum spp.	uni mo	nr	0.1	whorl	green	1–3	t 8–15	st 5–27	1

Sex expression: bi = bisexual, uni = unisexual, di = dioecious, mo = monoecious, andmo = andromonoecious, gynmo = gynomonoecious, poly = polygamous; Dicho/Homogamy: protogyn = protogynous, protand = protandrous, homo = homogamous, nr = not relevant; Phyllotaxis: spir-whorl (outer elements spiral, inner elements whorled), whorl-spir (outer elements whorled, inner elements spiral); Perianth number: s = sepals, p = petals, t = tepals; No. Stamens/Staminodes: sta = stamens, sto = staminodes (ou = outer, in = inner); empty fields = data not known or not found.

Table 2. Floral biology and pollination of basal angiosperms

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
ANITA								
Amborellales								
AMBORELLACEAE								
Amborella trichopoda	diu noc	up p	po	no	no	col dip hym lep wind	gen	oblout
Nymphaeales								
HYDATELLACEAE								
Trithuria spp.		no		no	no	wind water	ane hyd	comp in bi
CABOMBACEAE								
Cabomba caroliniana	diu	no	po ne	no	no	dip hym	gen	
Brasenia schreberi		no	po	no	no	wind	ane	comp
NYMPHAEACEAE								
Nuphar spp.	diu	p sweet fruity	po ne	no	no	hym dip col	gen	comp
Euryale ferox	diu		po	no	no	dip hym	gen	comp
Barclaya spp.	diu	fruity	po ne	no	no	dip	myi	
Nymphaea ondinea (former *Ondinea*)	diu	no	po	no	no	hym col	gen	

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
Nymphaea subgen. *Nymphaea, Brachyceras, Anecphya*	diu	no s aromatic	po stiex	no	no	dip hym col lep	gen	comp
N. subgen. *Hydrocallis, Lotos*	noc	p pungent	po tiss	yes	yes	col	canth	comp
Victoria	noc	s fruity	po foob	yes	yes	col	canth	comp
Austrobaileyales AUSTROBAILEYACEAE								
Austrobaileya scandens	diu	s up	po brood	no	no	dip (col)	sapmyi (sapcanth)	incomp
SCHISANDRACEAE								
Schisandra glabra	diu		po brood	yes	no	dip	myi	
S. henryi	diu	no	po	no	no	dip	myi	oblout
S. sphenanthera	noc diu	sweet	po	no	no	dip thr col lep hym	gen	
Kadsura longipedunculata	noc	s fruity	po	yes	no	dip	myi	comp
Illicium floridanum	diu noc	s up	ne po	yes	no	dip col hym lep	gen	
I. dunnianum	noc	no	brood	yes	no	dip	myi	incomp
I. tsangii	noc	no	brood	yes	no	dip	myi	incomp
TRIMENIACEAE								
Trimenia moorei	diu	s fruity	po	no	no	dip hym col wind	gen	incomp

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
BASAL MONOCOTS								
Acorales								
ACORACEAE								
Acorus spp.	diu noc	sweet	po	no	no			
Alismatales								
ALISMATACEAE spp.	diu	sweet	po ne	no	no	dip hym lep col	gen	comp incomp
ARACEAE spp.	diu noc	s p up	po tiss perfume ne	no yes	no yes	dip col hym	myi canth mel	comp incomp
MAGNOLIIDS								
Canellales								
CANELLACEAE spp.								
WINTERACEAE								
Takhtajania perrieri						dip	myi ?	apomixis
Tasmannia piperita	diu	sweet	po ne* stiex	no	no	dip hym col	gen	oblout
Drimys brasiliensis	diu	aromatic	po ne* stiex	no	no	col dip thr	gen	comp
Pseudowintera colorata		w p sweet	po stiex	no	no	col dip (thr lep)	gen	incomp
Zygogynum crassifolium, Z. pancheri, Z. pauciflorum	diu	w sweet	po stiex	no	yes	thr	thy	comp (*pancheri*)

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
Z. baillonii, Z. pomiferum, Z. stipitatum	diu	s fruity	po stiex tiss	no	yes	col (lep)	canth	
Piperales								
ARISTOLOCHIACEAE								
Saruma henryi								
Asarum europaeum	diu noc	s up p	po	no	yes	no	self-poll	comp
Asarum caudatum and other spp.	diu	w no fungi	po	no	yes	dip	myi	comp
Aristolochia spp.	diu	s carrion up fruity no	po ne	no	yes	dip	myi sapmyi	comp incomp
LACTORIDACEAE								
Lactoris fernandeziana	diu noc	no	po	no	no	wind	ane	comp
HYDNORACEAE								
Hydnora spp.	noc diu	s up putrid carrion	po	yes	yes	col (dip)	sapcan sapmyi	
Prosopanche americana and spp.			po	yes	yes	col	sapcan	
PIPERACEAE								
Piper spp., *Pothomorphe* spp. and *Peperomia* spp.	diu	w sweet-lemmon	po (ne)	no	no	hym col dip wind	gen	comp incomp

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
SAURURACEAE								
Saururus cernuus		s sweet	po	no	no	hym dip col wind	gen	incomp
Laurales								
CALYCANTHACEAE								
Idiospermum australe	diu	s fruity	po tiss	no	yes	col thr dip lep hym	gen	
Chimonanthus praecox	diu	s sweet	po ne	no	no	hym dip	gen	
Calycanthus occidentalis and *C. floridus*	diu	s fruity	po foodb	no	yes	col	canth	
Calycanthus chinensis		no	po tiss	no	yes	col	canth	comp
SIPARUNACEAE								
Siparuna spp.	noc (diu)	s lemmon	po brood	no	no	dip	myi	
GOMORTEGACEAE								
Gormortega keule	diu	no	po ne	no	no	dip hym	gen	
ATHEROSPERMATACEAE spp.				no	no	dip hym	gen	
HERNANDIACEAE								
Hernandia nymphaeifolia	diu	s sweet	po ne	no	no	hym and ?	gen	
Sparattanthelium botocudorum	diu	s sharp	po	no	no	dip hym col	gen	incomp

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
MONIMIACEAE								
Mollinedia spp.	diu	no	po brood	no	yes	thr	thy	oblout
Wilkiea huegeliana	diu	no	po brood	no	yes	thr	thy	oblout
Tambourissa spp. group 1 (6 spp.)	diu	s fruity	po stiexs	no	yes	dip	myi	
Tambourissa spp. group 2 (4 spp.)	diu	s fruity		no		col	can	
LAURACEAE spp.	diu	s p up spermatic	po ne	no	no	hym dip col (lep)	gen	often incomp
Magnoliales								
MYRISTICACEAE								
Myristica spp.	noc diu	p sweet up musky	po	no	yes	hym dip thr col	gen can	
DEGENERIACEAE								
Degeneria spp.		up p	po	no	yes	col	can	
HIMANTANDRACEAE								
Galbulimima spp.		p aromatic	po	no		col	can?	
MAGNOLIACEAE								
Magnolia ovata and *Magnolia* spp. Neotropics	noc	s p fruity	po tiss	yes	yes	col	can	comp
Magnolia spp. *Liriodendron* spp. Temp. Zones	diu	s p aromatic	po ne tiss	no	yes	col hym dip thr	gen	comp (incomp)

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
EUPOMATIACEAE								
Eupomatia spp.	diu noc	s fruity musky	po tiss	no	yes	col	can	comp
ANNONACEAE								
Anaxagorea spp.	diu	s p fruity	po stoex stiex	yes	yes	col (small)	can	comp
Guatteria spp. and other genera (small flowers)	diu noc	s p fruity	po stiex	yes no	yes	col (small)	can	comp
Annona spp. and other genera (large flowers)	noc	s p fruity, sharp	po tiss stiex	yes	yes	col (large)	can	comp
Bocageopsis and other genera	diu	w p sweet up rancid	po	no	yes	thr	thy	
Pseuduvaria and other genera	diu	s up	po	no	no	dip	myi sapmyi	
Uvaria elmeri	noc	s up mushroom	po stiex	no	no	cockroaches	cockroaches	incomp
Unonopsis spp.	diu	p spearmint lemmon	po perfume	no	no	hym	mel	
Chloranthales								
CHLORANTHACEAE								
Chloranthus fortunei	diu	w aromatic	po	no	no	thr	thy	
C. serratus	diu	w p	po	no	no	thr	thy	

Taxa	Anthesis	Scent	Resources	Thermo-genesis	Poll. chamber	Pollinators	Pollination mode	Breeding system
C. spicatus	diu	s lemmon	po	no	no			incomp
Sarcandra chloranthoides	diu	s up	po	no	no			agamospermous
S. glabra	diu	w fruity	po	no	no			
Ascarina rubricaulis	diu	no	po	no	no	wind	ane	oblout
Hedyosmum mexicanum	diu	no	po	no	no	wind	ane	oblout
Ceratophyllales								
CERATOPHYLLACEAE								
Ceratophyllum spp.	diu noc	no	no	no	no	water	hyd	comp

Anthesis: diu = diurnal, noc = nocturnal; Scent: w = weak, s = strong, p = pleasant, up = unpleasant; Resources: po = pollen, ne = nectar, stiex = stigmatic exudates, stoex = staminodes exudates, tiss = nutritious tissue, foob = food bodies, brood = brood site; Pollinators: col = coleopters (beetles), dip = dipters (flies), hym = hymenopters (bees), thr = thrips (thysanopters), lep = lepidopters (butterflies, moths); Pollination mode: gen = generalist, canth-cantharophilous, sapcan = saprocantharophilous, myi = myiophilous, sapmyi = sapromyophilous, mel = melittophilous, thy = pollination by Thysanoptera, ane = anemophilous, hyd = hydrophilous; Breeding system: comp = self-compatible, incomp = self-incompatible, oblout = obligate outcrossing; Empty fields: data not known or not found; * nectar glands on stamens.

Endress & Igersheim (2000) investigated the reproductive structures of *Amborella* and found that the flowers are unisexual but with an underlying bisexual organization, since at least the pistillate flowers regularly have one or two staminodes outside the gynoecium. Moreover, the staminodes of the pistillate flowers look like fertile stamens. Evidence for ancestral bisexuality in *Amborella* to Poluszny & Tomlinson (2003) comes from the similar ontogenetic synorganization of pistillate and staminate flowers, while the presence of outer staminodia in most pistillate flowers also provides similar evidence, as does the occasional presence of central carpels in staminate flowers. The presence of bisexual floral organization is a strong indication for a basal state of this condition in angiosperms (Endress & Igersheim 2000). The relatively frequent occurrence of functionally unisexual flowers among basal angiosperms, to Endress & Igersheim (2000) "… may be a method to support outbreeding in a group in which self-incompatibiliy systems are lacking or unelaborated."

Thien et al. (2003) found that flowering of female and male plants of *Amborella* within populations is synchronous and that *A. trichopoda* is both insect- and wind-pollinated. Bud opening in staminate and pistillate flowers is throughout the day and night. Staminate flowers last 4 to 5 days from bud opening to complete anther dehiscence. Pistillate flowers last 3 to 4 days and stigma receptivity extends to 24–30 hours. Floral odor, not always perceptible, was faint and smelled like licorice, scented hay, and sometimes also like feces. A wide variety of mostly forest litter dwelling insects (1 mm to 7 cm length) was observed visiting flowers and leaves of *A. trichopoda* (Thien et al. 2003). Two species of Curculionidae (Cryptorhynchinae) were found to be common pollinators along with a tenebrionid beetle (*Neoadelium fauveli*). Large cerambycid beetles, as well as members of Homoptera, Hemiptera, Microlepidoptera, parasitic Hymenoptera and cecidomyiid Diptera were additional pollen transporters and potential pollinators. Tests with jelly-covered microscope slides proved that clumps of pollen grains, apparently held together by pollenkitt, were transported by wind.

Amborella has a generalist pollination system, where several species of pollen-eating and pollen-transporting insects belonging to different groups, as well as the wind can be effective in pollination. The insects probably visit pistillate flowers because of the mimetic role of the staminodes, contributing to the overall similarity of both flower types and presumably also because of the floral odor.

Nymphaeales

Hydatellaceae, are a group of small grass-like aquatic or subaquatic herbs, which formerly were placed among monocots. The phylogenetic placement of this family together with Cabombaceae and Nymphaeaceae in the order Nymphaeales, however, is well supported by both molecular and morphological data (e.g. Rudall et al. 2007, Saarela et al. 2007, Sokoloff et al. 2013). Analyses supported placement of Hydatellaceae as sister to Cabombaceae plus Nymphaeaceae (Saarela et al. 2007). The sole genus *Trithuria* (Sokoloff et al. 2008) as currently recognized has 8 species endemic to mainland Australia, while one species each occurs in Tasmania, New Zealand and India, and one last species occurs in both Tasmania and mainland Australia (Sokoloff et al. 2011). The "reproductive units" in this seemingly highly reduced and modified group,

are interpreted as aggregations of reduced unisexual apetalous flowers (Rudall et al. 2007, Endress & Doyle 2009, Taylor et al. 2010). Four of the twelve species have bisexual reproductive units, four are dioecious, and four are monoecious. For example, of two Western Australian species, *T. austinensis* is dioecious and thus obligately outcrossing, while *T. submersa* is bisexual and selfing (Taylor & Williams 2012). It is not very clear whether *Trithuria* is pollinated in the air or in the water (Endress 2010). Wind pollination has been hypothesized for several species and water pollination in two permanently submerged species (Rudall et al. 2007). In *T. submersa* which has bisexual reproductive units, buds opened and pollen matured under water, but anthers were never dehiscent in submerged reproductive units. Submerged reproductive units never received pollen. Only emergent reproductive units received pollen. The species is characterized as mainly self-pollinated, self-compatible and primarily autogamous; it occasionally also exhibits wind pollination. Stigmas are receptive before and during anther dehiscence (Taylor et al. 2010). Thus, most *Trithuria* species have similar reproductive features as *T. submersa*, which are associated with wind pollination; two exceptional perennial species having permanently submerged reproductive units are probably pollinated underwater (Taylor et al. 2010).

The monotypic *Amborella* and also Hydatellaceae, the latter consisting of very specialized, aquatic species, which are presumably highly modified related to the environment in which they grow, do not really provide many insights into early diversification of angiosperms.

The aquatic family **Cabombaceae** consists of the genus *Cabomba*, having five species in tropical and temperate regions of the Americas, and the monotypic *Brasenia schreberi*, distributed in tropical and temperate regions of the Old and New World. The emergent flowers of *Cabomba caroliniana* are trimerous and 2.5 cm in diameter when fully open. The six white tepals are in two whorls and nectaries occur on the adaxial side of the inner tepals (Vogel 1998a, Erbar 2014). Schneider & Jeter (1982) observed that the protogynous flowers have receptive stigmas on the first day of flowering. On the second day, the flowers are in the staminate stage, the filaments are elongated and anthers dehisce above the nectaries, while the non-receptive stigmatas are pressed together at the center of the flower. Autogamy does not occur because of the strict dichogamous protogyny. The breeding system itself, self-compatibility or -incompatibility, was not tested. Two ephydrid flies, *Notiphila cressoni* and *Hydrellia bilobifera*, were observed in both first-day and second-day flowers consistently moving from flower to flower and were seen applying their mouth parts to the yellow nectaries. Flowers were interpreted to be myiophilous, since other flower visitors, such as the halictid bee *Lasioglossum* sp., a curculionid beetle and brachonid wasps were occasional visitors or did not contact the reproductive parts of the flowers. The yellow flowers of *C. aquatica* growing near Belem, Amazonia, were observed by Vogel (1998a) to emerge in the morning of the first day of anthesis and enter into the pistillate stage, to close in the afternoon, and then to be redrawn into the water. The second day, flowers similarly emerged and unfolded but entered into the staminate stage; filaments elongated and anthers occupied superficially the former position of the stigmas. At the end of the second day, flowers closed and submerged definitely. Vogel (1998a) observed nectar- and pollen-collecting stingless bees (Meliponidae) and concluded that instead

of classifying *Cabomba* as myiophilous he would rather classify them as allophilic, exhibiting unspecialized entomophily.

The emergent flowers of *Brasenia schreberi* have many more stamens (18–36) than *Cabomba* species (3 or 6) and have long filaments. Anthesis of the bisexual, protogynous flowers also lasts for two days, with the pistillate stage on the first day and the staminate stage on the second. Flowers of *Brasenia* are primarily wind-pollinated, but were also visited by several insects mainly for pollen collection (Osborn & Schneider 1988). Seed set after pollination experiments in cages using pollen of the same plant proved self-compatibility in this species (Osborn & Schneider 1988).

Nymphaeaceae have a global distribution and originally comprised the six genera *Nuphar, Barclaya, Euryale, Ondinea, Nymphaea* and *Victoria*, together representing about 70 extant species. Similar to the other two families in the Nymphaeales, they are also all herbaceous aquatics.

The most basal genus of the family is thought to be *Nuphar* (Borsch et al. 2008). Formerly, the genus was considered monotypic comprising a single variable species, *N. lutea*, distributed throughout the temperate northern hemisphere. After molecular studies, 13 distinct lineages were recognized, five species in Europe and Asia, and eight species in North America (summarized in Lippok et al. 2000). The literature on the floral biology of *Nuphar* is vast and goes back to Sprengel (1793). Schneider & Moore (1977) reviewed the observations of other authors and provided new data from studies of *N. lutea* subsp. *macrophylla* (=*N. advena*), in Texas. The yellow flowers are protogynous and anthesis occurs over a period of several days. First-day flowers emit an intense sweetish scent, somewhat like brandy or papaya fruits. During this first-day pistillate stage, the stigmatic disc is covered with a sticky, mucilaginous secretion. The authors observed numerous insects visiting first-day flowers, especially Coleoptera, Hemiptera, Homoptera and Hymenoptera. The most numerous visitors of the flowers were the beetle *Donacia piscatrix* (Chrysomelidae) and bees of the genera *Halictus* and *Apis* hypothesized to be attracted by the yellow perianth and strong scent. The dorsal side of the inner tepals produce nectar and have been called "honey leaves" (Müller 1893). In Erbar's recent detailed comparative study of nectaries, she remarks that *Nuphar* is the only genus of Nymphaeaceae in which nectar is presented in distinct drops (Erbar 2014). Schneider and Moore (1977) found that during the night, first-day flowers closed their tepals over the stigmatic disc and enclosed many of the beetles. The stamens reflexed and pollen was shed. In the second morning of anthesis, the tepals re-opened, the stigmatic disc began to dry, and the pollen-covered beetles could be observed to emerge from the flowers and to fly to first-day and older flowers. Although the *Donacia* beetles and the *Halictus* and *Apis* bees appeared to be efficient pollinators, Schneider & Moore (1977) thought that the overall floral structure, scent emissions, tepal closing during the night, in addition to other characteristics, represent primary adaptations for beetle pollination. Subsequent studies have shown, however, that *Nuphar* pollination is somewhat more complex. Michels (1993) studied the floral biology of *N. lutea* from the river Lahn close to Giessen, Central Germany, where flowers were visited by 30 different insect species, including chrysomelid (*Donacia clavipes*) and nitidulid (*Meligethes aeneus*) beetles, and flies of the families Calliphoridae, Ceratopogonidae, Empididae, Ephydridae, Muscidae, Sarcophagidae,

Scatophagidae, Sepsidae, Syrphidae and Tachinidae, Heteroptera, Homoptera and Hymenoptera (*Apis mellifera* and *Bombus* spp.). Insects collected pollen as well as imbibed nectar and stigmatic exudates. The most frequent visitors were flies (70%), especially syrphid flies. In the summer months, during the flowering period the visitor spectrum of insects varied strongly. Flies preferred to visit second-day and older flowers in the staminate stage and were 3.6 times more common than on first-day flowers in the pistillate stage. In contrast, bees visited pistillate stage flowers as often as staminate stage flowers. Beetles were only rarely found in the receptive first-day flowers. Thus, the most efficient pollinators of *N. lutea* at Giessen were bumblebees (*Bombus terrestris/lucorum* complex), followed by honeybees and flies, especially syrphid flies, as well as the *Cabomba/Nuphar/Nymphaea* specialists *Hydrellia* (one species), *Notiphila* (two spp., Ephydridae), and *Hydromyza livens* (Scatophagidae) (see also van der Velde & Brock 1980). Ervik et al. (1995) investigated *N. lutea* in Norway, and found that besides *Apis mellifera* and *Bombus* spp., syrphid flies were efficient pollinators. The chrysomelid beetle *Donacia crassipes* played a minor role in pollination. The authors concluded that in Norway, *N. lutea* appears to have shifted from a typical beetle pollination system, as suggested by Schneider & Moore (1977) for *N. advena*, to a non-specific pollination syndrome. In a later study, Lippok & Renner (1997) compared *N. lutea* and *N. pumila* at sites in Norway and southwest Germany. Flies were the main pollinators in both species, while the beetle *Donacia crassipes* played an insignificant role for both *Nuphar* species in Norway and was absent at the German site. In the study of *N. pumila* by Zhou & Fu (2007) in China, no beetle visits occurred and halictid bees and flies were the most frequent visitors to flowers. Lippok & Renner (1997) had already hypothesized that the open bowl-shaped flowers of *Nuphar* having accessible nectar and pollen ". . . might simply sample locally available insects", and thus, there seems to be no specialization to any particular insect group. At that time, however, it was not yet clear whether New World *Nuphar* species have a tendency to be principally beetle-pollinated. To resolve this question, Lippok et al. (2000) re-studied *N. advena* in Texas and also studied *N. ozarkana* in Missouri, and concluded that. . ."The comparison of pollination spectra in the two Old World and the three New World *Nuphar* species studied so far suggests that the relative contribution of flies, bees, and beetles to pollen transfer in any one population depends more on these insects' relative abundances (and in the case of *Donacia*, presence) and alternative food sources than on stamen length differences between Old World and New World pond-lilies."

Lippok & Renner (1997) and Lippok et al. (2000) confirmed self-compatibility for *N. lutea*, *N. pumila* (see also Zhou & Fu 2007) and *N. advena* and strong protogyny of their flowers, preventing automatic selfing; hence, insect pollination is necessary for seed production. Also Michels (1993) found *N. lutea* to be self-compatible and pollination experiments with pollen of the same plant, including 16 first- and second-day flowers, resulted in a 100% fruiting success and 95% seed-set.

The two Asian genera *Euryale* and *Barclaya* were reported to have cleistogamous and chasmogamous flowers; sometimes both types occur within a single individual (Schneider and Williamson 1993). The sole *Euryale* species, *E. ferox* has cleistogamous, self-pollinating submerged flowers that appeared more than one month earlier

than chasmogamous ones; chasmogamous flowers were fewer than chleistogamous ones and were already self-pollinated at opening, some occasional small flies (*Notiphila* spp.) and solitary bees did not enter the floral tube or touch the stigmatic surface and, thus, were not responsible for seed set (Kadono & Schneider 1987). The four species of the genus *Barclaya* have been studied by Williamson & Schneider (1994). Both, *Barclaya longifolia* and *B. kunstleri* were observed to have only cleistogamous, self-pollinated flowers. On the other hand, *B. motleyi* produces chasmogamous, self-pollinated flowers; no flower visitors were seen during a three-week observation period. In *B. rotundifolia* which has aerial, chasmogamous flowers, the outer tepals are greenish to white and inner tepals and stamens are purplish. For three days, individual flowers open in the morning and close at dusk; they emit a pungent, fermented odor. Unidentified small- to medium-sized flies were collected around the flowers, which occasionally suffocated in the mucilage that covers the surface of the stigmatic cup. The occurrence of flies in the flowers, the floral construction, color and odor suggest myiophily for this species. The cleistogamous and chasmogamous flowers are self-pollinated, the latter type facilitated partly by flies in emergent flowers. Three of the four species were tested and found to be self-compatible.

After careful study, it was discovered that the former Australian monotypic genus *Ondinea* was nested in *Nymphaea* and so was recently transferred under the new name *N. ondinea* (Löhne et al. 2009). It is unusual because it is atepalous, the original distinction between *Ondinea* and *Nymphaea*, however a second subspecies having violet tepals was discovered later. Study of the floral biology of the tepal-bearing subspecies (Schneider 1983, Schneider et al. 1984) indicated that anthesis lasts for 3 days. First-day flowers are in the pistillate stage and characterized by reflexion of the purple perianth and stamens. The stigmas secrete a fluid that fills the stigmatic cup. Second- and third-day flowers are in the staminate stage and present pollen. The most common visitors in both stages were bees (*Trigona* spp.) besides some minor pollinators, curculionid and chrysomelid (*Donacia*) beetles. In first-day flowers, bees approached the stigmatic area where pollen carried by the insects was washed off by the fluid. On the second and third day of anthesis, the stamens assume a vertical erect position forming a cone and again trigonid bees were observed to land on the stamens to collect pollen.

Nymphaea, the largest and most diverse genus of the family, consists of about 50 species, has a world wide distribution, and species have more or less large (up to 20 cm diam.), showy, white, yellow, red or blue flowers, which may or may not be scented. Anthesis of water lilies can occur over a 2–5 day period, depending on the species. There are diurnally flowering species (subgen. *Nymphaea, Brachyceras, Anecphya*) with tropical and temperate zone representatives, which are jointly visited and pollinated by a wide array of Diptera, Hymenoptera and Coleoptera (e.g. Robertson 1889, Knuth 1898/1899, Schmucker 1932, Meeuse & Schneider 1979/80, Schneider 1982a, 1982b, Capperino & Schneider 1985). For example, *N. odorata*, examined in Texas by Schneider & Chaney (1981) opens its flowers each morning and closes them about noon for three successive days. The flowers are protogynous and first-day flowers are receptive having secreting stigmas; the fluid, which contains a surfactant responsible for washing pollen off the bodies of visiting insects, fills the stigmatic cup (Wiersema 1988). Pollen quickly germinates in the stigmatic secretions

and pollination is achieved (Williams et al. 2010). During the following two days, the stigmas of *N. odorata* become non-receptive, anther dehiscence occurs and pollen is offered to insect visitors. After the third day of anthesis, the flowers submerge. Beetles belonging to the families Chrysomelidae (among others *Donacia piscatrix*), Curculionidae and Scarabaeidae, as well as syrphid flies and Hymenoptera were observed visiting the flowers. The bee *Lasioglossum versatum* (Halictidae) appeared to be the most efficient pollinator. Another well-studied species is *N. alba*. Michels (1993) studied this species for a whole flowering season at several lakes and ponds around Giessen, Central Germany. In total, 24 insect species belonging to four orders visited the flowers. Bees, beetles and butterflies were negligible as pollinators. The most important pollinators of *N. alba* at that site were ephydrid flies, namely three species of *Hydrellia* and two species of *Notiphila*. These insects collected pollen and were also seen absorbing the sweet, 2.8–3.8% sugar-containing stigmatic exudates (see also Baker et al. 1973).

The derived groups of *Nymphaea*, species of the subgenera *Hydrocallis* (Neotropics) and *Lotos* (Paleotropics) (Borsch et al. 2008), also have protogynous flowers with nocturnal anthesis over two nights (at least in Neotropical species) and emit a strong scent. Exclusive pollinators are nocturnally active, large dynastid scarab beetles (Scarabaeidae: Dynastinae) of the genus *Cyclocephala*. Cramer et al. (1975) found *C. castanea* as pollinator in flowers of *Nymphaea blanda* var. *fenzliana* and *N. rudgeana* in Surinam. A third species, also in Surinam, *N. amazonum*, was found by the above authors to be pollinated by *C. verticalis* (see also Prance & Anderson 1976). In a later paper, Prance (1980) found *N. amazonum* in the Pantanal of Mato Grosso to be pollinated by *C. mollis*. Although not measured, it can be deduced from similar phenomena in *Magnolia*, Annonaceae, Araceae and other groups, that the flowers of all these nocturnal, dynastid scarab beetle-pollinated Neotropical *Nymphaea* species are probably thermogenic, warming-up during the night hours. One of the two known Paleotropical representatives of the tribe Cyclocephalini (Ratcliffe et al. 2013), *Ruteloryctes morio*, visits and pollinates (besides certain bees) the African *N. lotus* in Ivory Coast (Hirthe & Porembski 2003; Krell et al. 2003); the protogynous flowers are nocturnal, with anthesis lasting 4 to 5 days. Flower temperature increased in the first half of the night, with recorded values of 5°C on the first, and 7°C on the second, night above ambient air; the temperate difference was less on subsequent nights. In Senegal, Ervik & Knudsen (2003) found the same species, *N. lotus*, to be exclusively pollinated by *R. morio*. At their site, *Apis mellifera* was observed to collect only pollen but did not touch the stigma. Thus, *N. lotus*, at least in Senegal, appears to be exclusively beetle-pollinated.

Nymphaea lotus was tested and found to be self-compatible (Hirthe & Porembski 2003), as were *N. rudgeana* and *N. ampla* in the vicinity of Manaus (Prance & Anderson 1976), in addition to eight other *Nymphaea* species mentioned by Wiersema (1988), among them the temperate species *N. alba* (see also Michels 1993).

The two Amazonian species of *Victoria, V. amazonica* (Fig. 1) and *V. cruziana*, exhibit exclusive cantharophily. In both species the very large (up to 25–30 cm diam.) protogynous flowers have a two-night rhythm, warming up strongly during the first night of flowering (5–11 °C above ambient air temperature in *V. amazonica*) followed

by a lower temperature increase in the second evening when the beetles leave. Heat was generated mainly in the floral chamber on the first evening and by the stamen complex on the second (Seymour & Matthews 2006). The strong temperature elevation of the first night is accompanied by a potent, fruity, pineapple-like fragrance. During the second day, the originally white inner tepals become purplish-red and lose their fruity scent. By the afternoon, the anthers shed pollen and finally, in the evening, the pollinators emerge from the flowers, squeezing through the pollen-shedding stamens. The most common beetle species is *Cyclocephala hardyi*, along with three other more occasionally visiting *Cyclocephala* species (Prance & Arias 1975, Kite et al. 1991). The starch-containing carpellary appendages are eaten by the beetles while they are inside the floral cavity. Self-pollination in the self-compatible *V. amazonica* resulted in fruit- and seed-set (Prance & Arias 1975). The flowers of *Victoria cruziana*, apparently also self-compatible, behave in a similar manner to *V. amazonica*, and were found to be pollinated in Argentina by a species of *Chalepides*, a beetle also belonging to the group of Cyclocephalini dynastid scarabs (Valla & Cirino 1972, Skubatz et al. 1990, Lamprecht et al. 2002).

Fig. 1. *Victoria amazonica.* A. Second-day flower (diam. of expanded petals ca. 25–30 cm.) with internal petals starting to change color from white to red. B. First-evening flower with closed white petals, in pistillate stage, being approached by its pollinating beetle, *Cyclocephala hardyi*. C. Cut flower showing the pollination chamber and one beetle. D. Reddish, second-evening flower with expanded petals, in staminate stage. The beetles, covered with pollen grains, are coming out of the pollination chamber; some beetles are mating before flying off.

Austrobaileyales

Austrobaileyaceae is a monotypic family represented by the relict *Austrobaileya scandens,* a liana endemic to North Queensland, Australia. Its bisexual, large (5–6 cm diam.), showy, solitary flowers are pendent and phyllotaxy is spiral throughout. The perianth exhibits a series of appendages transitional from small green bracts to large yellowish petal-like organs. Inner staminodes and stamens are yellowish. The protogynous flowers emit a strong scent of decaying fish and were visited by flies, some of which oviposited there (Endress 1993a); beetles were also observed (Thien et al. 2009). The combination of an unpleasant odor, coloration of the stamens and staminodes, dark brown spots on a yellow background pattern of the perianth, and observed visitors, strongly suggest that *Austrobaileya* is mimicking rotten organic matter. The carpels are covered by the connivent parts of the staminodes and are not visible from outside. It is thought that the visiting flies may reach the stigmatic region by slipping through the gaps between the stamens and staminodes, which form a labyrinth-like structure (Endress 1980c). Apparently, the bisexual flowers of *A. scandens* are self-incompatible (Prakash & Alexander 1984).

The **Schisandraceae** now consist not only of the two genera *Schisandra* (25 spp.) and *Kadsura* (22 spp.), having mostly Southeast Asian species, but also of *Illicium* (formerly Illiciaceae with 30–40 species; Morris et al. 2007; APG III 2009), which has a distribution in Southeast Asia and southeastern North America. Ueda (1988) reported on labile sex expression and sex change in the woody vine *Schisandra chinensis*, which can produce staminate flowers one year, and pistillate and rarely even bisexual flowers in another year. The study of Zhao et al. (2013) showed that this species is mainly monoecious and that gender expression and reproductive output is age-dependent, with young and old plants having lower female ratios. Labile sex expression is mentioned also for *Kadsura japonica* and might occur in other species of Schisandraceae (Ueda 1988).

The only species of *Schisandra* occurring outside Asia is *S. glabra*, which grows in southeastern United States and Mexico. It was shown that this monoecious plant has thermogenic pistillate and staminate flowers, which function as a host site primarily for Diptera and also small Coleoptera that inadvertently pollinate while ovipositing (Liu et al. 2006). The woody vine *S. henryi*, studied in South-Central China by Yuan et al. (2007), was found to be strictly dioecious, having small (several mm diam.) pendulous flowers with green or yellow tepals. It is not thermogenic and did not emit any detectable scent. The small diameter of the floral orifice and the small space inside the flower interior only permit small insects to enter. Of several insects observed, only adult females of *Megommata* sp. (Cecidomyiidae, Diptera), that eat pollen grains, are effective pollinators. As pollen is the only food resource for the insects, the pistillate flowers of *S. henryi* attract pollinators by deceit. Wind pollination was not ruled out, but the authors conclude that the drum-shaped, pendulous flowers have such small orifice that wind pollination would likely be prohibited. Another, dioecious species, *S. sphenanthera*, from Central China has an extragynoecial compitum and it was observed that pollen tubes can easily cross *via* this compitum from one carpel to another (Du & Wang 2012). The observed populations of this species were male

biased, and, principally, diurnally-active gall midges (*Reseliella* sp., Cecidomyiidae) and thrips (*Thrips flavidulus*) were the most common visitors to flowers (floral diam. 1.6–1.8 mm, tepal color red or yellow, fragrance sweet); additional visitors included a few hoverflies, beetles and butterflies. The gall midges, which fed on pollen, were more common in staminate flowers and thrips were more common in pistillate flowers. Du et al. (2012a) thought that the pistillate flowers attracted pollinators by deceit.

The monoecious *Kadsura longipedunculata* was studied by Yuan et al. (2008) in the same area as *S. henryi*. It has larger flowers (1.5–2.6 cm diam.) than the aforementioned *Schisandra* species. Its tepals are yellow and stamens may be yellow or red. Tepals of the staminate flowers are reflexed when open, while pistillate flowers form a drum-shaped chamber. Both pistillate and staminate flowers are thermogenic during the night and emit a strong fragrance. This species, like *S. henryi*, is pollinated by female, pollen-eating cecidomyiid flies (*Megommata* spp.); pistillate flowers, which do not offer any nutritive tissues are visited by deceit. This species combines an extragynoecial compitum, which distributes the pollen tubes to the individual free carpels, with a dry-type stigmatic tissue (Lyew et al. 2007). Tests showed that this species can form some fruits after selfing and therefore shows a degree of self-compatibility (Yuan et al. 2008). *Kadsura japonica*, as opposed to *K. longipedunculata* has a nectary tissue located on the adaxial surface of the inner tepals (Saunders 1998).

Illicium floridanum, studied in Louisiana (Thien et al. 1983) has showy (ca. 7 cm diam.), deep red or purple, thermogenic (Thien et al. 2009) flowers which, in a functional stage, last for 12–14 days and emit an intense, unpleasant odor, smelling like freshly caught fish. A wide spectrum of insects emerging from the surrounding leaf litter and stream in the riverine community visited the flowers. Principally Diptera were pollinators. Hymenoptera and Hemiptera visited the flowers only occasionally and Coleoptera rarely, the last usually approaching only partially opened flowers. The insects fed on nectar that was produced in very small quantities at the base of the inner tepals and stamens. Flowers exhibited complete dichogamy. The original report of pre-zygotic self-incompatibility of this species (Thien et al. 1983) is now thought to be due to inbreeding depression, although late-acting post-zygotic ovarian self-incompatibility cannot be ruled out (Koehl et al. 2004). Williams et al. (1993) reported on intercarpellary growth of pollen tubes in the apocarpous *I. floridanum*. An apical residuum with its associated unfused carpel margins acts as an extragynoecial compitum for pollen tube transfer between carpels. A compitum is thought to be a mechanism by which more ovules can be fertilized and thus may increase the efficiency of seed set. The small-flowered (floral diam. ca. 0.8 cm), protogynous *I. parviflorum* of eastern Florida produces o faint sweet scent. Flowers last 2–3 days and open during the day and night; the pistillate stage lasts for the first 24 hours. Mainly gall midges (Cecidomyiidae), along with some psychodid and ceratopogonid flies were the principal pollinators; these insects, among others probed on stamen nectaries (White & Thien 1985). As compared, in particular to *I. floridanum*, the Malayan species *I. peninsulare*, *I. tenuifolium* and *I. ridleyanum* have relatively small, inconspicuous flowers, which are pale yellow or white and only faintly scented; although not observed, Keng (1993a) hypothesizes that they are insect pollinated. *Illicium dunnianum* (self-incompatible) and *I. tsangii* from China, both having bisexual flowers (floral diam. 1–1.5 cm) with no

perceptible floral scent, are exclusively pollinated by gall midges that use the flowers as brood sites and not for pollen feeding. First-night flowers were in the pistillate stage and second- or third-night flowers in the staminate stage. There was a slight floral heating of ca. 1.6°C above-ambient temperature, mainly during the pistillate stage and the later larval nursing phase following the staminate stage of flowers; experiments showed that this post-anthetic warming benefited larval development of the gall midges, not fruit development (Luo et al. 2010).

Trimeniaceae consists of a single genus having 5–8 species distributed from Celebes to eastern Australia and the Southwest Pacific (Philipson 1993b, Bernhardt et al. 2003). *Trimenia papuana* and *T. neocaledonica* were both found to be andromonoecious, with small, inconspicuous flowers. Most flowers were bisexual, but a few were staminate and had the gynoecium reduced or lacking. No nectar is produced. The pollen was found to be dry and easily dispersed by wind (Endress & Sampson 1983). *Trimenia moorei* is also andromonoecious and both male and bisexual (protogynous) flowers (ca. 1 cm diam.) were found to be strongly scented. Hover flies (Syrphidae), sawflies (Pergidae) and several bees (Apidae, Colletidae and Halictidae) carried pollen of *T. moorei* and acted as pollinators. Pollen is also shed directly into the air, permitting wind pollination. This species was found to be self-incompatible (Bernhardt et al. 2003).

Pollination in basal monocots

Acorales

There is strong support that *Acorus* (**Acoraceae**) is sister to all other monocots (e.g. APG III). The inflorescences and flowers of the two to four species bear superficial similarities to those of Araceae, and for a long time, *Acorus* was considered to be a member of that family. The distribution of this northern hemisphere genus is temperate to tropical. The bisexual flowers are protogynous. Ever since Knuth (1899), the entomophilous characters, e.g. sticky pollen, sweet scent of *Acorus* inflorescences have been stressed, but apparently there are no observations of insect visits to flowers. One hundred years after reports by Knuth, the situation has not much improved: "The pollinators or pollinating agency of *Acorus* are unknown; both entomophily and anemophily have been suggested, but entomophily appears more likely." (Bogner & Mayo 1998). Azuma & Toyota (2012) found a rare scent compound (for angiosperms) in *A. gramineus* and they, as have several other authors, suggested that the species was entomophilous.

Alismatales

Both Acorales and Alismatales are early-divergent monocot groups and most phylogenetic studies resolve Alismatales as the sister group to all other monocots except *Acorus* (Acorales). Alismatales is a cosmopolitan and diverse clade of monocots, comprising about 4500 species in 13 families (e.g. Iles et al. 2013).

Alismataceae consist of 12 genera and about 80 species of subcosmopolitan distribution. Flowers are bisexual or unisexual by abortion of either stamens or carpels. Sex expression of plants with unisexual flowers is commonly either monoecious (*Sagittaria*), polygamous (*Limnophyton, Sagittaria*), or dioecious (*Burnatia*). The petals are delicate and white, pink, or purple in color (Haynes et al. 1998).

Observed flower visitors and pollinators of *Alisma plantago-aquatica* are several species of syrphid and muscid flies and occasionally also a bee or a butterfly, which feed on nectar, and in case of Syrphidae also eat pollen. Nectar is produced by the carpels and accumulates at the base of the filaments. The homogamous flowers open between 9 and 11 a.m. and fade between 5 and 7 p.m. of the same day. Pollenkitt is not well developed in *A. plantago-aquatica*, such that the pollen is not only transported by insects, but also by strong air currents (Knuth 1899, Daumann 1965). Nectar production is reported not only for *Alisma*, but also for *Sagittaria, Damasonium, Baldellia, Caldesia* and some species of *Echinodorus*, such as *E. grandiflorus* (Pansarin 2008). Robertson (1929) observed 66 species of insects in four orders visiting both staminate and pistillate flowers of *Sagittaria latifolia* in Illinois. Flowers of *S. brevirostra* in Nebraska were found to be full of small insects, at least some of which are surely pollinators (Kaul 1979). Flowers of *S. guyanensis* in Bolivia were principally visited by bees, some beetles and an occasional butterfly (Gumbert & Kunze 1999), and in China occasionally by certain syrphid flies (Huang 2003). In contrast, at a site in China, *S. potamogetifolia, S. trifolia* and *S. pygmaea* were frequently visited by bees, flies and butterflies (Huang 2003). The two species, *S. australis* and *S. latifolia*, were both found to be visited in Ohio by a similar spectrum of generalist bees, and additionally by some flies, wasps, other bees, and a few butterflies (Muenchow & Delesalle 1994), and *Echinodorus grandiflorus* flowers in Bolivia by bees and additionally by Coleoptera, Lepidoptera and an occasional fly (Gumbert & Kunze 1999). Comparative studies on two *Echinodorus* species in São Paulo State revealed that *E. longipetalus* is gynodioecous (the first report for this sex distribution in the genus), offers only pollen as a reward, and is pollinated principally by several bees. The pistillate flowers, which do not offer any reward, attract by deceit. Other visiting beetles and hoverflies were not seen to contact the pistils, and thus have to be considered at least poor pollinators if pollinators at all (Pansarin 2008). In contrast, *E. grandiflorus* has bisexual flowers that offer pollen and nectar. Also this species was found to be pollinated nearly exclusively by social and solitary bees, which collected only pollen. The additional flower visitors were beetles, which fed on petals, stamens and pistils, and damaged them, and bombyliid flies which collected nectar without touching the stamens (Pansarin & Pansarin 2011). Since the authors report for the latter species that pollen-collecting bees appeared immediately when flowers opened, it can be deduced that the flowers of *E. grandiflorus* must be either homogamous or protandrous. Flower visitors of *Caldesia grandis and C. parnassifolia* in China were flies and bees, with the latter being more effective pollinators. *C. grandis* was found to be protandrous. Anther dehiscence occurs soon after flower opening at about 10:00 a.m., when the first flower visitors approach, and stigmas were found to be receptive between 12:30 and 1:00 p.m. (Gituru et al. 2002).

Kugler (1955) and Daumann (1965) tested *Alisma plantago-aquatica* and found it to be self-compatible. Self-compatibility was also found in *Sagittaria guyanensis* (Huang 2003) and in the five species of the genus *Damasonium*; four of the five species are homogamous and *D. californicum* is protandrous (Vuille 1987). *Baldellia ranunculoides* subsp. *repens* is self-incompatible, whereas *B. ranunculoides* subsp. *ranunculoides* and *B. alpestris* are self-compatible. The genus *Baldellia* is noted to

be primarily insect-pollinated with a trend toward self-pollination (Vuille 1988). *Caldesia grandis* and *C. parnassifolia* are also self-compatible (Gituru et al. 2002). In the gynodioecous *Echinodorus longipetalus*, individuals having bisexual flowers were found to be self-compatible (Pansarin 2008), whereas *E. grandiflorus*, wherein only bisexual flowers are known is self-incompatible (Pansarin & Pansarin 2011).

Another family of the Alismatales, the **Araceae**, comprise 120–130 genera and over 3300 species having a cosmopolitan distribution; Araceae are most abundant and diverse in tropical latitudes. Flowers and inflorescences of Araceae are very different in construction from other families in the order. The inflorescence is composed of an unbranched spike made of densely grouped flowers known as the spadix; this is subtended by a bract called the spathe. Flowers can have a perigon or be without it. The spadix itself can bear bisexual flowers only or can be specialized, having proximally pistillate flowers and distally staminate flowers, and there can be one or several zones of sterile flowers or entirely naked axial zones, and smooth or staminodial terminal appendices. The development of the spathe into a lower tube and an upper expanded blade is another differentiation. Araceae are all protogynous (Mayo et al. 1997). With regard to pollination, Araceae are principally pollinated, more or less exclusively, by flies, bees and beetles (Grayum 1984, 1990, Mayo et al. 1997). Since the literature on Araceae is extensive, I provide only a few examples each of myiophilous, melittophilous and cantharophilous species from observations of our group as well as other authors, and in the general discussion section there is reference to the hypothesized evolution of pollination in the family.

Pollination has been well-studied in several *Arum* species; they attract flies or beetles, searching for breeding sites in decaying organic matter, and are kept inside the inflorescence "kettle" during the pistillate stage, and later released covered with pollen, after the staminate stage. Several species are known to warm-up (e.g. Bermadinger-Stabentheiner & Stabentheiner 1995, Seymour et al 2009a, Linz et al. 2010). Not all *Arum* species attract their pollinators by deception, some provide resources to the insects (e.g. Lack & Diaz 1991, Albre et al. 2003, Diaz & Kite 2006). Species of *Arisaema* attract fungus gnats (Mycetophilidae and Sciaridae), which are released in the few monoecious species, but die inside the female inflorescences of the dioecious ones, after pollen deposition on stigmas (Vogel & Martens 2000, Barriault et al. 2010). *Anthurium* and *Spathiphyllum* species are known to have several different pollination systems, among which are some pollinated by euglossine bees (Williams & Dressler 1976, Croat 1980). For example, *Anthurium sagittatum, A. thrinax, A. rubrinervum*, and *Spathiphyllum humboldtii*, observed in French Guiana, are pollinated by scent-collecting male euglossine bees (Hentrich et al. 2007, 2010). Different bee species visited the inflorescences of the sympatric, simultaneously flowering Araceae in the pistillate and staminate stages. Analysis of the scent samples showed that each plant species emitted a specific floral bouquet that clearly differed from the bouquets of the other studied sympatric species. It was hypothesized that the different floral scents lead to clear separation of the main pollinating euglossine species, providing a directed and efficient intraspecific pollen flow that results in high reproductive success.

The large genus *Philodendron* with 500–700 species has a complex inflorescence morphology, with pistillate flowers proximally on the spadix, followed by a sterile

staminate zone and a distal fertile staminate zone. The large spathe forms a pollina-
tion chamber, known as a kettle at the spathes' base and which opens in the upper
part. The first correct description of pollination in *Philodendron*, probably of *P. lun-
dii*, growing at Lagoa Santa, Minas Gerais, was by Warming (1883). One hundred
years later, the two species, *P. selloum* and *P. bipinnatifidum* (both species, together
with *P. lundii*, belonging to the *P. bipinnatifidum* complex of subgen. *Mecanostigma*)
were compared. It was recognized that the inflorescences warm-up strongly in the first
night of flowering in the pistillate stage (*P. selloum*), or can warm-up also in subse-
quent nights in the pistillate and staminate stages (*P. bipinnatifidum*), and depending
on the spectrum of potent scent compounds emitted during heating (thermogene-
sis), attract species specific dynastid scarab beetles, namely *Erioscelis emarginata* in
P. selloum (Fig. 2) and *Cyclocephala variolosa* in *P. bipinnatifidum* (Gottsberger &
Amaral 1984). Studies on these species were extended and the olfactory and visual
attraction of the beetles to the inflorescences was tested (Gottsberger & Silberbauer-
Gottsberger 1991). Subsequently, we studied other *Philodendron* species in the
Amazon region (Silberbauer-Gottsberger et al. 2001). The scent compounds of two
species of the *P. bipinnatifidum* complex were analyzed and their attractivity to the
respective pollinating beetles was tested. The comparative data were refined and
placed in context of the population structure of the investigated species, their geo-
graphical distribution, the pollination processes, including anthesis and thermogene-
sis, and the behavior of the beetles (Dötterl et al. 2012, Gottsberger et al. 2013). The
results showed convincingly that pollination in *Philodendron* is very sophisticated
and highly specialized. Each species of *Philodendron* attracts usually only one spe-
cies of dynastid scarab beetle. The floral scent emissions that accompany the intense
heating (thermogenesis) of the inflorescences, which in *P. selloum* reaches a world
record for plant tissues, of greater than 45°C, and a relative heating of more than
30°C, are essential for attraction of the specific beetle species, as well as for their
behavior, maintenance and welfare inside the kettle. Studies on other *Philodendron*
species have revealed many further interesting details about this fascinating system
(see Gibernau & Barabé 1999, Gibernau et al. 1999, 2000, Seymour & Gibernau
2008, Maia et al. 2010, Pereira et al. 2014).

   With regard to the breeding system of Araceae, self-compatibility was found in
many cases, although some authors remarked that there was a lower fruit set in selfed
inflorescences as compared to out-crossed ones: *Pinellia tripartita* (Uhlarz 1985),
Dieffenbachia longispatha (Young 1986), *Spathiphyllum friedrichsthalii* (Montalvo &
Ackerman 1986), *Peltandra virginica* (Patt et al. 1995), *Montrichardia arborescens*
(self-compatible or apomictic, Gibernau et al. 2003), *Xanthosoma daguense* (García-
Robledo et al. 2004), *Arum maculatum* and *A. italicum* (Diaz et al. 2006), *Anthurium
acaule, A. cristalinum, A. fendleri, A. salviniae, A. spectabile, A. trinerve, A. upa-
lahense* (Chouteau et al. 2006), *Alocasia portei, Anthurium longistamineum* and
A. schlechtendalii, Dieffenbachia oerstedii, D. seguine (Chouteau et al. 2008) and
Taccarum ulei (Maia et al. 2013b). On the other hand, *Arisarum vulgare* was found to
be self-incompatible (Koach & Galil 1986). For A*rum maculatum* there are conflicting
results, because Dieterle (1999) found the species to be self-incompatible, while cer-
tain authors of the aforementioned found it to be self-compatible.

Fig. 2. *Philodendron selloum* (length of inflorescence ca. 25 cm). A. One individual of pollinating beetles (*Erioscelis emarginata*) is approaching a first-evening, pistillate stage inflorescence. After collision with the spathe the beetle will fall into the kettle where the pistillate flowers are in the receptive stage. B. During the second day, the accumulated beetles try to protect themselves against daylight at the base of the kettle. C. On the second evening, the distal staminate flowers of the spadix press out pollen grain chains. The spathe is closing and the beetles are obliged to move upwards and to pass the pollen-producing region. D. Pollen-covered beetles arriving at the top of the spadix, shortly before flying off.

Pollination in Magnoliids

The magnoliids comprise four orders, the clade Canellales and Piperales, which apparently are sister taxa to the clade Laurales and Magnoliales (APG III 2009).

Canellales

To the best of our knowledge, there are few reports on the floral biology of **Canellaceae**. The family comprises five or six genera and about 20 species in Madagascar, Africa, South and Central America and the Caribbean (Kubitzki 1993b). Flowers are bisexual having a basic trimerous or pentamerous organisation. Protogyny was observed in the Caribbean species, *Canella winterana*, and all flowers of a tree were strictly synchronized: they were either all in the pistillate or the staminate stage (Wilson 1982). The epidermal cells of the filament tube produce nectar (Erbar 2014), and, in addition to small insects, the flowers attract paper wasps, butterflies, leaf-cutting bees and hummingbirds (Wilson 1986). Kubitzki (1993b) remarked that in herbarium material of *Cinnamodendron dinisii* he found that the androecial tube was elongated and enclosed the stigma in a later stage.

Phylogenetic studies of **Winteraceae** (e.g. Ehrendorfer et al. 1979, Suh et al. 1993, Endress et al. 2000, Ehrendorfer & Lambrou 2000, Karol et al. 2000, Doust & Drinnan 2004) assign a basal position to the endemic Madagascan monotypic genus *Takhtajania*, which is sister to the remainder of the Winteraceae; the next branches are *Tasmannia* (7 spp., Philippines to Tasmania), *Drimys* (7 spp., distributed from southern Mexico to the south of South America), and *Pseudowintera* (3 spp., New Zealand). The former genera *Bubbia, Belliolum, Exospermum* and *Zygogynum* were combined into a single genus *Zygogynum s.l* (Vink 1993). The generic relationships in Winteraceae were re-studied by Marquinéz et al. (2009a), and their analyses based on nuclear and plastid sequence data corroborated monophyly of *Drimys, Tasmannia, Pseudowintera, Zygogynum s.l.* and they also corroborated the same phylogenetic relationships obtained by Karol et al. (2000) and Doust & Drinnan (2004). Flowers are usually bisexual (unisexual in *Tasmannia*) and are either small or relatively large, and petal color is white, yellow, yellow-purple or red.

Flowers of the apparently earliest-divergent Winteraceae, *Takhtajania perrieri*, were found to be visited by flies (pers. comm. in Thien et al. 2000). In the dioecious genus *Tasmannia*, staminate flowers having sterile carpels can occur and bisexual flowers are also sometimes been observed (Vink 1970, 1993, Frame 2003b). *Tasmannia insipida* has a ventral stigmatic crest running the length of the carpel. The sepals fuse laterally and form a protective cover, called calyptra. The carpel grows up as a completely open structure in the early stages of its development. Later the carpels close and cells of the stigmatic surface excrete a sticky fluid. First, there appeared calyptra-formed droplets on both pistillate and staminate flowers, which probably function as a "reward" to potential pollinators in advance of flower opening. Pollen tubes were observed to grow along epidermal cells of the stigmatic crest but did not germinate in the calyptra-formed droplets (Frame-Purguy 1996, Frame 2003b). In Papua New Guinea, individual plants of *T. piperita* had pistillate, staminate and bisexual flowers. The white-petaled flowers were functional for 10–12 days and did not close at night. Upon opening, the

stigmatic crests of the carpels of pistillate or bisexual flowers secreted large drops of sugar-containing fluid. Stamen connectives also secreted nectar. In addition to carpellary and staminal secretions, the base of the petals in some infraspecific taxa of this species also exuded a liquid upon which visitors fed. The only published account of insect pollination is that of Thien (1980), who found flies visiting the sweet-scented flowers of *T. piperita*, at very high altitudes (3200–3500 m). Coleoptera, Hymenoptera and Hemiptera were occasional visitors. At high elevation, where it is cold, flies usually replace other pollinators, which might be present at lower elevations. There are other species of *Tasmannia*, growing at lower altitudes, that may likely be insect pollinated. *Tasmannia* has open flowers, and there is nothing to prevent other insects visiting the flowers, such that it does not appear to have flowers specialized on flies, as it is definitely not a trap flower, nor is the flower foul smelling (pers. comm. Dawn Frame, 2015). It is possible too, that some species may be wind-pollinated, in view of the large fraction of *Tasmannia* pollen recorded in regional pollen rain in Australia (Sampson 1987).

Drimys brasiliensis, studied in southeastern Brazil, was found to open its flowers for the whole day, without any synchronization. As the bisexual white flowers (2 cm diam.) open, they are already in the pistillate stage; stigmas are covered in exudates, but anthers are still closed (protogyny). From about the second or third day of flowering, stamens start to shed pollen, and this pistillate-staminate stage can last for a few days until the flowers pass into the final, purely staminate stage (Gottsberger et al. 1980). The open flowers emitted a slight, pleasant odor, principally from the petals, recalling the scent of vanilla or violets, and which was especially strong during the day hours. During the first and second night, as long as the flowers are in the purely pistillate stage, the petals bend over the flower center, until the flower is closed, and unfold again the following morning. A broad spectrum of insects visited the flowers. The most common visitors were small Coleoptera (Curculionidae, Nitidulidae, Mordellidae, Anobiidae, Tenebrionidae, Chrysomelidae, Dermestidae), and Diptera (Bibionidae, Scatopsidae, Sciaridae, Syrphidae, Chloropidae) and Thysanoptera, and occasionally also Lepidoptera, Hemiptera and Collembola. On very hot days, flies outnumbered beetles. With regard to the beetles, curculionids searched regularly for pollen and stigmatic exudates often in one and the same flower. Further effective pollen eaters and transporters were nitidulid, mordellid and tenebrionid beetles; flies and thrips visited the top of the stamens, probably to feed from small anther glands found there, as well as on the sticky stigmas. The endemic species *D. confertifolia*, on Juan Fernández Island was found to have nectarless, anemophilous flowers and to be self-compatible (Anderson et al. 2001). *Drimys granadensis*, studied close to Bogotá, Colombia was visited by 29 morpho-species representing 21 families of Coleoptera, Diptera, Hymenoptera, Psocoptera, Neuroptera and Thysanoptera; considering the pollen loads carried by the insects, four species of beetles (Curculionidae and Chrysomelidae) and two species of flies (Bibionidae and Empididae) probably were the most efficient pollinators (Marquinéz et al. 2009b). Several of the flower visitors were preyed upon by spiders (12 morpho-species belonging to seven families), which have camouflage colors and were observed also to forage on stigmatic exudates (Marquinéz et al. 2010).

The greenish-white, protogynous flowers of *Pseudowintera colorata*, studied in New Zealand (Lloyd & Wells 1992), have a pistillate stage lasting on average 6 days. Afterwards pollen is shed. Pollination occurred during the day, with flower visitors spanning a rather broad taxonomic range. Holodid beetles and chironomid flies of the genus *Smittia* were by far the most abundant visitors. The flies visited staminate phase flowers infrequently and probed the stigmatic exudates rather than fed on pollen. Flies were more common than beetles, but beetles carried more pollen and they visited both flower stages more consistently.

Zygogynum s.l. seems to be late-divergent among the Winteraceae (e.g. Karol et al. 2000, Doust & Drinnen 2004, Marquinéz et al. 2009a), and its approximately 40 species are distributed in Australia, New Guinea, Moluccas, New Caledonia and the Solomon Islands. Three New Caledonian species of *Zygogynum s.s., Z. pancheri, Z. pauciflorum* and *Z. crassifolium* were studied by Thien (1980). The relatively large, scented, yellow flowers, are protogynous and function all in a similar manner; they were all found to be pollinated by a single species of thrips, *Taeniothrips novocaledonensis*. The insects chewed on the stigmas and ate pollen.

Zygogynum baillonii and *Z. pomiferum* were also studied in New Caledonia (Thien 1980). The remarkable characteristics of the flowers of these two species are the thick and leathery petals, which make movements during anthesis. *Zygogynum baillonii* has yellow-orange, protogynous flowers with a strong burnt-orange scent. The upright flowers open over several hours in the morning. The outer petals extend, but the inner ones only open slightly, forming a kind of pollination chamber. The flowers close again in the late afternoon of the first day of anthesis. Early on the second day all petals open, the stigmas are no longer receptive and the anthers dehisce and release pollen. *Zygogynum pomiferum* has thick pale green petals and a strong banana-like scent; petal movement and duration of anthesis, with the pistillate stage during the first day and the short staminate stage during the morning of the subsequent day, are similar to the former species. Chrysomelid beetles in *Z. baillonii* and curculionids in *Z. pomiferum* were found to enter the floral chamber during the first day and to leave the flowers during the second day in the staminate stage when all petals expand. An additional flower visitor was a species of *Sabatinca*, a representative of the basal moth group Micropterigidae. In subsequent studies (Thien et al. 1985, Pellmyr et al. 1990) the importance of beetles and the micropterigid moth *Sabatinca* was shown. Adult *Sabatinca* moths have grinding mandibles and usually feed on spores of ferns and pollen. The moths use the flowers of *Zygogynum* as mating sites and eat the pollen which is immersed in a dense pollenkitt. Since fossil records of both the moth and the Winteraceae extend to the Early Cretaceous, it was assumed that this association is an ancient one. Visitors to several *Zygogynum s.l.* species were found to be two species of *Sabatinca* and three species of weevils (*Palontus* spp., Curculionidae). The *Palontus* beetles often carried pollen on their body, while the moth *Sabatinca* carried only light loads on their heads. Thien and co-workers concluded that the beetles are regular pollinators while *Sabatinca* is a more occasional pollinator. Thien et al. (1990) found densely packed polysaccharide granules at the inner surface of petals of several species of *Zygogynum* and interpreted them as "food-bodies", which function as pollinator rewards for beetles.

We found (Gottsberger et al. 1980) that cross-pollinated flowers of *Drimys brasiliensis* had a 24% higher fruit set than bagged self-pollinated flowers. Still, self-pollinated flowers formed normal ripe fruits and seeds, an indication that self-compatibility is a possible mode of reproduction in this species. Also Thien (1980) mentioned that bagged buds of *Zygogynum pancheri* set fruit after flowering. Adam & Williams (2001) reported of high levels of selfing in monoecious individuals of the otherwise dioecious *Tasmannia insipida*. On the other hand, *Pseudowintera colorata* did not form fruits after self-pollination (Godley & Smith 1981), and self-incompatibility in this species was later confirmed by Lloyd & Wells (1992; see also Sage & Sampson 2003 for *P. axillaris*). Sage et al. (1998) mention several authors which, recording to them, have reported on self-sterility in the genera *Belliolum, Bubbia, Drimys, Exospermum, Pseudowintera, Tasmannia* and *Zygogynum*, essentially deduced from the failure to produce fruit following self-pollination. Sage et al. (1998) studied *Pseudowintera axillaris* and *Drimys winteri* and found that ". . . self-sterility mechanisms in both species appear to result in failure of embryo sac development after double fertilisation has been effected by self-pollen tubes."

Piperales

According to the APG III (2009) classification, the order Piperales comprises families having a perianth, i.e. Aristolochiaceae and Lactoridaceae, and those lacking a perianth, i.e. Piperaceae and Saururaceae (e.g. Jaramillo et al. 2004). The relationships of the holoparasitic Hydnoraceae is unclear within Piperales, but molecular and morphological data indicate that the two genera of Hydnoraceae, *Hydnora* and *Prosopanche*, comprise a clade together with Aristolochiaceae *sensu lato* (including Lactoridaceae). This clade is sister to the other clade composed of Piperaceae and Saururaceae (Nickrent et al. 2002, Neinhuis et al. 2005). Recently, Christenhusz et al. (2015) reported that there is support for Lactoridaceae and Hydnoraceae being nested in Aristolochiaceae *s.l.*

Accepting two subfamilies in **Aristolochiaceae** *s.s.* has gained support especially in light of the study of Neinhuis et al. (2005). Subfamily Asaroideae has about 85 species occurring mainly in northern temperate regions, with a center in Asia; subfamily Aristolochioideae has about 420 species having a predominantly pantropical distribution. Results by the aforementioned authors also provides evidence that within Asaroideae, *Saruma* is sister to *Asarum*. The monotypic *Saruma henryi* from China is outstanding in Aristolochiaceae by possessing apocarpy, a free green outer, and yellow, inner perianth, free anthers and carpels, and sulcate pollen. This species also has small, trimerous polysymmetric flowers, and superficially similar to Annonaceae flowers (Dickison 1992, Leins & Erbar 1995). A cladistic analysis and examination of the pollination mechanisms of the protogynous flowers in the genus *Asarum* seems to support the conclusion that herkogamy (short filaments and spatial isolation of dehisced anthers and stigmas), and thus obligate insect pollination, is derived from a plesiomorphic condition of autonomous self-pollination (stamen movements with deposition of copious amounts of pollen directly on the stigmatic surface) (Kelly 1997). Such a plesiomorphic condition, for example, occurs in *A. europaeum*, which despite an intense unpleasant or pleasant scent (various authors have either perceived the scent

differently or there exist mutants having different scents) was never found to be visited by insects and is self-pollinating (e.g. Kugler 1934, Daumann 1972). On the other hand, *Asarum caudatum* and other *Asarum* species are regularly pollinated by fungus gnats (e.g. *Fungivora fungorum*, Mycetophilidae) (Vogel 1978, but see criticism by Lu, 1982). The fungus gnat flowers of *Asarum* species are fungi mimics and attract midges, which mate on the flower and even oviposit; the subsequent larvae, incapable of eating flower tissue, die before anthesis ends. Pollination by brood-site deception appears to be common in *Asarum* and also occurs in *Aristolochia* (Vogel 1978, Burgess et al. 2004).

Flowers of the Aristolochioideae are also basically trimerous, functionally protogynous and the perianth is mostly gamophyllous. Most species depend on insects for pollination and they are all myiophilous or sapromyiophilous. The basic floral mechanism of *Aristolochia* has been known since Sprengel (1793). Huber (1993) summarized characters typically associated with fly pollination, such as flower gigantism, something not intuitively obvious given the small size of the pollinators (e.g. Hipolito et al. 2012); caudate perianth lobes often bearing osmophores (Vogel 1962); flower parts imitating fruiting bodies of mushrooms (including their lamellae), and the flowers indeed being pollinated by fungus gnats (Vogel 1978); in some species there are limb-born floral nectaries or nectarioles, which play a role in attraction of certain flies (Daumann 1959, Vogel 1998b, Murugan et al. 2006), and in some cases the nectar functions as food to guarantee survival of the imprisoned pollinators, in which case the nectaries are of the trichomatous type located inside the utricle (e.g. Vogel 1998c, Erbar 2014); dark purple, brown to black coloration, often set against yellow or green background; a musky, fruit-, fungus-, urine- or carrion-like odor in several species; and the perianth tube converted into a trap, which commonly retains the visitors by a smooth, oily inner surface or by stiff "trap hairs". These hairs allow the visitors to enter the basal part of the perianth tube, the utricle, harboring the stigmas and anthers, but inhibits their exit until hairs wilt after pollination. For new data on the contribution of trapping trichomes to the capture, retention and release of pollinators see Oelschlägel et al. (2009). Oelschlägel et al. (2015) described an extraordinary kleptomyiophilous strategy for *A. rotunda*. The main pollinators are female chloropid flies. The flies are food thieves that feed on secretions of true bugs (Miridae) while these are eaten by arthropod predators. Freshly killed mirids and *A. rotunda* flowers release the same scent compounds that chloropids use to find their food sources. Most species of *Aristolochia* have a floral longevity of 2–3 days, however, *A. chilensis* and other species occurring in arid and low productive environments, produce flowers lasting up to 8 days. This might be correlated with the low abundance of pollinators in dry and unfertile habitats (Stotz & Gianoli 2013). Data presented in Endress (1994), Murugan et al. (2006), Nakonechnaya et al. (2008), Berjano et al. (2009) and Stotz & Gianoli (2013) indicate that flies of the following families visit and eventually pollinate *Aristolochia* species: Agromyzidae, Anthomyiidae, Asillidae, Bibionidae, Borboridae, Calliphoridae, Cecidomyiidae, Ceratopogonidae, Chironomidae, Chloropidae, Dolichopodidae, Drosophilidae, Empididae, Ephrydidae, Fanniidae, Heleomycidae, Heteromyzidae, Lauxanidae, Lonchaeidae, Millichiidae, Muscidae, Mycetophilidae, Neriidae, Ortalidae, Otitidae, Phoridae, Piophilidae, Pipunculidae, Platystomatidae,

Psychodidae, Richardiidae, Sarcophagidae, Scatopsidae, Sciaridae, Sepsidae, Spaeroceridae, Syrphidae, Tachinidae, Tephrididae, Trypetidae and Ulididae.

With regard to the breeding systems of Aristolochiaceae, as mentioned previously, studies of *Asarum* indicate that self-compatibility (Kugler 1934, Daumann 1972, Lu 1982), partly with autonomous self-pollination is basal in the genus, while herkogamy with obligate cross-pollination by insects, seems to be derived; it is not clear whether the herkogamous species have a self-compatible or self-incompatible breeding system (Kelly 1997). The genus *Aristolochia* has both self-compatible (e.g. *A. argentina*, Trujillo & Sérsic 2006) and self-incompatible species. For example, Nakonechnaya et al. (2008) attribute (partly based on the literature) self-pollination and self-compatibility for *A. manshuriensis, A. littoralis, A. barbata, A. brasiliensis, A. bracteolata. Aristolochia arborea* (Cammerloher 1922) and *A. paucinervis* (Berjano et al. 2006) have autonomous self-pollination leading to fruit set. Cleistogamy occurs in *A. serpentaria* (Pfeifer 1966). Murugan et al. (2006) found self-compatibility in *A. tagala* and note that few *Aristolochia* species are self-incompatible, as for example *A. maxima, A. gigantea* and *A. grandiflora*.

The monotypic *Lactoris fernandeziana* (**Lactoridaceae),** endemic to the Juan Fernández Islands, has small, green, trimerous, solitary flowers (or few-flowered inflorescences); the unisexual flowers have vestiges of staminodia or pistils (Kubitzki 1993e). The study by Bernardello et al. (1999) and Anderson et al. (2001) has shown that this species is gynomonoecious and wind-pollinated. Bisexual flowers are herkogamous and protogynous. Based on experimental hand self-pollinations, the plant is self-compatible (geitonogamous) and capable of outcrossing. The coupling of wind pollination and self-compatibility in *Lactoris* might by a consequence of the scarcity of pollinators on Juan Fernández Islands (Anderson et al. 2001).

Members of the holoparasitic family **Hydnoraceae** have a rhizome-like underground organ on which flower buds develop and emerge from the soil at anthesis. The actinomorph protogynous flower is a more or less large (5.5–11 cm diam.), cylindrical, fleshy tube having fleshy lobes, which bear the reproductive organs on the inner tube wall and on its base. Hydnoraceae comprises two genera, *Hydnora* and *Prosopanche. Hydnora* has seven species and is distributed in Africa, Réunion, Madagascar and Saudi Arabia. Three species of *Prosopanche* are known and occur in South and Central America (The Plant List 2013). In *Hydnora* only the perianth lobes and sometimes part of the floral tube emerge above the soil. In *H. africana*, osmophores on the thick, orange-red tepal lobes emit a putrid, carrion-like odor that attracts beetles, which drop into the deep floral tube of the protogynous flower. The smooth inner surface and the vertical inclination of the tube prevents most visitors from escaping. After about 3 days of strong odor production in the pistillate stage, anthers open and shed pollen. At about this time, too, the surface of the floral chamber begins to change, creating a surface that facilitates release of the pollen-impregnated insects. Among the 10 beetle species that visit flowers, the most common one (77% of all visits) was *Dermestes maculatus* (Dermestidae), which is known to oviposit exclusively on carrion (Bolin et al. 2009). Recently, a new *Hydnora* species, *H. visseri* was recognized upon segregation from *H. africana* (Bolin et al. 2011). The primary pollinator of *H. visseri* was found to be *Dermestes maculatus* (no fly visitors), while *H. africana* was found to attract numerous

flesh flies (Sarcophagidae) in addition to beetles. It appears that different floral scent compounds of these two *Hydnora* species attract a different insect spectrum. *Hydnora triceps* also attracts dermestid beetles and blow or carrion flies (Calliphoridae), and *H. johannis* is pollinated by scarab beetles (Musselman & Visser 1989, Bolin et al. 2009). Hence, *Hydnora* flowers can be classified as exhibiting brood-site mimicry with imprisonment. Low thermogenesis (in *H. abyssinica* 2.8 °C and in *H. esculenta* 3.8 °C above ambient temperature in the pistillate stage) appears to be associated with scent production. On the other hand, in *H. africana* no temperature elevation could be measured (Seymour et al. 2009b). The pollinating carrion beetles and carrion and flesh flies of *Hydnora* apparently do not oviposit while inside the flowers (Bolin et al. 2009). Among American members of the Hydnoraceae, flowers of the South American *Prosopanche americana*, which exhibit thermogenesis (Cocucci & Cocucci 1996), also emit an unpleasant smell and were found to be pollinated by nitidulid (*Neopocadius nitiduloides*) and curculionid (*Oxycorynus hydnorae*) beetles. Both beetle species, besides being considered effective pollinators of *Prosopanche*, have been observed to oviposit in the floral tube; their larvae fed on tube tissue and they completed their development underground on the plant (Bruch 1923). The second Argentinian species, *P. bonacinae*, is associated with two weevil species, *Hydnorobius hydnorae* and *H. parvulus* (Ferrer & Marvaldi 2010). Thus, several members of Hydnoraceae are strictly cantharophilous (saprocantharophilous), while others (e.g. *H. africana*, *H. triceps*) eventually have a mixed saprocantharophilous/sapromyiophilous pollination system. The role of fly-mediated pollination, however, was not yet been fully worked out (Bolin et al. 2009). At present, nothing is known about the breeding system of Hydnoraceae (see Bolin et al. 2009).

Piperaceae are pantropical, but the great centers of diversification are in the Neotropics and Southeast Asia. They are poorly represented in Africa wherin there are only two native species of e.g. *Piper* (Smith et al. 2008). Piperaceae are notable for their spicate or racemose inflorescences having minute perianthless flowers, each subtended by a single bract. Flowers are bisexual or unisexual; in the latter case species are monoecious or dioecious (Tebbs 1993). Early on, largely due to their inconspicuous flowers and inflorescences, many researchers thought that Piperaceae had abiotic pollination, by wind and/or rain water (e.g. Martin & Gregory 1962). This despite even earlier workers e.g. F. Müller (1922) and Wettstein (1935), having mentioned flies, bees and beetles as visitors of the inflorescences and from this deducing entomophily for Piperaceae. Semple (1974), Vogel (1998a) and Figueiredo & Sazima (2000) have shown that insects regularly visit and pollinate Piperaceae flowers. In the study by Semple (1974) in Costa Rica, *Piper aduncum, P. auritum, P. friedrichsthalii, P. villiramulum* and *Pothomorphe peltata* were investigated. The flowers of all studied species are bisexual and protogynous, the stigmas being exserted several days before anther dehiscence. Several species of *Trigona* (Apidae) besides *Augochloropsis* and *Lasioglossum* bees (Halictidae) and several small unidentified beetles visited the inflorescences of these species. *Trigona* bees were the most common, and small beetles were the next most numerous, visitors. *Trigona* seemed to be the most efficient pollinater, because these bees collected large amounts of pollen by working up and down the spikes, and they were observed to fly from spike to spike. Up to six bees

were observed on a spike at a time. Individual bees were seen flying from one *Piper* species to another, indicating weak species constancy on single foraging trips. Wind pollination was found to be unlikely because of the sticky nature of the pollen grains. The author found that even after rain storms pollen still was present on the spikes. The study of Figueiredo & Sazima (2000) in southeastern Brazil included eleven species of *Piper*, two species of *Ottonia* and *Pothomorphe umbellata*. The majority of the species studied exhibited incomplete protogyny, *Piper mikanianum* showed complete protogyny, *P. xylosteoides* incomplete protandry, and *P. regnelli* homogamy. All but one species had bisexual flowers; the exception was *Piper arboreum*, which had some inflorescences having only staminate flowers and others only bisexual ones. Prior to this, andromonoecy had not been recorded in Piperaceae. In *Peperomia fraseri* another unique sex distribution was found by Remizowa et al. (2005), here, the lower flowers of each spike are bisexual and the distal region of the same inflorescence bears pistillate flowers (gynomonoecy). The inflorescences of the species studied by Figueiredo & Sazima (2000) were creamy, yellowish or whitish in color, and most of them (except *Piper aduncum*) produced a sweet, lemon-like odor. Nectar was not discernible in the flowers, although heretofore observed by other authors. Pollen of all species was found to be dry. Insects visited inflorescences of all species for pollen, moving up and down the inflorescences. The most important were syrphid flies and apid bees, while some Coleoptera and Hemiptera behaved as herbivores and appeared not very important for pollination. Wind pollination was found to occur additionally to entomophily in at least seven species, leading to the conclusion that the investigated Piperaceae showed attributes commonly associated with entomophily and anemophily and have therefore to be considered ambophilous. These authors studied eight further *Peperomia* species (Figueiredo & Sazima 2007). Pollination by wind and Syrphidae was confirmed for two self-incompatible species. The remaining six species are self-compatible and their high fruit set was accounted by autonomous self-pollination or agamospermy. In *Peperomia magnoliifolia* (protandrous with a distinct fruity smell reminiscent of *Alocasia odorata*) and some related taxa, Vogel (1998a) described nectarioles on the floral bracts, which are extrafloral but nuptial in function; these produced a sugar-containing liquid that attracted sciarid and muscid flies. On the basis of his observations, Vogel hypothesized a sapromyiophilous syndrome for the study species. *Piper marginatum*, studied north of Recife, Northeast Brazil, was revealed to have bisexual, also protandrous flowers (Ulbricht 2006). The cream-colored, sweet-aromatic-scented inflorescences were visited by a broad spectrum of insects between 7:30 a.m. and 4 p.m., which consisted principally of bees (*Tetragonisca angustula, Exomalopsis* sp., *Augochloropsis* sp., *Apis mellifera*), flies (5 spp. of Syrphidae), lacewings (one species of Chrysopidae, Neuroptera) and beetles (among others Chrysomelidae).

The breeding systems in Piperaceae are known for only few species. The Paleotropic *Piper nigrum* and the Neotropical *P. arieianum* are reported to be self-compatible (Martin & Gregory 1962, Marquis 1988, Sasikumar et al. 1992), while the Paleotropical *P. methysticum* is self-incompatible (Prakash et al. 1994). Five of the eleven species investigated by Figueiredo & Sazima (2000) show a substantial degree of self-compatibility (of these five species, *Piper aduncum* and *Pothomorphe umbellata*, may be agamospermous, since all inflorescences developed fruits), while the

other species evinced a low degree of self-compatibility or were self-incompatible. *Piper marginatum* was revealed to be self-incompatible (Ulbricht 2006).

Saururaceae (6 species) have a disjunct distribution in North America and East and Southeast Asia. The inflorescences are dense spikes, which in *Houttuynia, Anemopsis* and *Gymnotheca* have showy bracts at the base of the spike, giving the inflorescence a pseudanthial appearance. The flowers are bisexual and without perianth (Cheng-Yih & Kubitzki 1993). The nectarless flowers of *Saururus chinensis* have a faint scent and were found to be visited by many insects, especially syrphid flies (Tanaka 1979). *Saururus cernuus,* investigated in southern United States near New Orleans (Thien et al. 1994), has sweet smelling, protogynous flowers, pollinated by wind, bees, flies and beetles. When large insects land on the spike, small clouds of pollen are released into the air (insect-mediated wind pollination). Thien and collaborators concluded that wind, insect-mediated anemophily and insects alone or in combination contribute to fruit set in this self-incompatible species.

Laurales

Based on evidence from both molecular and morphological data, the order Laurales consists of seven families (Renner 1999, see also APG III 2009). The Calycanthaceae (including *Idiospermum*) are sister to the remaining six families, which form two groups, the Siparunaceae-Gomortegaceae-Atherospermataceae clade and the Hernandiaceae-Monimiaceae-Lauraceae clade (Renner 1999, Renner & Chanderbali 2000).

The deepest split within **Calycanthaceae** is between the monotypic tropical *Idiospermum australiense* (Idiospermoideae) and the temperate shrubs of the two other genera (Calycanthoideae) (Li et al. 2004, Zhou et al. 2006). Flowers of nearly all ten species of the family are bisexual and protogynous, and have a cup-shaped or urceolate receptacle (Kubitzki 1993).

Flowers of *Idiospermum australiense*, a canopy tree in tropical rainforests of North Queensland, are relatively large (ca. 3.5 cm in diam.), with some populations of the species being andromonoecious while others having only bisexual flowers (Worboys & Jackes 2005). Just as in other Calycanthaceae, tepals of *I. australiense* become progressively smaller distally, grading into persistent, rigid inner tepals, which cover the androecium. The stamens and their extended connective appendages exhibit a transitional series into staminodes. Food bodies on tepals, staminodes and stamens such as found in *Calycanthus*, or nectar production on tepals as in *Chimonanthus*, are not present in *Idiospermum*. The anthesis of an individual flower of *Idiospermum* lasts three to four days, although the wilting flowers remain attached up to 10–16 days. Tepals are creamy white during the initial pistillate stage, and strongly fragrant throughout the day. Moreover, during the staminate stage, which starts on the third day after tepal opening, fragrance is still strong, and tepals have meanwhile turned to a dull purple color. From the fourth day on the fragrance fades and flowers start to wilt. In the center of the flower, the inner tepals, together with the staminal appendages and staminodia form a crater, providing access to the stigmas for insects. A wide diversity of arthropods, including Diptera and 13 species of beetles, and most commonly thrips visited the flowers. Particularly thrips were most abundant in pistillate and staminate stage flowers. The authors conclude that *Idiospermum* has a generalist pollination

system, and that thrips and beetles are the main pollinators, rewarded by pollen and/
or floral tissue.

Vogel (1998a) found the strong-smelling flowers of the Chinese *Chimonanthus praecox* to have melittophilous characters. The outer tepals are cream or light yellow and the inner ones are smaller and dull purple with yellow spots. In the pistillate stage, the stamens are bent toward the tepals and thereby expose the pistils. After two days, the stamens commence to bend toward the floral center (which may take from one to four days) until they enclose the pistil, thereafter the anthers shed their pollen (Azuma et al. 2005). Flowers of cultivated plants in Europe attracted bees (*Osmia cornuta* and honeybees), as well as syrphid, anthomyiid and drosophilid flies (Vogel 1998a). All insects imbibed the freely exposed nectar produced by nectarioles (Erbar 2014), an assemblage of glandular cells arranged around a single stomatal sap-hole on the inner petaloid tepals. Studies in China have confirmed that this species is pollinated by *Apis* bees as well as syrphid and muscid flies (Azuma et al. 2005).

The large, dark red flowers of *Calycanthus occidentalis* emit a wine-like, fermented fragrance at anthesis and were found to last 12–36 hours. After opening of the outer tepals and the beginning of the pistillate stage, the inner tepals maintain their semi-closed position and form a kind of pollination chamber. The innermost tepals, stamens and inner staminodes have pearl-white food bodies on their tips. In California, the nitidulid *Colopterus truncatus* (about 3 mm long) was found to be the main pollinator of this species (Grant 1950); the beetles eat the food bodies, which contain high levels of protein and low quantities of lipid and starch (Rickson 1979). At other places in the U.S., other nitidulid species of the genera *Colopterus* and *Carpophilus* were found to be effective pollinators of *C. occidentalis* and *C. floridus* (Nicely 1965, Williams et al. 2008).

The Chinese *Calycanthus chinensis* has flowers of 4–7 cm in diameter. The outer tepals are whitish with a tinge of pink, while the inner tepals are pale yellow to white with maroon markings; they are fleshy and form a kind of pollination chamber. The flowers are scentless and do not produce nectar. The distal margins of the petals and the connective appendages were found to bear a warty cover. Several subjacent cell layers were rich in cytoplasm and quite similar in consistence to the food bodies of the North American *Calycanthus* species. They represent food tissue rather than distinct food bodies as occur in the other two *Calycanthus* species. Vogel (1998a) suggested that the flowers of this species might reveal to be cantharophilous. Li & Del Tredici (2005) confirmed that this species is indeed pollinated by small beetles.

Information regarding breeding systems in Calycanthaceae is quite scarce. *Calycanthus chinensis* was found to be self-compatible and not apomictic (Zhang & Jin 2009) and *Chimonanthus praecox* to be self-compatible (Zhou et al. 2006, Du et al. 2012b).

Siparunaceae comprises two genera, the West African *Glossocalyx* and the New World tropics *Siparuna*. Flowers of *Siparuna* are strictly unisexual, small (a few mm in diameter), and sex distribution is monoecious (15 species) or dioecious (the remaining 38 spp. of *Siparuna*, as well as also *Glossocalyx*). The monoecious species are proposed to be evolutionarily basal to dioecious species (Renner & Hausner 2005). Reproductive organs in *Siparuna* are completely enclosed in massive cup-like

receptacles. A membrane, called floral roof or velum covers the reproductive organs except for a small pore in the center. At anthesis, the styles and anthers emerge through this pore. The styles may fuse postgenitally at the height where they emerge from the massive receptacle, resulting in a joint transmission track for pollen tubes that originally landed on different stigmas (Renner et al. 1997). Pollination has been studied in 13 dioecious species in Ecuador and Colombia (Feil & Renner 1991, Feil 1992, Peña Paz 2000), and six monoecious species in Central Amazonia (Schulz-Burck 1997). Data for these 19 species in addition to data from herbarium material suggest that pollination mode is identical throughout the genus (Renner & Hausner 2005). Flowers of dioecious species in Ecuador were found to be pollinated by gall-midges (*Asynapta* sp., *Clinodiplosis* sp., *Dasineura* sp., Cecidomyiidae, Diptera). Female cecidomyiids are attracted at night by the lemon-scented flowers and try to insert their abdomen into the pore of the floral roof of pistillate and staminate flowers in an effort to deposit an egg into the flowers' interior. Egg laying was chiefly in staminate flowers because they are more readily accessible than pistillate ones; pistillate flowers are almost entirely closed, with only the stigmas protruding, and thus unsuited for the ovipositing gall-midges. Pistillate flowers also aborted if eggs were laid in them. As insects moved during oviposition in the staminate flowers, their abdomens become covered in pollen. Mature larvae of cecidomyiids, drop from their host plants and construct silk cocoons in the soil. Holes have been observed in the receptacles of a few staminate flowers of *Siparuna* species that may have been created by exiting midges (Renner & Hausner 2005).

Gomortega keule, of monotypic **Gomortegaceae,** from Central Chile, produces small (4–5 mm diam.), white, protogynous flowers. Based on the size and shape of its flowers and the presence of large nectary glands at the bases of the filaments of outer staminodes (Kubitzki 1993c), Renner et al. (1997) postulated that it is pollinated by small flies and bees. Lander et al. (2009) collected 34 insects of six families at the flowers, 26 syrphids and 8 non-Syrphidae (among others one species each of lauxanid flies, sphecid and vespid wasps, a colletid bee and a Psocidae). Syrphid flies were the most common flower-visiting insects, carried the largest proportion of *G. keule* pollen and appeared to be effective pollinators of the species.

The **Atherospermataceae** may have unisexual or bisexual flowers (protogyny in bisexual flowers of *Daphnandra* confirmed by Endress 1992). Staminal appendages in *Laurelia, Daphnandra* and *Atherosperma moschatum* secrete nectar (Sampson 1969, Endress 1992, Erbar 2014). Sampson (1969) observed a considerable number of bees and blowflies (Calliphoridae) visiting the flowers for nectar; Schodde (1969) found them to be pollinated by flies and bees.

Flowers of the pantropical **Hernandiaceae** are bisexual or unisexual, in the latter case the plants are polygamous or monoecious, rarely dioecious. The filaments are usually provided with a pair of nectariferous glands and in pistillate flowers nectariferous staminodes are present; the anthers dehisce by valves (Kubitzki 1993d). For the strongly scented monoecious *Hernandia nymphaeifolia*, Endress & Lorence (2004) described a novel type of heterodichogamy of unisexual flowers not yet known for angiosperms. Within a population, two kinds of individuals occurred: individuals having pistillate flowers that open in the morning and staminate flowers that open in the afternoon,

while other individuals exhibited the reverse behavior. Heterodichogamy is considered a strategy to promote outbreeding; nonetheless, in *H. nymphaeifolia* geitonogamy is possible because anthesis of the morning and afternoon flowers overlap during midday. Pollination by small flies and bees was postulated for the family (Renner et al. 1997). The nectar-producing flowers of *Illigera* and *Hernandia* are mentioned as pollinated by bees or flies, and the small-flowered species of *Sparattanthelium* and *Gyrocarpus* said to be wind-pollinated (Michalak et al. 2010). Studies of *Sparattanthelium botocudorum*, in Atlantic forests in Northeast Brazil (Ulbricht 2006), found that the bisexual flowers (which initially emitted a sharp smell) opened between 4:00 and 5:00 a.m. and exhibited four or five, whitish, extended tepals (ca. 2 mm length), and presented an apparently receptive stigma as well as filaments and anthers; it was not observed if the flowers are slightly protogynous or not. From 8:00–9:30 a.m., tepals and stamens changed color becoming beige and finally brown. At the end of this stage, flowers scent was more sweetish and fruity. This stage lasted until about 10:30 a.m., as flowers became progressively browner, the scent faded and the flowers (from about 3:30 p.m. on) finally wilted. Pollination experiments indicated self-incompatibility for this species. Flower visitation, observed over two days, occurred during a relatively short period in the early morning hours when the flowers were still whitish and emitted their sharp scent, viz. between 5:45–7:45 a.m. in September and 4:45–8:00 a.m. in October. Observed flower visitors were five different unidentified fly species, two beetle species and two bee species (*Exomalopsis* sp., Apidae; and an Anthidiini, Megachilidae). Flies and bees were the most abundant visitors and appeared to be the most effective pollinators.

Among the pantropical **Monimiaceae**, most species have unisexual flowers (monoecious or dioecious), but several basal genera, e.g. *Hortonia* (Hortonioideae), *Dryadodaphne, Nemuaron, Doryphora* and *Daphnandra* (Atherospermatoideae) (Perkins & Gilg 1901) have regular bisexual flowers; protogyny has been confirmed in *Hortonia* and *Daphnandra* (Endress 1992). In *Hortonia angustifolia* and *Peumus boldus*, filaments bear two basal appendages, which are probably nectariferous (Erbar 2014). Under its present circumscription (Renner 1998), Monimiaceae are distinguished by having a massive cup-like receptacle that shows a trend towards enclosure of the reproductive organs (Endress 1979, 1980a, 1980b, 1994).

The genus *Mollinedia* is always dioecious. *Mollinedia floribunda* and *M. widgrenii*, investigated in Brazilian upland Atlantic rainforests in São Paulo and Botucatu, both in São Paulo State (Gottsberger 1977), were found to bear small roundish flowers of ca. 4–5 mm diam. Four tepals close the small opening of the receptacle during the bud stage. Buds and open flowers are greenish and had no perceptible smell. Female thrips (Thysanoptera) punctured the still closed pistillate and staminate buds in the region of the closed tepals with their ovipositor and deposited their eggs in the interior of the receptacle. When the flowers opened, their interior contained thrips eggs, larvae and adults. Adults not only stay inside flowers but can fly off; movements from staminate to pistillate flowers lead to pollination. Emerged female thrips also oviposited in new buds. Thrips visiting *M. floribunda* were identified as *Liothrips seticollis* (Phlaeothripidae) and *Heterothrips* sp. (Heterothripidae). Similarly, Mound and Marullo (1996) identified the heterothripid *Lenkothrips sensitivus* in large numbers in

the flowers of *Mollinedia latifolia* in Ecuador, and David H. Lorence (pers. comm. in letter, December 16, 1988) wrote that he had collected thrips from flowers of *M. viridiflora* in Veracruz, Mexico, indicating that thrips-pollination may be the standard mode of pollination within the genus. Also *Wilkiea huegeliana* in Australian subtropical rainforests is exclusively pollinated by thrips (Williams et al. 2001, Frame 2013), by the sole species *Thrips setipennis.* Similarly, in this species, both pistillate and staminate flowers serve as brood sites, with the difference that the entry of the thrips is always *via* the small apical ostiole of open flowers.

Endress (1979) discovered a most interesting structure, a "hyperstigma", unique to angiosperms, in *Tambourissa purpurea*. It is a secretary zone in the narrow entrance of the floral cup. At anthesis, the pistillate flowers of *T. purpurea* produce a mucilaginous plug in the apical floral entrance, and inside the floral cup there is a continuous mucilaginous film from the floral entrance to the carpels. Pollen grains deposited on the outer surface of the mucilaginous plug germinate and the pollen tubes grow through the mucilage to the carpels. Hyperstigmas not only occur in *Tambourissa* but also in *Wilkiea*, *Kibara* and *Hennecartia* (Endress 1980b). Anthesis of flowers of different *Tambourissa* species lasts 10–15 days. Flower color can be purple, pale white, cream, pink or pale orange, and floral scent of observed species has been recorded as more or less strong, fruity, sweet, sour, fermented, rancid or musky. All eleven species investigated produced mucilage on the free surface of the carpels, and *Tambourissa purpurea*, as described above, additionally produced mucilage at the hyperstigma. Staminate flowers do not produce any mucilaginous secretion. Flies (Drosophilidae, Lauxaniidae and Syrphidae) were visitors in six of the seven *Tambourissa* species studied, whereas beetles (Hydrophilidae, Nitidulidae, Rhizophagidae and Staphylinidae) were the main visitors of the four species *T. ficus, T. quadrifida, T. sieberi* and *T. tau* (Endress & Lorence 1983).

Experiments provide evidence of self-incompatibility for *Tambourissa quadrifida, T. tau* and *T. purpurea*, while *T. sieberi* was partly self-compatible (Endress & Lorence 1983). Pollinator exclusion experiments with the usually monoecious (sometimes dioecious) *Wilkiea huegeliana* were inconclusive but indicated possible facultative agamospermy (Williams et al. 2001).

Lauraceae have relatively small (1-)2–8(-20) mm diam. flowers, organized in compact or loose inflorescences. Flowers are open and easy accessible for most insects and their color usually is greenish, yellowish or white. Flowers are mostly trimerous, bisexual and protogynous, or unisexual. Plants with unisexual flowers are monoecious or dioecious. Tepals are in two whorls and stamens usually in four whorls, of which the innermost is sterile or lacking; sometimes other stamen whorls are sterile or lacking. Anthers open by valves. Stamens of the third androecial whorl of many Lauraceae have a pair of nectar glands (staminal glands) at their base (Rohwer 1993). Most Lauraceae having bisexual flowers possess an additional fourth androecial whorl that is sterile but provided with a glandular tissue (staminoidal glands). In the initial pistillate stage of these bisexual flowers, the staminoidal glands (whorl IV) produce nectar, whereas in the later staminate stage, the staminal glands (whorl III) produce nectar. These two different, short-use nectaries occur in heterodichogamous Lauraceae having bisexual flowers (Kurz 1982, Rohwer 2009). In such heterodichogamous species there exist

two cohorts of individuals in a population. Some individuals open their bisexual flowers in the morning in the pistillate stage and become staminate in the afternoon. The reciprocal individuals open their flowers in the afternoon (pistillate stage) and enter the staminate stage the next morning. The stamens do not open until the stigma of the same flower wilts. It was described in some species that the flowers close after the pistillate stage and open again at the onset of the staminate stage. Nectaries in both sexual stages are certainly useful to attract insects to visit both pistillate and staminate stage flowers. In Lauraceae, heterodichogamy with flower closing after the pistillate stage was early described for *Persea* species by Stout (1927) and Skutch (1932, 1945).

Amazonian heterodichogamous species of *Aniba, Clinostemon* and *Licaria* were visited by several small species of *Trigona* (Meliponinae), while dioecious unpleasant smelling species of *Ocotea* were visited by unidentified bees, flies, wasps and moths (Kurz 1982, Kubitzki & Kurz 1984). Six dioecious species of *Lindera* in Kyoto, Japan, were visited by a large number of mainly Coleoptera, Diptera and Hymenoptera, typical visitors of the generalist-pollinated Lauraceae flowers (Dupont & Kato 1999). The Brazilian cerrado species *Cinnamomum hausknechtii* has bisexual greenish-yellow flowers that emit a distinct sperm-like odor during the initial pistillate and the later staminate stage. Probably because of the spermatic odor, the spectrum of visitors was dominated by flies (eight families), and to a lesser degree visited by bees and wasps; beetles were rather rare pollinators (Gottsberger & Silberbauer-Gottsberger 2006). The dioecious *Laurus azorica* studied in the Canary Islands (Forfang & Olesen 1998) has a male-biased sex ratio. The population consisted of 2.5 times more male than female trees. Additionally, males produced more flowers and their inflorescences lasted longer. Flowers were visited by ten different species of Hymenoptera, Diptera, Lepidoptera, Coleoptera and Hemiptera, however, the bees *Halictus* sp. and *Lasioglossum* spp. (Halictidae) and the fly *Tachina canariensis* (Tachinidae) accounted for 97% of the total number of insect visits. The bees collected pollen and nectar and the fly collected nectar from flowers of both sexes. *Laurus nobilis* in Italy was mainly visited by *Apis mellifera*, *Bombus*, other bees, as well as flies and wasps (D'Albore & D'Ambrosio 1982). Another cultivated species, avocado, *Persea americana*, studied in its region of origin, Mexico, was visited by about 100 different insect species (Hymenoptera, Diptera, Coleoptera and Heteroptera) at undisturbed sites and backyards. The most efficient pollinators were 8–10 relatively small species of stingless bees, as well as *Apis mellifera* and the wasp *Brachygastra mellifica.* In commercial orchards sprayed with insecticides, only a small number of visitors were observed, and those were predominantly honeybees (Ish-Am et al. 1999). In the Neotropics, *Apis mellifera* is an introduced bee species and it is unlikely to be the most efficient pollinator of this small-flowered *Persea* species (Westerkamp & Gottsberger 2000). Avocado is cultivated in many regions having a Mediterranean climate where honeybees commonly dominate. *Apis*, however, is an inadequate pollinator because of its preference for flowers of other species, which limits fruit set of *P. americana* in e.g. Israel (Ish-Am & Eisikowitch 1993, 1998, Afik et al. 2006).

Thus far, all studies have shown that Lauraceae species have generalist pollination by pollinators consisting of a mixture of small to medium-sized beetles, flies, bees and wasps. In the tropical canopy tree *Nectandra umbrosa* the number of beetles attracted

to inflorescences was considerable (723 individuals representing 121 species, collected during two flowering periods for a total of sampling hours) and came mostly from the following subfamilies: Cerambycinae, Cryptocephalinae, Eumolpinae, Galerucinae, Baridinae and Curculioninae, however, only a subset of these are likely pollinators, nor were other insect visitors recorded in this study (Ødegaard & Frame 2007).

Artificial geitonogamous pollination in *Aniba panurensis, A. roseaodora, Licaria guianensis* and *Clinostemon maguireanum*, led to no fruits being formed, indicating self-incompatibility; agamospermy or apomixis apparently did not occur (Kurz 1982, Kubitzki & Kurz 1984). Self-incompatibility, although not tested, appears likely for *Ocotea tenera*, too (Gibson 1995, Gibson & Diggle 1998). *Persea americana* was found to set fruits due to spontaneous self-pollination in Florida, however, this does not occur in the cooler Mediterranean climate in Israel (Ish-Am & Eisikowitch 1998).

Magnoliales

As presently circumscribed, Magnoliales includes six families. Myristicaceae apparently is sister to two clades: one in which Degeneriaceae and Himantandraceae are sister to Magnoliaceae, and another comprising Eupomatiaceae and Annonaceae (e.g. Qiu et al. 1999, 2006, Doyle & Endress 2000, Sauquet et al. 2003, Endress & Doyle 2009, APG III 2009). All extant Magnoliales are trees, shrubs or rarely lianas, and flowers are typically large (with the exception of Myristicaceae), bisexual (here again with the exception of Myristicaceae) and have an apocarpous gynoecium (excepting Myristicaceae and Degeneriaceae, which are monocarpellate).

Pantropical **Myristicaceae** are mostly dioecious, with monoecy occurring in a few genera. Flowers are in inflorescences and quite small (4 to 6 mm diam.), actinomorphic, funnel-shaped, campanulate, or urceolate, and flower color may be yellowish-white, yellow, pink or red (Kühn & Kubitzki 1993). The dioecious *Iryanthera macrophylla* and *Virola calophylla* in Central Amazonian forests (Ackerly et al. 1990), as well as *Myristica fragrans* in plantations in India and *M. insipida* in rainforests of northern Queensland (Armstrong & Drummond III 1986, Armstrong & Irvine 1989a) showed male-biased sex ratios. Male plants of *Myristica fragrans* produced over 50 times as many flowers as female plants, and its P/O ratio of 801,000:1 was found to be extremely high for an insect-pollinated plant. Both pistillate and staminate flowers of this species are light cream to yellow, and flowers have a sweet, musky scent during the night. Three species of beetles were observed to visit the flowers of *M. fragrans* for pollen foraging, but only *Formicomus braminus* (Anthicidae, an ant-mimicking beetle) was collected from inside the staminate flowers. This beetle is too large to enter the interior of the pistillate flowers, but probing attempts by the beetles would, nonetheless, deposit pollen on the stigma. It was concluded that the pistillate flowers, which provide no reward, are probably mimics of the staminate flowers (Armstrong & Drummond III 1986). *Myristica insipida*, investigated in northern Queensland, has a floral biology similar to *M. fragrans*. Female and male trees flowered synchronously, producing display maxima between 6 p.m. and 6 a.m., and male trees produced three times the number of flowers of female trees. Although this species inititates anthesis at night, arrival of flower visitors was observed to begin only the next morning. The most frequent visitors and most efficient pollinators were small beetle species of the families

Curculionidae, Mordellidae, Nitidulidae, Scolytidae and Staphylinidae. Thrips were less effective visitors. The perianth of the pistillate flowers excludes beetles from the floral interior, but during brief visits to pistillate flowers they may touch the stigmas; as beetles do not receive any reward, the pistillate flowers seem to function here again by automimicry (Armstrong & Irvine 1989b, Armstrong 1997). The dioecious *Myristica dactyloides* in India showed a generalist pollination system (Sharma & Shivanna 2011) wherein Thysanoptera (one species of Phlaeothripidae and one species of Thripidae), which used flowers and buds as brood sites (a situation similar to *Mollinedia* in the Monimiaceae), and beetles (mainly Staphylinidae and Curculionidae), bees (mainly Halictidae) and flies (Syrphidae and Phoridae) carried pollen from staminate to pistillate flowers. The authors cited earlier research (Givnish 1980, Bawa et al. 1985a, 1985b) which suggests that other species of *Myristica* conform to a generalized, small insect pollinator type, too, and not only to a cantharophilous one. Increased research and sampling intensity in *Myristica* and other genera of the family will probably reveal a more diverse pollinator assemblage than presently known. To our knowledge nothing is known about the breeding system of monoecious Myristicaceae species.

Degeneriaceae historically have been regarded as monotypic, with the single species *Degeneria vitiensis* endemic to the Fiji Islands. Miller (1988, 1989) described a second species, *D. roseiflora*, which occurs on the islands of Vanua Levu and Taveuni, while the former species *D. vitiensis* occurs about 60 km distant on the island Viti Levu. Either species may reach tree heights of 35 m. *Degeneria roseiflora* has different (smaller) flowers, coloration (pinkish white to rose or magenta), floral smell (a musty rose smell) and several other differences in flower characteristics as compared to *D. vitiensis.* Both species have pendulous flowers and are protogynous. The perianth is differentiated into a calyx having 3 sepals and 12–25 petals. The stamens are followed by inner staminodes and a monocarpellate gynoecium. Anthesis of flowers lasts 9–11 h. Fragrance is already emitted before the imbricate buds open in the early evening. By 9 p.m. the flowers are completely open. Upon opening, the yellow petals and staminodes of *D. vitiensis* spread, revealing the single carpel. The staminodes secrete a thick, slimy yellow substance and emit a foul odor (for other authors it resembles the pleasant smell of *Cananga*; Miller 1989). After the first night of flowering, the petals and staminodes close over the flower center and on the second evening the petals and dehisced stamens reflex again, the staminodes, however, remain curved over the carpel. Many male and female individuals of the nitidulid *Haptoncus takhtajani* were found in both pistillate and staminate stage flowers of this species and are its likely pollinators (Thien 1980, Miller 1989). As far as we know, there are no data on the breeding system of *Degeneria*.

Himantandraceae, comprising two species of *Galbulimima*, occurs in New Guinea, the Moluccas, Celebes and Queensland. Their flowers are 2–4 cm in diam., bisexual, probably protogynous and cream-colored. There are no sepals or petals, but there is a floral envelope consisting of two caps formed by bracts. Stamens are between outer and inner staminodes. Secretory regions occur on the inner stamens and inner staminodes. Apparently, there are no observations about pollination or the breeding system; however, a number of floral features seem to point to cantharophily (Endress 1984a, 1993c, 2010).

In former times, **Magnoliaceae** was one of the families thought to be evolutionarily basal of extant angiosperms. Their large, solitary flowers having an elongated receptacle, on which numerous stamens and free carpels are spirally arranged, were long held to be prototypical of "primitive" flowering plants (see Frame & Gottsberger 2007). However, as previously noted, new phylogenetic data do not support this concept. Modern interpretations treat Magnoliaceae as having two subfamilies, Liriodendroideae with two species of *Liriodendron*, and Magnolioideae with 220–240 species, of a single genus, *Magnolia*, itself further subdivided into three subgenera and 12 sections (Figlar & Nooteboom 2004, Figlar 2006). The extant members of the family exhibit disjunct tropical/subtropical/temperate distributions in the Americas and in East and Southeast Asia.

One of the earlier studies on floral biology and pollination of temperate species was that of Heiser (1962), who studied *Magnolia tripetala, M. grandiflora, M. macrophylla* and *M. virginiana*, all North American natives to the U.S.A., and worked mainly with cultivated individuals in Bloomington, Indiana. He discovered that the large, white-petaled flowers were protogynous, strong smelling and attracted principally beetles, which were the main pollinators of these *Magnolia* species; flies and bees were less important. Eight *Magnolia* species native to the southeastern United States were investigated by Thien (1974), here, too, they are pollinated by several species of beetles that entered buds as well as closed and open flowers, and fed on stigmatic exudates and on pollen and petal secretions. Individual flowers last from two to four days and undergo a series of petal, stigma and stamen movements that assure beetle pollination, and even exclude other insects, such as bees. Thien (1974) mentioned visitation of bees to flowers, but attributed to them a very low if any importance for pollination, and classified the flowers of *Magnolia* as highly specialized for exclusive pollination by beetles. In a later paper, Thien et al. (1995) admitted that at least in *M. macrophylla, M. ashei* and *M. dealbata* (the petals of the last mentioned species have fluorescence patterns in ultraviolet light), beetles and bees were pollinators. Allain et al. (1999), after observations of cultivated individuals of *Magnolia grandiflora* in South Louisiana (which also exhibits floral UV reflectance patterns) concluded that although beetles were occasional floral visitors and carried pollen, . . . "bees (non-native *Apis mellifera* and indigenous *Lasioglossum bruneri*) were frequent floral visitors and were the only floral visitors whose behavior showed any correlation with the array of floral changes that occurred over the 3–4 day flowering period." In their study, Hymenoptera and Thysanoptera accounted for 87% of the insect visits, while the remaining 13% of insect visits were by Coleoptera, Diptera, Hemiptera, Homoptera and Plecoptera. The Japanese *M. stellata* is said to be pollinated principally by rove beetles (Staphylinidae) and Thysanoptera, but rarely also by bumblebees, honeybees, and flies (Hirayama et al. 2005, Setsuko et al. 2008). Likewise, *M. praecocissima* in Japan is principally pollinated be beetles. About 78% of its visitors crawling on stigmas and stamens were Coleoptera (Chrysomelidae, Curculionidae, Nitidulidae, Oedemeridae, Scraptiidae and Staphylinidae), and the remaining 22% were Diptera and Hymenoptera (Ishida 1996). Studying eight *Magnolia* taxa native to Japan, Yasukawa et al. (1992) found that a very large spectrum of insects visited the flowers, including not only Coleoptera, but also a number of Diptera and Hymenoptera, which nearly all played at least some role as pollinating agents. The picture is not much different for species in China. In

Liriodendron chinense, bees, flies and beetles behaved as generalist foragers, and none of them seemed to be especially adapted to the flowers (Huang et al. 1999). Again, in *Magnolia coriacea*, insects of the three orders Coleoptera, Diptera and Hymenoptera were flower visitors. The most effective pollinators appeared to be chrysomelid beetles, flies (Fanniidae) and *Bombus* (Apidae) (Zhao & Sun 2009). Strong indications that not only the mainly pollen- and tissue-eating beetles but also nectar-sucking insects are pollinators of the above mentioned *Magnolia* species, are provided by Daumann (1930) and especially Erbar & Leins (2013), who investigated *M. stellata* in detail and found an epithelial nectary involving the epidermis of the entire carpels. Nectar production is limited mainly to the pistillate phase of anthesis. This way, the attractiveness of the flowers is also assured in the initial non-pollen presentation stage of anthesis.

In conclusion, one gets the impression that in nearly all northern hemisphere temperate *Magnolia* species studied so far, beetles are important for pollination, and in some sites may even be the predominant pollinators, but that also other insect groups, especially bees, flies and thrips are more or less important and effective co-pollinators, too.

Studies of Neotropical species of *Magnolia*, however, have revealed strict cantharophily. Gibbs et al. (1977) found the large thick-petaled flowers of the Brazilian species *M. ovata* to be nocturnal; anthesis is protogynous, the flowers open and close in a two-night rhythm and are pollinated by large dynastid scarab beetles. Later it was found that the flowers of this species are thermogenic in both the pistillate and staminate stages, attaining 6.0 and 10.6 °C above ambient air, in the pistillate and staminate stages, respectively (Seymour et al. 2010). Female and male individuals of only one beetle species, *Cyclocephala literata* (Dynastinae: Scarabaeidae), are attracted to the scented, warm flowers in both pistillate and staminate stages (Fig. 3). Once inside the flowers they feed on petal tissue (in pistillate stage flowers) and on pollen (in the staminate stage) and also mate inside the flowers (Gottsberger et al. 2012). The two Mexican species, *M. schiedeana* and *M. tamaulipana* apparently also have nocturnal anthesis and are visited and pollinated by *Cyclocephala* species (Dieringer & Espinosa 1994, Dieringer et al. 1999). The flowers of the Paleotropical species *M. persuaveolens*, observed for a short time at Mt. Kinabalu, Sabah, Borneo (Gottsberger, pers. obs.), were found full of small flies but contained no beetles at all.

With regard to the breeding system, *Magnolia ovata*, a member of the most early divergent section *Talauma* was found to be self-compatible (Gibbs et al. 1977). Two other tropical American species, the Mexican *M. schiedeana* and *M. tamaulipana* are also self-compatible (Dieringer & Espinosa 1994, Dieringer et al. 1999). The North American species *M. tripetala, M. virginiana, M. grandiflora, M. macrophylla* and *M. ashei* likewise revealed self-compatibility (Heiser 1962, Thien 1974, Allain et al. 1999), and this breeding system was also found in the Japanese species *M. praecocissima* var. *borealis, M. obovata*, and *M. stellata* (Ishida 1996, 2008, Ishida et al. 2003, Isagi et al. 2004, 2007, Hirayama et al. 2005, Setsuko et al. 2008, Matsuki et al. 2008, Tamaki et al. 2009, Setsuko & Tomaru 2011) and in the Chinese species *Liriodendron chinense, Magnolia coriacea* and *M. denudata* (Huang & Guo 2002, Zhao & Sun 2009, Wang et al. 2010); notwithstanding, some of these species showed breeding depression. The two North American species *M. fraseri* and *M. pyramidata* are mentioned as being self-incompatible (Thien 1974).
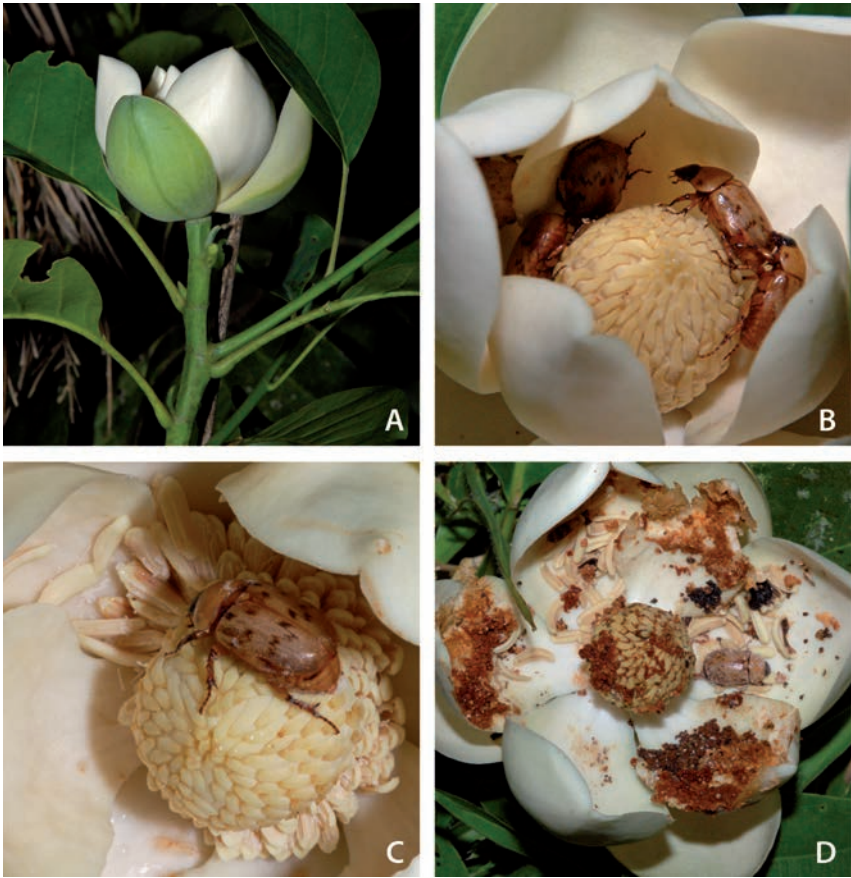
Fig. 3. *Magnolia ovata.* A. Half-open first-evening flower in the pistillate stage (expanded petals ca. 13 cm diam.). B. Pollinating beetles (*Cyclocephala literata*) after arriving in a pistillate stage flower. Some beetles are gnawing at the inner side of the inner petals and others are initiating to mate. C. Flower in staminate stage, in the second-evening. A beetle is feeding on pollen. D. Open flower in the late-staminate stage with expanded petals, showing one beetle covered with pollen. Feeding marks caused by beetles are visible mainly at the inner side of the inner petals.

The three species *Eupomatia laurina, E. bennettii* and *E. barbata* (**Eupomatiaceae**) occur in eastern Australia and New Guinea and have relatively large (3–4 cm diam.), bisexual, protogynous flowers, which are interpreted as lacking a perianth, having petal-like stamens and staminodes instead. Protection of the bud is by a calyptra, an amplexicaul bract. The petal-like inner staminodes produce sticky, oily exudates and emit a strong, fruity-musky smell (Endress 2003, Kim et al. 2005). Anthesis lasts one day in *E. laurina*, which has cream-colored flowers, and two days in *E. bennettii*, which has yellow flowers and innermost staminodes that are purple. In the initial

pistillate stage, the staminodes expand and function as organs of visual and olfactorial attraction. In a later stage, the staminodes bend over the center of the flower and hide the gynoecium, while the stamens shed their pollen (Endress 1984b, 1993b). Several species of *Elleschodes* (Curculionidae) visit and pollinate *Eupomatia* flowers. As many as 80 beetle individuals would congregate in a single flower, feeding on staminodes, contacting the stigmas, and in a later stage, impregnated with pollen, leave the flowers. They also oviposited in the flowers; later, when the androecium abscised as a synandrous unit, it served as a place of feeding for the beetles' larvae until they pupated in the soil (Hamilton 1897, Diels 1916, Hotchkiss 1959, Endress 1983, Armstrong & Irvine 1990). For *E. laurina* and *E. bennettii* self-compatibility was confirmed (Endress 1984b).

Flowers of the large, pantropical family **Annonaceae** are mostly bisexual and protogynous, commonly having a trimerous perianth consisting of one whorl of sepals and two whorls of thick, fleshy, strongly scented petals. The numerous stamens, commonly having broad connective shields, and the apocarpous carpels have a helical arrangement. Stigmatic exudates function as a compitum, distributing the growing pollen tubes to the carpels. The family is predominantly pollinated by beetles, but in some genera and species, thrips (Thysanoptera), flies, cockroaches and even bees are the exclusive pollinators of flowers (Gottsberger 2012). There are two major sorts of beetles pollinating flowers of Annonaceae. The large majority of cantharophilous species of Annonaceae are pollinated by small beetles (Nitidulidae, Curculionidae, Staphylinidae, Chrysomelidae), having a body length up to 7 mm, and a smaller group of species attract Scarabaeidae (Dynastinae, Rutelinae, Cetoniinae, Trichiinae), which are large beetles having a body length of 14–20 mm.

The earliest-divergent genus in Annonaceae is *Anaxagorea* (Scharaschkin & Doyle 2006). Where studied, flowers have been found to have a diurnal, 2-day flowering rhythm, with the pistillate stage occurring during the first day and the staminate stage during the second. In *Anaxagorea brevipes, A. manausensis*, and *A. phaeocarpa*, investigated in the Central Amazon of Brazil (Webber 1996), and in *A. dolichocarpa*, studied in the northeastern Atlantic forests (also Brazil) (Braun & Gottsberger 2011), flower temperature rises approximately 1.5–6 °C above ambient air temperature in the pistillate and staminate stages, a phenomenon that accelerates the emission of fruit-like odors, which attract the pollinators, species of *Colopterus* (Nitidulidae). *Anaxagorea prinoides*, studied in French Guiana, was found to be heterodichogamous; its flowers did not warm up and were also pollinated by *Colopterus* species (Teichert et al. 2011). *Anaxagorea* flowers have inner staminodes, which make movements during anthesis. In the pistillate stage they spread outwards, making space around the stigmas for the incoming beetles, and in the staminate stage they incline towards the carpels thereby facilitating beetle access to the pollen-providing stamens.

Many Annonaceae in the Neotropics and Paleotropics have diurnal or nocturnal flowers, with or without thermogenesis which are pollinated by small beetles, such as in the genera *Annona, Cathostemma, Deeringothamnus, Duguetia, Enciosanthum, Fissistigma, Friesodielsia, Goniothalamus, Guatteria, Haplostichanthus, Isolona, Meiogyne, Melodorum, Monocarpia, Piptostigma, Polyalthia, Sapranthus, Tetrameranthus, Uvaria* and *Xylopia* (e.g. Gottsberger 1970, 1999, Webber 1981a, 1981b, 1996, Deroin 1989,

Nagel et al. 1989, Olesen 1992, Andrade et al. 1996, Küchmeister et al. 1998, Momose et al. 1998a, Bernhardt 2000, Silberbauer-Gottsberger et al. 2001, 2003, Norman 2003, Ratnayake et al. 2006, 2007, Weerasooriya & Saunders 2010, Gottsberger et al. 2011, Teichert et al. 2012, Paulino-Neto 2014).

In the Neotropics, pollination by large dynastid scarab beetles, mostly of the genus *Cyclocephala*, occurs in nocturnal, large-flowered species of the genera *Annona, Cymbopetalum, Duguetia, Fusaea, Malmea, Porcelia* and others (e.g. Webber 1981a, Gottsberger 1989a, 1989b, Schatz 1990, Webber 1996, Momose et al. 1998a, Braun et al. 2011). Their petals are very fleshy with nutritious tissue principally at the base of the inner petals (Gottsberger et al. 1989a). Thermogenesis can be remarkable high, reaching temperatures up to 12 °C above ambient air, and co-incident scent emissions are very strong and either sharp or fruity. The beetles, which often stay inside the pollination chamber for as long as 24 hours, are rewarded by nutritious tissue and pollen, they are protected against predators and, as beetles of both sexes are attracted, they can mate. Elevated temperatures inside the floral chamber permit beetles to expend less energy to keep warm and in this way promotes their activities (Seymour et al. 2003). *Asimina* species in Florida are pollinated by scarabs, but by members of the subfamilies Trichiinae and Cetoniinae (Norman & Clayton 1986), and large-flowered African species of *Uvariodendron* are pollinated by scarabs of the subfamilies Trichiinae and Rutelinae (Gottsberger et al. 2011).

Thrips are the exclusive or additional pollinators in species of *Bocageopsis, Xylopia, Popowia, Oxandra* and *Cananga* (e.g. Kessler 1993, Webber & Gottsberger 1995, Webber 1996, Momose et al. 1998b), fly-pollination occurs in unpleasant scenting flowers of *Pseuduvaria* and *Uvariopsis* (Morawetz 1988, Silberbauer-Gottsberger et al. 2003, Gottsberger et al. 2011), and *Uvaria elmeri* was verified in Malaysia to be pollinated by cockroaches (Nagamitsu & Inoue 1997). A highly sophisticated case of bee pollination was described for species of the genus *Unonopsis*. Males of *Euglossa* and *Eulaema*, so called "orchid bees" (Euglossinae) collect perfume at osmophores produced on the inner side of the inner petals of *Unonopsis* flowers and pollinate them (Carvalho & Webber 2000, Silberbauer-Gottsberger et al. 2003, Teichert et al. 2009).

Inner flower petals of some Annonaceae species can provide nectar. In *Pseuduvaria* both staminate and pistillate flowers secrete nectar through small slits from a multi-layered mesophyllary nectary, which is a resource for the pollinating flies (Silberbauer-Gottsberger et al. 2003). Nectaries are indicated also in species of *Orophea* (Kessler 1988), and nectaries of the epithelial type were described by Erbar (2014) for *Asimina* species; this nectar might be consumed by visiting and pollinating beetles, flies and thrips (e.g. Kral 1960).

Annonaceae have developed a number of sophisticated and highly specialized pollination syndromes. The large majority of species are beetle-pollinated, but different lines of cantharophily have evolved: pollination by small beetles *versus* pollination by large beetles, diurnally *versus* nocturnally active flowers, and flowers with thermogenesis (especially notable in nocturnal species). Other lines of specialization are evident in the few species pollinated by thrips (e.g. very narrow pollination chambers linked to small flower size), cockroaches, flies (often unpleasant scent or nectaries) and bees. A more or less closed pollination chamber as found in cantharophilous flowers, would

be an obstacle for flies, cockroaches and bees trying to reach to the flower reproductive organs. As an adaptation to these "free working" pollinators, the myiophilous, melittophilous or cockroach-pollinated Annonaceae have open flowers with reflexed petals which gives pollinators free access to the flower center. Small and elongate thrips do not need an open flower to penetrate into its center, and thrips adapted flowers are either closed or semiclosed.

As in cantharophilous flowers, non-cantharophilous flowers have characteristics related to the behavior and senses of their respective pollinating insects. Still, non-cantharophilous species often retain one or more cantharophilous associated characters, e.g. thick, fleshy petals, flattened and sclerified connective shields, or protogynous dichogamy (Gottsberger 2012).

Studies on breeding systems in Annonaceae have shown that self-compatibility is prevalent in most studied species. In *Anaxagorea*, self-compatibility was found to occur in *A. phaeocarpa, A. crassipetala* and *A. dolichocarpa* (Webber 1996, Armstrong & Marsh 1997, Braun & Gottsberger 2011); in the species *A. manausensis, A. brevipes* and *A. prinoides*, self-compatibility is likely (for example, as indicated by p/o-ratio) but has not been confirmed by other studies (Webber 1996, Teichert et al. 2011). In *Annona*, the majority of studied species were found to be self-compatible: *A. cacans, A. cherimola, A. exsucca, A. glabra, A. montana, A. mucosa, A. muricata, A. nitida, A. reticulata, A. sericea, A. squamosa* (e.g., Wester 1910, Webber 1981a, 1982, 1992, Murray & Johnson 1987, Nagel et al. 1989, Gottsberger 1989b, Gazit et al. 1982, Richardson & Anderson 1996, Paulino Neto & Oliveira 1998, Tsukada et al. 2008, Gonzáles & Cuevas 2011). Only the African *Annona senegalensis* was found to be self-incompatible (Deroin 1989). Self-compatibility was further found in *Asimina parviflora, A. obovata* and *A. triloba* (Norman & Clayton 1986, Norman et al. 1992, Menges & Matthias 2002), *Deeringothamnus pulchellus* and *D. rugelii* (Norman 2003), *Cardiopetalum calophyllum, Duguetia lanceolata* and *D. pycnastera* (Paulino Neto & Oliveira 1998, Webber 1996), *Guatteria megalophylla* and two other unidentified *Guatteria* species occurring close to Manaus (Webber 1996), *Cymbopetalum torulosum* and *Cymbopetalum* sp. (Schatz 1984, Bawa et al. 1985a), *Mitrephora heyneana* (Weerasooriya & Saunders 2010), *Polyalthia* cf. *cauliflora, P. littoralis, P. coffeoides* and *P. korinti* (Okada 1990, Ratnayake et al. 2006), *Pseudoxandra coriacea* (Webber 1996), *Uvaria concava* (Silberbauer-Gottsberger et al. 2003), *Xylopia amazonica, X. aromatica, X. benthami* and *X. brasiliensis* (Andrade et al. 1996, Paulino Neto & Oliveira 1998, Webber 1996,). Conversely, *Cymbopetalum costaricense* (Schatz 1987), *Polyalthia glauca* and *P. hypoleuca* (Rogstad 1994), as well as *Popowia pisocarpa* (Momose et al. 1998b), *Sapranthus palanga* (Bawa 1974) and *Uvaria elmeri* (Nagamitsu & Inoue 1997), were found to be self-incompatible. *Xylopia championii* appears to be intermediate between being self-incompatible and self-compatible (Ratnayake et al. 2007). *Cymbopetalum brasiliense* apparently is apomictic (Braun et al. 2011).

Pollination in Chloranthales and Ceratophyllales

Chloranthaceae diverged at some point above the ANITA grade, but below the divergence of magnoliids (e.g. Doyle et al. 2003), and there seems to be still some

evidence that Chloranthaceae may be sister to magnoliids (e.g. Bell et al. 2010). The Ceratophyllaceae (Ceratophyllales) have shifted back and forth in different phylogenies, but in more recent publications they are considered sister to Chloranthaceae, and most recently, both families combined are suggested to be the older sister clade to eudicots (Zeng et al. 2014).

Chloranthaceae, the sole family of Chloranthales, consists of ca. 75 pantropically distributed species. Their habit varies from herbs and subshrubs (*Chloranthus* and *Sarcandra*) to shrubs and large trees (*Ascarina* and *Hedyosum*). Flowers are bisexual (*Chloranthus* and *Sarcandra*) or unisexual (*Ascarina,* dioecious, rarely monoecious; *Hedyosmum*, monoecious or dioecious) (Todzia 1993). All species of *Chloranthus* and *Sarcandra* have protogynous, long-lasting flowers with a dry stigma (Hristova et al. 2005). The pistillate phase begins five to seven days before the staminate phase and continues during the staminate phase (Balthazar & Endress 1999). Usually the flowers lack a perianth and consist of an extremely low number of organs, often only of one stamen and one carpel. Endress (1987) affirms that *Chloranthus* and *Sarcandra* have entomophilous characteristics, such as bright colors and a penetrating scent from the androecium in, e.g. *S. chloranthoides*, and a fruity scent in *S. glabra*, while *Ascarina* and *Hedyosmum* show tendencies to wind pollination, which, however is quite pronounced in *Hedyosmum*. Endress (1987) found Chloranthaceae to be an instructive example "... that floral biological differentiation into certain entomophilous and anemophilous groups took place already in the initial stages or at least very early in angiosperm evolution."

Two *Chloranthus* species, *C. serratus* and *C. fortunei* were studied by Luo & Li (1999) in China. Anthesis of a single flower of *C. serratus* lasted 5–6 days and flowers are slightly protogynous. Flowers started to emit a scent when the androecium became white. Both species are entomophilous with thrips as exclusive pollinators (see also Ma et al. 1997 for *C. holostagius*). Some chrysomelid beetles visited the flowers as well, but were too large to enter the floral-axial chamber. The beetles were blocked by the androecial appendages and, thus, can be dismissed as pollen vectors.

Sarcandra glabra was investigated in its natural habitat in Japan (Tosaki et al. 2001). The small (ca. 0.3 cm diam.), protogynous flowers having a weak fragrance bear one stamen having a creamish white connective and thecae, which turn orange or reddish-brown upon dehiscence (several days after the beginning of stigma receptivity). Stigma receptivity dropped off significantly following anther dehiscence. The authors found that pistillate-stage and bisexual-stage flowers were visited by several beetles, bees, hemiptera, flies and rarely ants that foraged for pollen and/or small droplets of liquid that occasionally were secreted by the carpels and inflorescence axes. Pollination experiments showed that fruit set of *S. glabra* after experimental crossing and selfing was not significantly different, and automatic selfing sometimes occurred when pollen fell from upper flowers onto the stigmas of lower flowers.

After different pollination treatments (Luo & Li 1999) it was concluded that *Chloranthus serratus* and *C. fortunei* form fruits after cross-pollination, self-pollination and by agamospermy, but with a substantially higher fruit set after cross-pollination. Similar treatments by Balthazar & Endress (1999) indicated *Sarcandra glabra* to be self-compatible, *S. chloranthoides* agamospermous and *Chloranthus*

spicatus self-incompatible. However, the results on breeding systems, especially on self-compatibility of *Sarcandra glabra* were contested by Hristova et al. (2005), affirming that self-fruit/seed set can occur in the presence of a leaky self-incompatibility system. Their opinion is that "... all conclusions regarding the presence of agamospermy, SI or SC in any species of Chloranthaceae are inconclusive.", and demand that "... more rigorous studies are required to provide definite evidence of the presence or absence of the phenomenon in any of the species with bisexual flowers in the Chloranthaceae."

The small aquatic family **Ceratophyllaceae** (Ceratophyllales) consists of a mono-typic cosmopolitan genus having six submergent species. This family has proven diffi-cult to place in phylogenetic schemes and has changed its position several times. Probably on the basis of a shared aquatic habit, *Ceratophyllum* was usually aligned with Nymphaeales, and it has also been placed near other early diverging groups prior to the divergence of monocots and dicots (Les 1993). The family has been even proposed to represent the most basal clade of extant angiosperms, which was con-tested by e.g. Endress (1984c). At present, Ceratophyllaceae are considered sister to Chloranthaceae (e.g. Zeng et al. 2014).

All species of *Ceratophyllum* are hydrophilous, i.e. pollination occurs below the water surface. They are monoecious and sex ratio is commonly male-biased. The pis-tillate flowers occur near the shoot apex while the staminate flowers develop more basally. Pistillate flowers seem to be receptive somewhat prior to pollen release from the staminate flowers. The stamens, with a remarkable behavior of successive matu-ration, are lighter than water and detach from the flower and become buoyant with a tendency to rise. Stamen dehiscence and pollen release occurs while stamens are still attached to the flower or during their rise to the water surface. After their release, the water is full of pollen grains and some of them may reach the stigmatic opening and leading to pollination (Knuth 1899, Endress 1984, Les 1993). Studies have indicated self-compatibility of several species, which permits sexual reproduction in clonal pop-ulations. Related to this, it was found that outcrossing rates and genetic diversity of populations is quite low (Les 1993).

General discussion

Floral characteristics and sex expression

A few representatives of the ANITA group have very small flowers or reproductive units (viz. Hydatellaceae), usually less than 1 cm diam., such as *Amborella* and *Trithuria.* Flowers somewhat larger, up to 2 cm diam. occur in *Brasenia schreberi, Schisandra glabra, S. henryi* and *Trimenia moorei.* Medium-sized flowers up to 4 cm diam. are characteristic for *Cabomba caroliniana, Nuphar* spp., *Euryale ferox, Nymphaea ond-inea* and *Illicium floridanum. Austrobaileya scandens* (up to 6 cm flower diam.) and core *Nymphaea* species and *Victoria* have large to very large flowers: *Nymphaea* subgenera *Nymphaea, Brachyceras* and *Anecphya* have flowers up to 14 cm diam., *Nymphaea* subgenera *Hydrocallis* and *Lotos* up to 20 cm diam., and *Victoria* exhibits the largest flowers of the whole order having flowers up to 25–30 cm diam. Moreover, in the basal monocots, magnoliids and the clade Chloranthales plus Ceratophyllales, there also is a large variation in flower size, from very small to small, often reduced

flowers, such as in *Acorus*, Araceae, Chloranthaceae, Ceratophyllaceae, Lactoridaceae, Piperaceae, *Siparuna*, some Monimiaceae, Lauraceae and Myristicaceae, to large and very large flowers in other groups, where flower diameter or length of petals can reach 5–6 cm in species of *Zygogynum* (Winteraceae), 8–12 cm in *Asarum* and even occasionally 100 cm in *Aristolochia* (Aristolochiaceae), 5–11 cm in Hydnoraceae, 4–8 cm in *Calycanthus* (Calycanthaceae), 6–7 cm in Degeneriaceae, 16–20 cm in Magnoliaceae, and 3–8 cm in Annonaceae. Nearly all of the large to very large flowers belong to groups either specialized for beetles or flies. The possible reasons for the evolution of floral gigantism especially in beetle- and carrion-fly-pollinated species are discussed in Davis et al. (2008).

Flower color ranges from cream in *Amborella trichopoda* and *Trimenia moorei* and greenish in *Trithuria* spp., to green, yellow and brown in *Austrobaileya* s*candens*, and further to green, yellow, orange, crimson, red and purple in several species of Schisandraceae. Probably the broadest color range in the ANITA group is found among flowers of Cabombaceae/Nymphaeaceae, which possess white, yellow, pink, purple, red and blue (Table 1). True blue flower color is chemically complex and quite rare in basal angiosperms, only occurring in *Nymphaea*, which belongs to the first herbaceous clade of the angiosperms. Blue flowers occur in those taxa of the angiosperms characterized by an evolutionary trend towards the herbaceous habit, and are increasingly more abundant in the more advanced monocots and herbaceous higher dicots (Gottsberger & Gottlieb 1980, 1981).

Unisexual flowers exhibiting dioecious or monoecious sex expression (see also e.g. andromonoecy in *Trimenia moorei*, gynomonoecy in *Lactoris fernandeziana* or gynodioecy in *Echinodorus longipetalus*) occur in *Amborella*, *Schisandra* and *Kadsura* species (ANITA), partly in Alismataceae and Araceae (monocots), partly in Winteraceae (*Tasmannia*), partly or totally in Piperaceae, Siparunaceae, Hernandiaceae, Monimiaceae, Lauraceae, Myristicaceae and Annonaceae (e.g. in *Pseuduvaria*), all belonging to the magnoliids, in *Ascarina* and *Hedyosmum* (Chloranthaceae) and Ceratophyllaceae. Bisexual flowers are typical for some *Trithuria* species, Cabombaceae, Nymphaeaceae, *Austrobaileya* and *Illicium* (ANITA), *Acorus*, several Araceae and Alismataceae, the majority of the magnoliid families and for *Sarcandra* and *Chloranthus* (Chloranthaceae).

Dichogamy was broadly discussed by Lloyd & Webb (1986) and Bertin & Newman (1993), and many factors for the prevalence of either protogyny or protandry were mentioned. For basal angiosperms having bisexual flowers, it is remarkable that nearly all have protogynous dichogamy. Only in some Piperaceae and Alismataceae, homogamy or even protandry have been observed. It appears that protogyny is an archaic characteristic in angiosperms. It may find an explanation in the principal visitors to their flowers, mainly beetles, flies and thrips which, contrary to bees, butterflies, birds and mammals move slowly or little during their flower visits and often remain on and in an individual flower or inflorescence for a long time; in some cases, beetles and thrips, or trapped flies, may remain 24 hours or more in a flower. In this situation, receptive stigmas at the insects' arrival and pollen shedding stamens at their departure provides the best and most efficient mechanism to promote outcrossing. Even in abiotically pollinated plants, e.g. by wind, protogyny is more appropriate and more efficient than protandry, because

only then it is guaranteed that the available pollen during the initially pistillate stage of a flower is exclusively from another flower. Although the incoming pollen can be from other flowers of the same individual, still the probability that it is coming from other individuals is higher than it would be in protandrous flowers. In a bisexual protandrous anemophilous flower the first pollen available would be from its own flower, a situation which might even "clog" the stigmas and thus, make difficult or even inhibit cross-pollination. Other reasons for this kind of dichogamy may be found in flower construction of basal angiosperms, which often have many densely crowed reproductive organs and stamens lacking long filaments, or anthers and filaments without clear delimitation, so that pollen presentation is close to potentially receptive stigmas.

The few cases of homogamy and protandry observed in some Alismataceae and Piperaceae, two generalist pollination families, may be the first signs of a reversal and an adaptation to more rapidly-acting pollen- and/or nectar-searching visitors, bees. Indeed, in a few species of both families, bees become dominant or even exclusive flower visitors and pollinators. However, such a reversal is not a general trend in basal angiosperms, especially not in families with specialist pollination. For example, both Araceae and Annonaceae have specialist pollination, Araceae apparently starting with beetles and/or flies, and Annonaceae with beetles as basic pollinators. Some *Anthurium* and *Spathiphyllum* species (Araceae) and *Unonopsis* (Annonaceae) are specialized for perfume-collecting male euglossine bees, but even so their flowers exhibit protogyny. It may be that specialist families of basal angiosperms are too fixed or canalized in their original function such that their members have not been able to adapt and switch to the seemingly more appropriate condition of protandry.

Breeding systems

As the pistillate and staminate stages in bisexual flowers of basal angiosperms are in most cases completely separated, insect-mediated self-pollination can be avoided. This is important in cases where species are self-compatible. On the other hand, the breeding systems of basal angiosperms might have become self-compatible because their flowers are strongly dichogamous without overlapping of pistillate and staminate stages in an individual flower. However, as was remarked by Endress (1994), dichogamy can only be an efficient outcrossing factor, when there are other temporal mechanisms at the level of inflorescences, the individuals or the populations (see also Lloyd & Webb 1986, Bertin & Newman 1993).

In the present paper, a special effort was made to document data on the breeding systems in basal angiosperms. Several authors apparently are convinced that angiosperms have started as a group with obligatory oucrossing, viz. having a self-incompatible breeding system. The main argument for the prevalence of outcrossing of early angiosperms was the explosive development of angiosperm groups, evident from Cretaceous fossil records (e.g. Friis et al. 2011). It is believed that such a rapid speciation and diversification could only have been possible in groups having principally outcrossing breeding systems.

Some authors, myself included, are puzzled 1) by the high number of species, genera and even families of basal angiosperms bearing unisexual flowers, and 2) principally also by the high number of self-compatible species found in these groups.

A good documentation of the breeding system of a plant is a difficult job and it is not sure that all data about breeding systems in the literature are good data. On the other hand, we cannot neglect the abundant reports about self-compatibility in basal angiosperms and certainly not all data are wrong.

As cited above, also Endress & Igersheim (2000), after the study of *Amborella trichopoda*, referred to the frequent occurrence of functionally unisexual flowers among basal angiosperms, mentioning that this might be one method to support out-breeding in a group in which self-incompatibility systems are lacking or unelaborated.

In the first clade of ANITA with bisexual flowers, the Nymphaeales, all tested species of *Trithuria, Brasenia, Nuphar, Euryale, Barclaya, Nymphaea* and *Victoria* revealed to be self-compatible. The situation is somewhat different in the Austrobaileyales. *Austrobaileya scandens, Trimenia moorei* and *Illicium dunnianum* are self-incompatible, *Kadsura longipedunculata* appears to be self-compatible, and for *Illicium floridanum* it is not yet clear whether it is self-incompatible or self-compatible.

In the basal monocot family Alismataceae, five tested taxa of Alismataceae were self-compatible and one was self-incompatible. In the literature I found 20 accounts for self-compatibility in Araceae species and one account for self-incompatibility.

In the magnoliids, *Drimys brasiliensis, D. confertifolia, Tasmannia insipida*, and per-haps *Zygogynum pancheri* are self-compatible, while *Pseudowintera colorata, P. axil-laris*, and *Drimys winteri* are self-incompatible. In the Aristolochiaceae, the larger number of species was found to be self-compatible, and also the monotypic *Lactoris fernandeziana* is self-compatible. In the Piperaceae about the same number of self-compatible and self-incompatible species are reported. *Saururus cernuus* (Saururaceae) is self-incompatible, and *Calycanthus chinensis* (Calycanthaceae) was found to be self-compatible. *Sparattanthelium botocudorum* (Hernandiaceae) is self-incompatible. In different species of the genus *Tambourissa* (Monimiaceae) both types of breeding sys-tems were found. In the few species of Lauraceae tested, self-incompatibility prevailed. In the Magnoliaceae self-compatibility is much more common than self-incompatibility. Two tested species of *Eupomatia* are also self-compatible. In the Annonaceae self-compatibility is numerically dominating by far over self-incompatibility.

For the Chloranthaceae there are several data for species being either self-compatible or self-incompatible, but all results about breeding systems in this family were con-tested by Hristova et al. (2005), who affirm that self-fruit/seed set can also occur in the presence of a leaky self-incompatibility system. Self-compatibility was confirmed in several species of *Ceratophyllum* (Ceratophyllaceae).

The data above indicate that self-compatibility in basal angiosperms is a common phenomenon and that this phenomenon also exists in the Nymphaeales, the earliest-divergent bisexual clade.

Thus, one might ask whether unisexuality and protogyny in bisexual flowers, both well established in basal angiosperms, are perhaps indeed characteristics to avoid self-ing in plants that predominantly have a self-compatible breeding system? Might it be possible that the basal angiosperms have started as self-compatible lines, which at their beginning evolved and developed relatively slowly, and which only much later and after the acquirement of self-incompatible breeding systems had their broad and rapid diversification mainly along the Cretaceous?

Resources for pollinators: pollen, nectar, nutritious tissues and floral heating

Pollen is likely the first and oldest resource provided for angiosperm flower visiting insects and pollinators (e.g. *Amborella*). Pollen continues to be a main resource for most flower visitors, but in the Cabombaceae and Nymphaeaceae, nectar, an energetically much richer food than pollen, as well as abundant stigmatic secretions or less abundant stigmatic exudates are additional important resources (for a review of the occurrence of nectar and nectaries see Erbar 2014). Both pollen and/or liquid secretions, the latter containing sugars, amino acids and many other substances, are the main resources provided by the majority of angiosperm flowers. Several groups of plants, especially cantharophilous basal angiosperms, provide another resource for their visiting beetles, namely more or less specialized nutritious tissues, provided on tepals, petals and staminodes and even food bodies on several floral organs. Small beetles often eat pollen and also feed on tepals, petals or staminodes during their extended stay in the interior of their flowers, in the so-called pollination chamber. The cantharophilous flowers of certain *Zygogynum* species seem to have food bodies on the petals. A very sophisticated case of food-providing to small beetles occurs in the genus *Calycanthus*. In the Chinese *C. chinensis*, the distal margins of the tepals and the connective appendages bear a warty cover which, together with the subjacent cell layers, seem to represent a kind of food tissue for the visiting beetles. In the North American species *C. occidentalis* and *C. floridus*, the innermost tepals, the stamens and inner staminodes have whitish food bodies on their tips, which contain high levels of protein and are eaten by *Colopterus* and *Carpophilus* (Nitidulidae) species during their visits to the flowers.

In flowers that are pollinated by the large-sized beetles of the Dynastinae, Rutelinae, Cetoniinae and Trichiinae (all Scarabaeidae), either the whole tepals or petals, especially the inner sides, are eaten by the beetles, or the flowers provide specific nutritious regions on tepals or petals. *Victoria* (Nymphaeaceae) species have starch-containing carpellary appendages that are eaten by the large beetles. In *Philodendron* species, beetles not only nourish themselves on stigmatic exudates and large amounts of pollen but also on sterile and fertile staminate flowers. In *Magnolia ovata*, beetles start eating at the nutritious tissue at the base of the inner petals and after consumption of these regions extend their gnawing to the whole petals. In Annonaceae, pollinated by dynastid scarab beetles, we found that after their arrival, beetles preferentially fed on special areas of the inner side of the three inner petals. These food areas apparently are a preferred resource for beetles during the initial pistillate flower phase; during the staminate phase the beetles feed also on pollen. In species of the annonaceous genera *Annona, Malmea, Cymbopetalum* and *Duguetia*, histochemical studies revealed the presence, in a more or less concentrated form, of starch, lipids, tannins (including polyphenols in a compact polymerized form) and mucilage cells (Gottsberger et al. 1998) in the nutritious tissues. Starch and lipids, besides being eaten by the large beetles, also provide fuel for flower thermogenesis.

Another resource or reward, especially for beetles, is provided by the ability of some plants to raise flower temperature above ambient temperature through metabolic heat production, resulting in a warm floral chamber. Besides being an aid in

strongly volatilizing the floral scent compounds for attracting the pollinators, warming of flowers helps beetles, which are facultative endotherms and need a great deal of energy for reducing thermoregulatory costs, to increase their activity levels in mating, locomotion, digestion and growth (Seymour & Schultze-Motel 1997, Seymour et al. 2003, 2009a, Seymour 2010, McCallum et al. 2013).

Thermogenesis occurs earliest in the ANITA grade, in the clade Nymphaeales, however, in the derived subgenera of *Nymphaea* and in *Victoria*, and it is associated with pollination by large dynastid scarab beetles. Also, in species of *Schisandra* and *Illicium* (Austrobaileyales) thermogenesis occurs, and for *Illicium dunnianum* it was found that the slight floral heating during the pistillate stage and the later nursing phase (after the staminate stage) benefits larval development of the pollinating gall midges. Flower heating is found in the cantharophilous genera *Hydnora* and *Prosopanche* (Hydnoraceae), too. The slight heating in *Hydnora* species was associated with scent production only. In Magnoliaceae, thermogensis was found in tropical American species being pollinated by dynastid scarab beetles. Several small-flowered and large-flowered cantharophilous Annonaceae, which are pollinated either by small or large beetles, are also thermogenic. Annonaceae species pollinated by large beetles, exhibit stronger heating, probably because larger, thicker petals have more accumulated starch and lipids than species with smaller and less fleshy flowers associated with small beetles.

Flowers as mating, oviposition and breeding places

Mating on flowers by pollinating beetles is a common phenomenon. We observed it in flowers and inflorescences of *Victoria amazonica, Philodendron* spp., *Magnolia ovata* and many Annonaceae spp. As observed in *Philodendron selloum*, scent stimulated mating of its pollinating dynastid scarab, *Erioscelis emarginata* (Gottsberger & Silberbauer-Gottsberger 1991). The thick, fleshy tepals or petals of cantharophilous species are not only important for the pollination process itself and for the pollinating beetles, but are also used by many insects other than pollinators as oviposition and breeding places. For example, in *Anaxagorea crassipetala* (Annonaceae), Armstrong & Marsh (1997) found besides the pollinating nitidulid beetles also a weevil species (*Cyriomyx* sp., Baridinae, Curculionidae), which oviposited into young flower buds and afterwards its larvae were ovule predators. Another flower predator of this species was *Diathoneura tesselate* (Drosophilidae, Diptera), which oviposited into the thick and fleshy outer petals of immature flower buds on the tree, and even in postanthetic fallen flowers. Each of the outer petals might contain several larvae of this drosophilid fly (Collier & Armstrong 2009). The petals of *Annona coriacea* were found to be oviposited and used as breeding places by a moth of the family Stenomidae, whose larvae nourished themselves on petal tissue (Moreira de Barros et al. 2014). In *Sapranthus palanga* flowers, Olesen (1992) detected larvae of a mining moth (Pyralidae, Lepidoptera), and Braun et al. (2011) found in a population of *Cymbopetalum brasiliense* (also Annonaceae) the butterfly larvae *Oenomaus ortygynus* (Lycenidae) destroying ripe buds and open flowers by eating petals, stamens and the entire gynoeceum. Additionally, Gottsberger & Silberbauer-Gottsberger (2006) show for Annonaceae occurring in cerrado vegetation, that many species of

non-pollinating beetles belonging to Curculionidae, Nitidulidae, Staphylinidae, Chrysomelidae, Elateridae, Dermestidae, Meloidae, Elateridae and Scarabaeidae visited the flowers without entering the pollination chamber, and several of those beetles besides feeding on petal tissue, mated on and oviposited the petals. If time is too short for larvae to finish development in flowers on the tree, they can continue their development in the fallen flower and pupate in the soil. Likewise, predation of flowers of Amazonian Annonaceae was shown by Webber (1996).

There are few documented cases wherein pollinating beetles use their flowers as breeding places where they mate and oviposit. The examples belong to *Prosopanche* (Hydnoraceae) and *Eupomatia* (Eupomatiaceae), but these phenomena are probably more common than the few described cases would suggest.

Flies were found mating, ovipositing and/or breeding on flowers, as for instance in *Austrobaileya*, as well as in *Cabomba, Nuphar* and *Nymphaea* (flies of the genera *Hydrellia, Notiphila*, Ephydridae; and *Hydromyza*, Scatophagidae) (van der Velde et al. 1978, van der Velde & Brock 1980). In Schisandraceae (*Schisandra* and *Illicium*), and in Siparunaceae (*Siparuna*), cecidomyiid flies were found to oviposit and breed in flowers that they pollinate. Similar phenomena, albeit involving other fly groups or a much broader fly spectrum, occur in several Araceae and in most Aristolochiaceae.

In Monimiaceae, the cup-like receptacle of *Mollinedia* and *Wilkiea* is a ovipositing and breeding place for their exclusive thrips (Thysanoptera) pollinators. Also in *Myristica dactyloides*, flowers are used by thrips species as brood sites; the additional pollinators, beetles, bees and flies only exploit the pollen.

Floral scent

Scent emitted by flowers is usually regarded as a pollinator attracting cue, indicating food, oviposition places or even sexual partners, but certain compounds of an odor bouquet can also have antagonistic or defensive function and repel undesired or harmful flower visitors (Junker & Blüthgen 2010).

In Nymphaeales, basal monocots, magnoliids and Chloranthales, nearly all major classes of floral scent compounds can occur, such as C5-branched chain compounds, aliphatics, benzenoids and phenyl propanoids, monoterpenes, sesquiterpenes, diterpenes and irregular terpenes (Knudsen et al. 2006). Of the numerous studies on floral scent chemistry, just a very few will be mentioned here, in beetle-pollinated groups.

For example, the large magnoliid family Annonaceae is basically a beetle-pollinated group (see above) and species of the most early-divergent genus *Anaxagorea* are pollinated by beetles of the genus *Colopterus* (Nitidulidae). The flowers of *Anaxagorea* species have a fruit-like scent. Members of other genera of Annonaceae, such as *Duguetia, Annona, Guatteria* or *Xylopia*, also have banana-like, ananas-like, fruity-acetonic and fermenting scents, and are also pollinated by nitidulids, Staphylinidae, and in *Xylopia aromatica*, additionally by Thysanoptera. The analyzed scent compounds in *Anaxagorea* species consist mainly of esters and occasionally also of alcohols. The scents of *Duguetia asterotricha* consist of monoterpenes, those of *Annona insignis* of benzenoids and ketones, and *Xylopia aromatica* and *X. benthamii* have high amounts of benzenoids including alcohols (Jürgens et al. 2000, Teichert et al. 2011). The most abundant floral scent compound identified in *Anaxagorea prinoides* and in

A. dolichocarpa is ethyl isovalerate (greater than 50 %), and isobutyl isovalerate is also plentiful. Ethyl isovalerate is known to be produced by beetle-attracting species of Araceae, Cycadaceae and Magnoliaceae, whereas isobutyl isovalerate is known only from the floral scent of Annonaceae species (Knudsen et al. 2006). Both esters, which also occur in fruits, seem to be effective beetle attractants (Teichert et al. 2011). It was reported some time ago that several Annonaceae flowers are associated with nitidulid and other beetles that normally live, nourish themselves and breed on rotten bark and fruits. Fruit scents produced and given off in the closed, dark pollination chambers of several Annonaceae attract these same fruit-inhabiting beetles, which in response enter the interior of Annonaceae flowers and pollinate them (Gottsberger 1970, 1974).

Another Annonaceae species, *Duguetia cadaverica* has foul-smelling flowers, and among the 18 identified scent compounds were characteristic earthy odors of fungi, sulfides, and 4-methylpentanoic acid, molecules associated with carcass and cheese odors, respectively. The pollinator of *D. cadaverica* is likely a nitidulid beetle (*Pycnocnemus* sp.), which belongs to the *Oxycnemus* genus complex, known to have fungal hosts of the order Phallales. Thus, the flower of the saprocantharophilous *D. cadaverica* appears to be a stinkhorn (Phallales) mimic (Teichert et al. 2012). With respect to their odor, species of the Annonaceae genus *Unonopsis*, are quite the opposite to *D. cadaverica*, because they emit a pleasant, aromatic smell. Many monoterpenes were detected in the scent samples, among them trans-carvone oxide. This component and others occur in *U. stipitata*, but also in several orchids, Euphorbiaceae and Araceae, and attract male bees of *Euglossa* and *Eulaema* (Euglossini, Apidae) to visit flowers of these four families, in what is thought to be an example of convergence. The bees collect liquid scent, or "perfume", produced by the inner petals and doing so, become pollinators of the *Unonopsis* flowers, as well as of the flowers of the families mentioned above (Carvalho & Webber 2000, Silberbauer-Gottsberger et al. 2003, Teichert et al. 2009). A review of chemical composition, and summary of the diversity of scents, in Annonaceae is given by Goodrich (2012).

A very special situation occurs in dynastid scarab beetle-pollinated Annonaceae. For example, *Annona coriacea*, *A. crassiflora* and *A. dioica* were observed to grow sympatrically in the Brazilian cerrado vegetation. They exhibited staggered flowering peaks and all three species attract the beetle *Cyclocephala atricapilla* with the same single scent compound 4-methyl-5-vinylthiazole. Also *Annona montana* and *Caladium bicolo*r in Northeast Brazil attract their pollinators (*Cyclocephala vestita* in the former and *C. celata* in the later species) with the identical thiazole compound. This highly specific attraction linked to the presence of a single compound is an example of rarely documented, scent-driven, "private communication channels" (Maia et al. 2012). Such private communication channels involving basal angiosperms and dynastid scarab beetles were documented also for *Magnolia ovata* (Gottsberger et al. 2012), *Philodendron acutatum* (Maia et al. 2010), *P. selloum* (Dötterl et al. 2012, Gottsberger et al. 2013), *P. adamantinum* (Pereira et al. 2014), *Taccarum ulei* (Araceae) (Maia et al. 2013a), and occur probably also in species of *Nymphaea* subgen. *Hydrocallis* (Maia et al. 2014) and *Victoria* (Kaiser 2006). One further example shows the simplicity and at the same time complexity of these chemical and behavioral interrelationships of flowers, their scents and the beetles attracted. The C5-branched chain ester Methyl

2-methylbutanoate is the principal floral scent compound of *Magnolia ovata* and attracts the pollinating Cyclocephalini beetle *Cyclocephala literata* (Gottsberger et al. 2012). This compound occurs also in *Magnolia mexicana* and *M. hypoleuca* (Azuma et al. 2004). The same compound occurs in high proportion in *Nymphaea gardneriana* and *N. lasiophylla* (subgen. *Hydrocallis*), both known to attract *Cyclocephala* beetles (Cramer et al. 1975, Prance & Anderson 1976, Prance 1980, Maia et al. 2014), and it is also a major constituent in both *Victoria* species (*V. amazonica* attracts *Cyclocephala hardyi* and *V. cruziana* is associated with *Chalepides* sp., both tribe Cyclocephalini) (Kite et al. 1991, Kaiser 2006). Interestingly, the same Methyl 2-methylbutanoate was found by Kaiser (2006) to dominate the scent of the Paleotropic *Eupomatia laurina* (Eupomatiaceae), a species known to be pollinated by small curculionid beetles of the genus *Elleschodes*. Thus, *Magnolia ovata*, *Victoria* and *Nymphaea* species in the Neotropics, and *Eupomatia laurina* in the Paleotropics apparently use the same scent compound to attract their specific scarab or curculionid beetles.

Pollination generalists versus specialists

It is highly unlikely that angiosperms started as pollination specialists. To do so would have canalized the angiosperms from the beginning on, and likely slowing down or inhibiting their further floral development and radiation. Bearing in mind the thousands of different flower types and forms and their many different ways of functioning, then it is unconceivable that angiosperms were originally pollination specialists.

During much of the last century and even before, however, there was an ongoing discussion of whether prototypical angiosperms were pollination specialists. At that time, the "Ranales", or "Polycarpicae" and later, the Magnoliidae and related groups, were thought to represent the extant ancestral angiosperms. Temperate zone species of *Magnolia* and *Nymphaea* were reported to be exclusively beetle-pollinated (but see sections on Magnoliaceae and Nymphaeaceae); additionally, North American *Calycanthus* species and the tropical Australian *Eupomatia laurina* were found to be beetle-pollinated (Delpino 1868–1874, Hamilton 1897). Diels (1916) was the first to hypothesize that beetle pollination was characteristic of ancestral angiosperms. His reasoning was based on the fact that cantharophily was found in several extant angiosperms thought to be "primitive", as well as on the prevailing notion of that time that beetles were the only or most important potential flower visitors around the presumed time of the origin of the angiosperms; moreover, geologically older plants, such as the cycads, were recognized as having mutualistic relationships with beetles as pollinators. The study of beetle pollination in *Calycanthus occidentalis* by Grant (1950) increased interest in Diels' ideas. The interpretation of basal angiosperm flowers as cantharophilous was turned into conviction in the papers and books of van der Pijl (1960, 1961), Baker & Hurd (1968), and many others. Referring to the time during which angiosperms were thought to have first evolved, Faegri & van der Pijl (1979) stated: " So, if insects had any function in pollination at that time, we may safely assume that beetles stood at the cradle of the flower."

In my first paper on the floral biology of Brazilian Annonaceae (Gottsberger 1970), I also accepted the prevailing idea that beetles were the most basal pollinators in angiosperms. A few years later and after the study of *Drimys brasiliensis* (Winteraceae),

a species that has open and accessible flowers, which are not only visited and pollinated by beetles, but also by Diptera, Thysanoptera and other insect groups, my ideas about pollination of extant basal angiosperms were profoundly modified: "It is believed that most primitive, still unspecialized Angiosperm flowers were pollinated <u>casually</u> by beetles. Only in a later phase did they gradually become adapted to the more effective but more devastating type of beetle pollination. Together with this specialization, flower enlargement, reduction of inflorescences, numerical increase of stamens and carpels, and their more dense aggregation and flattening might have occurred.", and comparing the results of the *Drimys* studies with that obtained from Annonaceae, it was further stated that . . ."Attracting fruit beetles by deceit must have been a secondary acquisition of primitive flowers, just as offering nutritious tissues or other special structures to compensate the negative side effects of larger and more precise pollinators. It is in this direction that we have to see the large and solitary flowers of Magnoliaceae, Annonaceae, Calycanthaceae, Himantandraceae, Nymphaeaceae, and others." (Gottsberger 1974). These ideas, which for the first time denied that exclusive beetle pollination was the original pollination mode of basal angiosperms, have been elaborated in subsequent papers: "These results suggest that one of the trends in the flower evolution of Magnoliidae was connected with specialization in beetle pollination. *Drimys brasiliensis* apparently represents a primitive stage with very generalized, open and unprotected flowers. . . Day-active beetles, flies and Thysanoptera (all more or less old insect groups) arrive at the open flowers, eat from pollen and lick from stigmatic exudates. . . Specialization along the line of beetle pollination was connected with the exploitation of a different ecological niche." (Gottsberger et al. 1980; see also Gottsberger 1977, 1988, 1993). Apparently, other authors agreed with this new concept and (with reference also to Magnoliidae, Arecales, Cyclanthales and Dilleniales) thus arrived at the same conclusion: "When Bernhardt and Thien (1987) first reviewed the floral biology of basal angiosperms, they came to the conclusion that generalist pollination evolved first in the insect-pollinated early angiosperms. . . The first flowers received a wide variety of pollen vectors representing several insect orders. . . Beetle pollination in particular represents a derived, albeit early evolving, syndrome. . ." (Thien et al. 2009).

So, which are the pollination generalists and specialists in basal angiosperms and which of the considered families of basal angiosperms have developed such specialists? The different lines of specialization in the basal angiosperms need to be shown and evaluated, as well as the accompanying flower developments and adaptations to different pollinators. Which are most prevalent among basal angiosperms, pollination generalists or specialists? Is there a general tendency for specialization in the basal angiosperms or are there also reversals?

It was outlined above that the monotypic, dioecious *Amborella trichopoda*, the supposed sister to all other angiosperms is a prototypic pollination generalist, having insects of several orders and the wind as pollination agents.

In the Nymphaeales, the aquatic or subaquatic species of *Trithuria* (Hydatellaceae) are self-pollinated or occasionally wind-pollinated, and *Euryale ferox* and some *Barclaya* species (Nymphaeaceae) also have self-pollinating, partly only cleistogamous and partly cleistogamous and chasmogamous underwater and aerial flowers,

which in *B. rotundifolia* are additionally visited by flies. It is difficult to classify these plants as generalists or specialists, although each of their characteristics alone, namely self-pollination, cleistogamy, wind and underwater pollination have to be seen as functional specializations. *Cabomba* species are perhaps all pollination generalists. Fly pollination in *Barclaya rotundifolia* (Nymphaeaceae) is probably one of the first pollination specializations among the basal angiosperms.

Species of *Nuphar* and *Nymphaea* subgen. *Nymphaea, Brachyceras* and *Anecphya* are pollination generalists. Insect-pollinated specialists occur in the derived *Nymphaea* clade subgen. *Hydrocallis-Lotos* which might be sister to the *Euryale-Victoria* clade (Borsch et al. 2008). Species of *Nymphaea* subgen. *Hydrocallis* and *Victoria* have a tropical American distribution and are visited by large, nocturnally active dynastid scarab beetles, mainly of the genus *Cyclocephala*, which are attracted by strong scent emissions, probably partly intensified by heating of the flowers (thermogenesis). Similarly, the African species *Nymphaea lotus* (subgen. *Lotos*) is pollinated by the dynastid scarab *Ruteloryctes morio*.

However, beetle pollination *per se* is not an indication of antiquity of the phenomenon, especially not in scarab beetle-pollinated Nymphaeaceae, Magnoliaceae, Annonaceae, Araceae and others (Gottsberger 2012, Gottsberger et al. 2012). Although the order Coleoptera is an old insect group, the dynastid scarab beetles (Dynastinae, Scarabaeidae) are apparently late-comers in the evolutionary history of beetles and seem not to have developed before the Tertiary (e.g. Ratcliffe et al. 2005, Krell 2006, Ahrens et al. 2014, McKenna et al. 2015). The radiation of the extant core Nymphaeaceae, including *Nymphaea* and *Victoria*, was relatively recent, in the late Oligocene to Middle Miocene (Löhne et al. 2008). Thus, dynastid scarab beetle pollination in extant *Nymphaea* and *Victoria* obviously is a quite recent adaptation to a modern beetle group. Nymphaeaceae-like fossils from the Early Cretaceous, such as *Monetianthus mirus*, have very small flowers, and Friis et al. (2011) wonder about the possible pollination mode of this early Nymphaeaceae species, which might have been pollinated by small, unspecialized insects. The increase in flower size in extant Nymphaeaceae probably has to do with specialization in pollination as instructively demonstrated by *Nymphaea* and *Victoria*. Species of *Nymphaea* subg. *Nymphaea, Brachyceras* and *Anecphya* are pollination generalists, however with a more or less common component of beetles of relatively small size. Their flowers, although quite large (up to 14 cm diam), are smaller than the flowers of *Nymphaea* subg. *Hydrocallis* and *Lotos* (up to 20 cm diam.) and *Victoria* (up to 25–30 cm diam.), which are both visited by the large, voracious dynastid beetles. Thus, it appears that flower size, at least in the aforementioned Nymphaeaceae, is indeed influenced by the size, behavior and appetite of the pollinating beetles which are kept inside the pollination chamber for many hours.

In the Austrobaileyales, *Trimenia moorei* (Trimeniaceae), *Illicium floridanum, I. parviflorum, Schisandra sphenanthera* and *S. glabra* (Schisandraceae) are pollination generalists. Conversely, *Austrobaileya scandens* flowers appear to be sapromyiophilous and/or possibly saprocantharophilous, and several members of Schisandraceae, such as *Kadsura longipedunculata, Schisandra henryi, Illicium dunnianum, I. tsangii* and probably *I. arborescens* are specialists. Some of these species having specialist

pollination are exclusively visited by midges (cecidomyiid flies) for pollen in the staminate flowers, while the pistillate flowers function in pollination by deceit. In some species, warm bisexual flowers are used as brood sites. The observed post-sexual phase flower heating in *Illicium dunnianum* does not benefit seed development, but is essential for the midge larvae, which can only develop in heated flowers (while fed by flower secretions). Luo et al. (2010) proposed that early Schisandraceae were pollinated by flies and/or beetles with midges being co-pollinators, as in the New World species *Illicium floridanum* and *I. parviflorum*. Heat in these flowers enhanced scent emissions for scent-oriented pollinators. "Some midges, such as *Clinodiplosis*, then increasingly used the warm flowers for breeding, which set the stage for reciprocal coevolution between midges selecting for long-heated brood chambers and flowers responding by relying exclusively on *Clinodiplosis*... Under this scenario, flower heating is a trait that evolved "for" scent emission and that then became co-opted as a pollinator reward in flowers relying on flower-breeding insects, the larvae of which require moist, warm chambers for the duration of their development." (Luo et al. 2010). Thus, at least in Schisandraceae, which is the species-richest family in the Austrobaileyales, a development from insect pollination generalists to specialists can be observed.

For the most basal clade of monocots, *Acorus* (Acorales), entomophily is assumed by several authors, but strangly enough, until now no one has ever detected flower-visiting insects. The Alismataceae, a member of the Alismatales, another early-divergent monocot clade, have open flowers visited by a more or less large spectrum of insects, and perhaps nearly all species have to be classified as pollination generalists. However, some species are more exclusively visited by bees with tendencies to melittophily. Just the opposite has occurred in another family of this order, Araceae, wherein most members exhibit specialist pollination modes, pollinators mainly being either flies, beetles or bees. With respect to the pollinator-plant interaction types provided for the family (Chartier et al. 2013), an ancestral pollination mode could not be inferred. Fly pollination appears as early as beetle pollination. The specific pollination mutualism in the family involves rewards in the form of liquid food for adult insects, floral perfume for male euglossine bees, pollen for beetles or flies, or mating- and egg-laying sites, while the antagonisms mean pollinator trapping and consequently the reduction of their fitness. The authors deduced that deception has evolved at least five times, in two cases associated with beetles (*Stylochaeton* and *Amorphophallus*), and in three cases mainly with flies (Cryptocoryneae, *Arisarum* and Areae).

Flowers of the earliest-divergent Winteraceae (Cannellales), *Takhtajania perrieri*, were found to be visited by certain flies. Observations are too scarce to make any judgement about its overall floral biology. *Tasmannia* appears to be a pollination generalist, and *Drimys* and *Pseudowintera* species are definitely pollination generalists, with the exception of *D. confertifolia* which is anemophilous, perhaps in response to the insect-poor environment on Juan Fernández Island. Species of the late divergent *Zygogynum s.l.* are pollination specialists. Several New Caledonian species of *Zygogynum s.l., Zygogynum pancheri, Z. rivulare* and an undescribed species are all pollinated mainly by a single thrips species, *Taeniothrips novocaledonensis*. Several other *Zygogynum* species studied in New Caledonia, such as *Zygogynum baillonii, Z. pomiferum, Z. bicolor, Z. viellardii, Z. mackeei, Z. stipitatum* and *Z. pauciflorum* were found to be

pollinated by three species of the beetle genus *Palontus* (Curculionidae) and occasionally by species of the moth *Sabatinca*. The *Zygogynum* species mainly pollinated by beetles exhibit a typical pollination chamber formed by thick petals; the petals close and open to keep beetles inside the pollination chamber during the pistillate stage and release them in the staminate stage. In Winteraceae it seems there is a trend from generalist to specialist pollination, although more data on *Tasmannia* are necessary. In the late-divergent genus *Zygogynum s.l.*, some species are specialized for thrips and some others mainly for beetles.

In the Piperales, the Aristolochiaceae are a group nearly exclusively associated with a large variety of fly groups. Up to now, flies, representing 41 families have been found to visit and pollinate flowers of investigated *Aristolochia* species. In *Asarum* (Asaroideae) the condition of autonomous self-pollination was found to be plesiomorphic and pollination of herkogamous flowers by fungus gnats (Mycetophilidae) derived. In the genus *Aristolochia* (Aristolochioideae) the quite different floral scent emissions described as agreeable to unpleasant and non-perceptible (by the human nose) together with other flower characteristics attract an extremely broad spectrum of flies (e.g., fungus gnats by fungi-like scent, Drosophilidae probably by fruit-like scents, or Calliphoridae, Muscidae, Sarcophagidae, Sarcopsidae by unpleasant scents). With respect to their pollination, Aristolochiaceae are almost exclusive specialists having myiophilous and sapromyiophilous pollination modes.

Wind pollination in the monotypic *Lactoris fernandeziana* (Lactoridaceae) may be attributed to the scarcity of pollinators in the Juan Fernández Islands. The holoparasitic species of *Hydnora* and *Prosopanche* (Hydnoraceae) with their unpleasant smelling, brood-site imitating flowers seem to be highly specialized either exclusively for beetles or for beetles and flies, and thus can be classified as exclusively saprocantharophilous and/or having a mixed saprocantharophilous/sapromyiophilous pollination syndrome.

The perianthless families of the Piperales, Piperaceae and Saururaceae are apparently both pollination generalists. In Piperaceae, the inflorescences are visited by bees, flies and sometimes beetles and other insects. Wind pollination is another additional mode at least in some species. Moreover, inflorescences of *Saururus* (Saururaceae) species were found to be visited by flies, bees, beetles and additionally pollinated by wind.

The families of Laurales consist of genera and whole families that are either pollination generalists or specialists. For Calycanthaceae, Zhou et al. (2006) proposed that the pollination generalist *Idiospermum australiense* had diverged by the Upper Cretaceous, while the northern Hemisphere genera *Calycanthus* and *Chimonanthus* diverged from each other as late as the mid-Eocene. If this is so then one of the two late-divergent genera, *Chimonanthus*, apparently continued as pollination generalist, while the three *Calycanthus* species have become specialized for beetle pollination. *Gomortega keule* (Gomortegaceae), Atherospermataceae, Hernandiaceae and apparently all Lauraceae are pollination generalists. On the other hand, Siparunaceae, at least all species of *Siparuna*, are highly specialized, having pollination by gall midges, which oviposit in the flowers. Likewise, flowers of *Mollinedia* and *Wilkiea* (Monimiaceae) are used by pollinating thrips as brood sites. Several species of the genus *Tambourissa* (also Monimiaceae) were found to be visited by flies and/or beetles. Observations on only

a few species in three genera of the pantropical family Monimiaceae (ca. 200 species in 28 genera), is insuffcent to provide insight into the functional evolution of the family. However, as the recognized pollination specialists *Mollinedia* and *Wilkiea* do not belong to the early divergent genera (e.g., the South American *Mollinedia* clade is only 28–16 Myr old; Renner et al. 2010) future studies on more genera should eventually clarify whether in this family, too, a development from pollination generalists to specialists has occurred.

In the family Myristicaceae (Magnoliales), only a few species of *Myristica* have been investigated with regard to pollinators and pollinator spectrum. *Myristica dactyloides* and other species of this genus show a generalist pollination system with thrips (using buds and open flowers as brood-sites), as well as beetles, bees and flies transferring pollen from staminate to pistillate flowers. *Myristica insipida* is more restrictively pollinated by beetles of five families, and additionally by thrips, and *M. fragrans* is pollinated mainly by a single beetle species. This species sequence is suggestive of a development from pollination generalists to species pollinated by beetles of several families, and finally to species, which are exclusively cantharophilous and associated with a single pollinating beetle species. However, as I am not aware of a phylogenetic study of the genus *Myristica*, the direction of the development, either from pollination generalists to specialists or vice versa cannot be determined.

Two further, very small families of the Magnoliales, Degeneriaceae having two species and Eupomatiaceae having three species, are exclusively cantharophilous, and the two species of *Galbulimima* (Himantandraceae) are suspected to be beetle-pollinated.

Diversification of extant members of Magnoliaceae apparently occurred during the early Eocene, at about 55 Myr (Nie et al. 2008). The tropical American section *Talauma* of *Magnolia*, to which the Brazilian *M. ovata* belongs, branched off first, and then both the tropical Asian and the West Indies groups diverged (Azuma et al. 2001). These authors also affirm that their data show that tropical disjunctions occurred prior to the disjunctions of temperate taxa. It was hypothesized (Gottsberger et al. 2012) that *Magnolia* evolution started in the early Tertiary in tropical America and in association and under the influence of flower-visiting dynastid scarab beetles. The large, robust *Magnolia* flower probably is best explained as being an archaic structure, which stems from the initial association of tropical American species of the section *Talauma* and American dynastid scarab beetles; flower size and robustness was partly maintained during diversification of the genus. On the other hand, the types of flower/insect associations apparently became modified and adapted when *Magnolia* radiated from the Neotropics (large dynastid beetles) to the Old World tropics and temperate zones (mainly small beetles, as well as flies, bees and thrips). A re-adaptation to dynastid beetles was possible when members of the genus radiated back to the warmer American regions. Thus, *Magnolia* would be an example of a group whose earliest extant species started as extreme specialists, being pollinated usually by only one species of dynastid scarab beetles. Later species radiated and diverged in the Paleotropics and in the northern temperate zones and became mainly pollination generalists.

The largest family of the Magnoliales, Annonaceae, is another basically cantharophilous family. The earliest divergent genus, *Anaxagorea* (subfam. Anaxagoreoideae), is sister to all other Annonaceae. All other Annonaceae are classified as belonging

either to the subfamily Ambavioideae or the two large sister clades, the subfamilies Annonoideae and Malmeoideae (Chatrou et al. 2012). *Anaxagorea* species are pollinated by small Nitidulidae beetles. Similarly, members of Ambavioideae (e.g., *Cananga, Tetrameranthus, Mezzettia*) are visited by small beetles (Nitidulidae, Chrysomelidae, Curculionidae). In the Annonoideae, many genera are still pollinated by small beetles (e.g. *Xylopia, Artabotrys, Asimina, Duguetia, Guatteria, Goniothalamus, Annona, Isolona, Uvaria*), while other species, some in the same genera, have diversified into pollination by large beetles (e.g. *Cymbopetalum, Porcelia, Duguetia, Asimina, Annona, Uvariodendron*), others into pollination by thrips (e.g. *Xylopia*), flies (e.g. *Monodora, Hexalobus, Uvariopsis*), cockroaches (*Uvaria*) and bees (e.g. *Uvaria*). A similar diversification pattern of pollination systems as observed in Annonoideae also occurs in Malmeoideae, with small beetles (e.g. *Piptostigma, Haplostichanthus*), large beetles (e.g. *Malmea, Mosannona*), thrips (e.g. *Bocageopsis, Oxandra, Popowia*), flies (e.g. *Pseuduvaria*), and perfume-collecting euglossine bees (e.g. *Unonopsis*) (see Gottsberger 2012, Saunders 2012). The Annonaceae seem to have originated in the Cretaceous (Pierie & Doyle 2012) and supposedly were initially associated with small nitidulid beetles. Small-sized beetles as pollinators apparently accompanied the whole evolutionary history of the family. It seems probable that some time during the Tertiary, several species became adapted to pollination by large scarab beetles (Dynastinae, Rutelinae, Cetoniinae, Trichiinae) and to euglossine bees. Flower morphological characters associated with adaptation to large and voracious scarab beetles were larger pollination chambers and concomitantly overall larger flower sizes than in flowers pollinated by small beetles, as well as extremely thick petal tissue. Thick petal tissue in several species is also associated with nutritious tissue at the inner side of the inner petals. Petal tissue provides the necessary nutrition for the attracted beetles, and the accumulated starch and (sometimes) lipids, enables the flower to attain a high self-heating through respiratory processes (thermogenesis) which, as a consequence, makes scent emissions strong, attracts beetles more precisely and provides them a warm flower interior. In contrast, a more or less closed pollination chamber would be an obstacle to reach the reproductive organs of the flowers for flies, cockroaches and bees. As an adaptation to these "free working" pollinators, the myiophilous, melittophilous or cockroach-pollinated Annonaceae have open flowers and reflexed petals, which gives pollinators free access to the flower center. Small, elongate thrips do not need an open flower to crawl inside it. "Their" flowers are relatively small and more or less closed during the pistillate stage, have comparatively few stamens and carpels and floral scent is relatively weak, but mostly pleasant and sweet and, thus, quite different from the scent of beetle-pollinated species.

For Chloranthaceae (Chloranthales), morphological and molecular data indicate that the deepest split is between *Hedyosmum* and the remaining genera and that *Ascarina* is sister to *Sarcandra* and *Chloranthus* (Zhang & Renner 2003). The calculated time for *Hedyosmum* divergence from the three other genera was around 111.1 Myr, *Ascarina* separation from the other two genera, 95.7 Myr, and *Sarcandra* splitting from *Chloranthus*, around 63.8 Myr (Zhang et al. 2011). Thus, for this family, anemophily in *Hedyosmum* and *Ascarina* having unisexual flowers appears basic, and insect pollination in the bisexual flower genera *Sarcandra* and *Chloranthus*, derived. *Sarcandra*

glabra was found to be a pollination generalist, being pollinated by beetles, bees, flies and other insects. The two species of *Chloranthus, C. serratus* and *C. fortunei*, have been revealed to be specialists, pollinated exclusively by thrips. Thus, in this family, the data again indicate a tendency towards specialization for insect pollination, with basal wind pollination in *Hedyosmum* and probably *Ascarina*, and development of generalist insect pollination in *Sarcandra* and specialist insect pollination in *Chloranthus*. All species of *Ceratophyllum* (Ceratophyllales) are specialized for underwater pollination.

Characteristics of pollination specialists

The basal angiosperms exhibit mainly four lines of specialization with regard to pollination by insects, namely pollination by flies (myiophily and sapromyiophily), thrips, bees (melittophily) and beetles (cantharophily and saprocantharophily). Further specializations are the abiotic modes of exclusive pollination by wind (anemophily) and water (hydrophily). Each of these so-called specialization lines, however, consist of quite different adaptations in different groups of the respective insects, which may have different behaviors, and which are attracted by different means and may use the flowers for different needs.

Starting with flies, we may give some examples of the extreme differences in myiophily and sapromyiophily. *Austrobaileya scandens* apparently is pollinated by flies; the pollination process, however, is not yet well understood, although it is clear that scent and color of the flowers are important for attracting flies. Quite sophisticated cases of myiophily occur in Schisandraceae, a family which, among others, is associated with cecidomyiid flies, which either eat pollen or in a derived mode use the flowers as brood sites. In the last case, larval development is benefited by floral heating extending to the post-anthetic stage. Cecidomyiid flies that breed inside the closed floral interior occur also in *Siparuna*. Some myiophilous species of Araceae, e.g. species of *Anthurium*, attract flies exclusively by emitting special scent compounds, leading the flies to pass over the exposed spadix. In other genera of Araceae, e.g. *Arum*, flies are lured to enter the basal kettle and are imprisoned there for a while until pollen is shed. Such sophisticated cases of myiophily and sapromyiophily occur also in Aristolochiaceae, with fly imprisonment and "manipulation" of these pollinators by the flower. The importance of flies in *Hydnora* pollination has still to be elaborated. Thus, considering myiophily and sapromyiophily in basal angiosperms, at least three main lines or levels of specialization have occurred. One level comprises open and free accessible flowers or inflorescences (e.g. *Anthurium*); flies are apparently attracted mainly by special scent compounds, as well as floral color and available resources. Another specialization is restricted to cecidomyiid flies, which at a lower level just eat pollen and at a higher level oviposit in flowers, using the heated (*Illicium*) or unheated (*Siparuna*) flowers as breeding places. Another specialization occurs in Aristolochiaceae and Araceae, in which either flowers (e.g. *Aristolochia*) or inflorescences (e.g. *Arum*) form a basal kettle; flies are lured to enter the kettle and are imprisoned for the time necessary to become efficient pollinators. Fly pollination occurs also in Annonaceae, e.g. in unpleasant smelling flowers of *Uvariopsis* and nectar-providing flowers of *Pseuduvaria*, which present their petals open and spread, giving flies the necessary access to floral resources and reproductive organs.

Thrips (Thysanoptera) are minute elongate insects, many species of which like to hide, to nourish themselves and to breed in flowers. They are co-pollinators in many flowers but are not so commonly exclusive pollinators. Three *Zygogynum* (Winteraceae) species in New Caledonia having pale-yellow flowers, which produce a faint, sweet fragrance were all found to be pollinated by a single species of thrips; a high number of thrips larvae were found in the flowers, indicating this thrips breeds in the flowers. In *Chloranthus* (Chloranthaceae) thrips are the exclusive pollinators, and they are the only insects able to enter the small floral-axis chamber. In *Mollinedia* and *Wilkiea* (Monimiaceae) thrips species breed inside the cup-like receptacle and pollinate the flowers. In *Myristica dactyloides*, thrips species use the buds and urceolate flowers as breeding sites, nonetheless, they are not exclusive pollinators, but co-pollinators of this species. Other exclusively thrips-pollinated species occur in Annonaceae, in the genera *Bocageopsis, Xylopia, Popowia, Oxandra* and *Cananga*. Thrips-pollinated flowers in Annonaceae are relatively small and have semi-closed petals during the flower's pistillate stage. Flowers have comparatively few stamens and carpels and floral scent is relatively weak, but pleasant and sweet and thus quite different from the scent of e.g. beetle-pollinated species. In Monimiaceae and *Myristica*, the whole flower is more or less a closed structure.

Bees as exclusive pollinators were observed in a few *Echinodorus* (Alismataceae) and *Piper* (Piperaceae) species and occur, albeit in a much more sophisticated way, also in Araceae; some *Anthurium* and *Spathiphyllum* species are pollinated by scent-collecting male euglossine bees. Flowers and inflorescences of melittophilous Alismataceae, Piperaceae and Araceae seem to have no special morphological adaptations for bees, flowers are just exposed, and the resources, whether pollen, nectar or perfume are easily accessible for collection by these insects. In *Unonopsis* (Annonaceae) species, pollination by perfume collecting male euglossine bees occurs, and the flowers in this genus present open flowers having extended petals providing entry for the perfume-collecting bees.

Beetle-pollinated species have the tendency to produce thick, tissue-rich petals, such as seen in Winteraceae and others. While the thrips- or generalist-pollinated species of Winteraceae have "normal" thin petals, petals of the derived beetle-pollinated *Zygogynum* species are thick and leathery. Similar tendencies can be seen also in e.g. Nymphaeaceae, Calycanthaceae, Magnoliaceae, Annonaceae. Petals are not only thick, but they also curve over the flower center, or cover it partly, and form a dark interior, which is the most important structure to maintain the beetles inside the flower during the first part of anthesis until pollen is shed. The closing of flowers is a typical and important characteristics of cantharophilous flowers and was first described for Annonaceae and called a pollination chamber (Gottsberger 1970). A pollination chamber is able to keep the beetles inside a flower as long as it is necessary to make them effective cross-pollinators. The closed, dark interior of the flower also shields the beetles from light during the day hours, the chamber may be warm and scented, promoting the activities of the beetles, such as feeding, digesting and mating, and at the same time it protects the beetles against predatory birds and lizards. The odoriferous, dark floral chamber also serves to select the flower-visiting beetle spectrum and to retain the beetles inside the flowers while they are closed.

The large majority of cantharophilous basal angiosperms are pollinated by Nitidulidae, Curculionidae, Staphylinidae, Chrysomelidae, Mordellidae, and a few other families, which usually have a body length up to 7 mm. Several derived *Nymphaea* and *Victoria* species, species of *Philodendron* and other genera of Araceae, Neotropical *Magnolia* species and quite a number of Annonaceae attract Scarabaeidae (Dynastinae, Rutelinae, Cetoniinae, Trichiinae), which are large beetles having a body length of 14–22 mm.

Morphological flower characters associated with adaptation to the large and voracious scarab beetles are large pollination chambers and, concomitantly, overall larger flower sizes than in flowers pollinated by small beetles, as well as thicker petal tissue. As mentioned above, thick petal tissue is often associated with the presence of nutritious tissue and high self-heating (thermogenesis) which, as a consequence, makes scent emissions strong and attraction of beetles more precise and efficient (Gottsberger 2012). On the other hand, a heated flower provides beetles a warm pollination chamber, which is necessary for the beetles' proper activities inside the pollination chamber and to aid them to fly off at the end of anthesis.

Thus, petals have several functions. They attract beetles by strong odor emissions, often intensified by floral warming. Once having penetrated the dark, warm, energy-saving pollination chamber, the beetles find nutritious tissues or food bodies during the pistillate stage of a flower and abundant pollen in the later staminate stage. A pollination chamber is an ideal place for beetles to hide, feed and mate. As gnawing of petals and reproductive organs is a destructive behavior, beetle flowers have developed several devices against being destroyed, such as large flowers with large and thick, tissue-rich petals, instructively seen in flowers visited by the voracious scarab beetles, as also food bodies on petals, stamens and staminodes, nutritious tissues on the petals, or protective shield-like connectives in Annonaceae and abundant and sticky stigmatic exudates.

Flowers can easily "handle" their beetle pollinators. If they provide them a dark, odoriferous, if possible, warm pollination chamber with sufficient food then they can keep them as long as necessary to become efficient pollinators! Considering the overwhelming number of beetles, both richness and abundance, cantharophily in tropical basal angiosperms, was likely an easy way to become a pollination specialist. Some members of Nymphaeaceae, several Araceae, some derived Winteraceae and Calycanthaceae, Hydnoraceae, some Myristicaceae and Magnoliaceae, Degeneriaceae, Eupomatiaceae and probably about 90% of extant Annonaceae diversified and function on the basis of this efficient and successful form of beetle pollination.

Which pollination mode predominates, generalist or specialist, and what has been the direction of evolutionary events?

How many pollination generalists and specialists occur in the extant basal angiosperms? Since groups treated in this review total about 13,000 to 14,000 species, of which only a small portion has been studied, we can only make a wild "guesstimate" about numbers, and idealizing them, we may discern patterns and trends of likely evolutionary events in the reproductive biology of the basal angiosperms.

The following numerical assessments are based on accounts in The Plant List (2013), which provides numbers of accepted species, including in part some infraspecific names; however, some unassessed or unresolved groups are included (e.g. Trimeniaceae, Winteraceae). The 32 families treated in this review are represented by 13,196 accepted taxa, wherein the ANITA grade consists of 186, basal monocots treated in this paper, of 3583, magnoliids of 9344, and Chloranthaceae and Ceratophyllaceae together, of 83 taxa. In the following, for the sake of simplicity, all are referred to as species. The numbers given below are in most cases from The Plant List and not necessarily identical with numbers of species provided by specialists of the respective groups, mentioned in the text.

Generalists in the ANITA grade are *Amborella*, perhaps all species of *Cabomba* (5 spp.), as well as *Nuphar* (24 spp.), *Nymphaea* (50 spp.) subgenera *Nymphaea, Anecphya* and *Brachyceras*, perhaps one third each of the species of *Schisandra* (32 spp.), *Kadsura* (16 spp.) and *Illicium* (34 spp.) and perhaps all species of *Trimenia* (5 spp.). Fly-pollinated specialists seem to be *Barclaya rotundifolia* and *Austrobaileya*, as well as perhaps two thirds each of the species of *Schisandra, Kadsura* and *Illicium*. The fly pollination in *Barclaya rotundifolia* (Nymphaeaceae) is of a more open type, while in *Austrobaileya* and several Schisandraceae myiophily is quite sophisticated. The association of flowers with pollen-eating and breeding cecidomyiid flies in thermogenic flowers of Schisandraceae appears to be a highly specialized type of myiophily. There is another line of specialization in the beetle-pollinated *Nymphaea* species of subgenera *Hydrocallis* and *Lotos*, and *Victoria* (2 spp.), in total around 15 species. *Brasenia* and ten species of *Trithuria* (in total 12 spp.) are wind-pollinated, while two *Trithuria* species are pollinated under water. One species of *Barclaya* (in total 2 spp.) and *Euryale* (1 sp.) are obligate selfers.

Our very rough estimation for the numerical distribution of pollination syndromes in the ANITA groups gives the following numbers: In the ANITA grade around 90 species may well be insect pollination generalists, 60 species fly-pollinated, 15 beetle-pollinated (therefore, 75 insect pollination specialists), 11 are wind-pollinated, two species water-pollinated and two species are obligate selfers.

It appears that the first specialization in the ANITA grade has been for fly pollination. Although the Nymphaeales diverged before the Austrobaileyales, the specialized beetle pollination of the derived *Nymphaea* and *Victoria* species is certainly a more recent association than fly pollination in Austrobaileyales and *Barclaya*, especially also because the pollinating dynastid scarab beetles of the Nymphaeaceae apparently are late-comers in the evolutionary history of beetles (see above). The radiation of Nymphaeaceae into this "newcomer" beetle niche obviously occurred as late as the Tertiary.

In the basal monocots, *Acorus* (4 spp.) might turn out to have a generalist pollination system. The majority of Alismataceae (120) are generalists, however showing tendencies for exclusive bee pollination in a few species. In Araceae (3,459 spp.), a pollination specialist group, nearly all species seem to be specialized either for flies, bees or beetles, with fly- and beetle-pollinated species dominating by far over bee-pollinated ones.

In the magnoliids, species of Canellaceae (21 spp.) might be pollination generalists, while Piperaceae (2,717 spp.), Saururaceae (7 spp.), Gomortegaceae (1 sp.), Atherospermataceae (21 spp.), Hernandiaceae (57 spp.) and Lauraceae (3,027 spp.) are definitely pollination generalists. In Piperaceae a very few species show tendencies for bee pollination. In Winteraceae (38 spp., in The Plant List partly unresolved, therefore there are probably more species), the basal two genera *Takhtajania* and *Tasmannia* (7 spp.) are probably pollination generalists. *Drimys* and *Pseudowintera* are generalists, but *Drimys confertifolia* is anemophilous. The derived genus *Zygogynum s.l.* (7 spp. in the Plant List, but probably 30 or more species existing) has probably a lower number of species specialized for thrips and a higher number specialized for beetles. The Aristolochiaceae (643 spp.) may have a few generalist species, perhaps on the order of 10 to 20 species, and the other 99% being specialized for flies. The Calycanthaceae (11 spp.) have six species in two genera that are generalists wherein *Calycanthus* species are beetle-pollinated. Of the Siparunaceae (61 spp.), *Siparuna* (53–60 spp.) seems to be exclusively pollinated by gall midges (Cecidomyiidae, Diptera). Monimiaceae (135 spp.) might be an entirely specialist pollination group given their floral morphology, albeit only a few observations on a few species of *Mollinedia* and *Wilkiea* indicate specialization for thrips, and on *Tambourissa* either for flies or beetles. In a few species of Myristicaceae (177 spp.) either a generalist or specialist pollination is evident; for calculation of numbers, 80 species are considered generalists and the rest specialists. The three small families Himantandraceae (1 sp., in the literature usually 2 spp. are mentioned), Degeneriaceae (2 spp.) and Eupomatiaceae (3 spp.) are reported to be or are exclusively beetle-pollinated. The Magnoliaceae (275 spp.) might have about two-thirds of species that are generalists and the remainder are more or less exclusively pollinated by beetles. The Annonaceae (2,135 spp.) are a pollination specialist group. About 90% of all species are probably beetle-pollinated, whereas about 150, 100 and 50 species might be pollinated either by flies, thrips and bees, respectively; only one species is known to be pollinated by cockroaches. In Chloranthaceae (73 spp.), species of *Hedyosmum* (45 spp.) and *Ascarina* (12 spp.) are assumed to be all wind-pollinated, while species of *Sarcandra* (2 spp.) might be insect generalists and *Chloranthus* species (14 spp.) are perhaps thrips specialists. The submersed *Ceratophyllum* (10 spp.) species are hydrophilous.

All 13,000 to 14,000 basal angiosperms together, viz. the ANITA grade, basal monocots, magnoliids, Chloranthaceae and Ceratophyllaceae, might have around 6400 pollination generalist species, 3600 cantharophilous, 2400 myiophilous, 550 melittophilous, 160 thrips-pollinated, and one or eventually several cockroach-pollinated species. Additionally, there are about 70 species pollinated by wind and 12 species pollinated underwater. The greatest number of beetle-pollinated species are in the Annonaceae, with 1,900 estimated species, followed by Araceae (about 1500 calculated spp.), and the Myristicaceae and Magnoliaceae with about 80 species each. The most fly-pollinated species are in the Araceae (1500 estimated spp.), Aristolochiaceae (about 620 estimated spp.), followed by Annonaceae (150 spp.), Siparunaceae (61 spp.), Schisandraceae (60) and Monimiaceae (40 spp.). The bee-pollinated species are concentrated in Araceae (perhaps 500 spp.) followed by Annonaceae (50 spp.). Thrips pollination is perhaps most common in Annonaceae (with 100 spp.), Monimiaceae

(40 spp.) and Chloranthaceae (14 spp.). Wind-pollinated species are concentrated in Chloranthaceae (57) and Hydatellaceae (11 spp.); underwater pollination (12 spp.) occurs in *Ceratophyllum* and *Trithuria* species. Thus, beetle and fly pollination with an estimated 3,600 and 2,400 cases, respectively, are the most common forms of specialist pollination in basal angiosperms.

Based on the available data on extant basal angiosperms, what can be deduced about the direction of their development with respect to pollination modes? The earliest divergent clade, represented by *Amborella* is a pollination generalist. Generalist pollination apparently is a successful pollination mode, and was continued partly or totally by Cabombaceae, Nymphaeaceae, Schisandraceae and Trimeniaceae. As seen by the crude data estimated above, generalist pollination was continued also by whole families or genera in basal monocots, magnoliids and Chloranthaceae, and seems still to be represented by nearly half of all species of the basal angiosperms. However in Nymphaeaceae, *Austrobaileya*, and especially in Schisandraceae an early strong trend towards specialization for fly pollination is deducible. Specialization as a clearly derived phenomenon occurred also in the genera *Nymphaea* and *Victoria* with adaptations for scarab beetles; however, it is likely that this development was a quite recent event.

Not all families show a development from pollination generalists to specialists. The extant species of *Magnolia* apparently initiated development in the Tertiary as a scarab beetle-pollinated group in the Neotropics, later other species became largely pollination generalists in the Paleotropics and the northern temperate zones, and after a radiation back to the Neotropics, species became beetle-pollinated specialists again, which is an instructive example of a "reversal". Another example at the genus level, can be seen in the phylogeny of the genus *Annona*, which shows several shifts from large dynastid scarab-pollinated species having large flowers, to small flowers pollinated by small beetles and reversals back to large and small flowers in association with the respective beetle groups (Chatrou et al. 2009, Rainer, pers. comm.). Thus, from the examples given, it appears that a development from pollination generalists to specialists was common in the basal angiosperms but also reversals seem to have frequently occurred.

Basal angiosperms and the diversification of pollinating insects

Nearly all insect pollinators of flowering plants come from five out of the 32 orders of insects. Labandeira (2000) named them the "Big Five", Thysanoptera (thrips), an hemipteroid group of small insects, and the four holometabolous orders Coleoptera (beetles), Diptera (true flies), Lepidoptera (moths and butterflies), and Hymenoptera (sawflies, wasps, bees and ants). Among basal angiosperms, the dominant specialist pollinator groups are beetles and flies. Conversely, among eudicots, bees take the lead and in non-alpine regions usually dominate over beetles, flies, moths, butterflies, thrips, birds and bats together (e.g. Gottsberger & Silberbauer-Gottsberger 2006). As previously mentioned, members of each of these five insect orders are very heterogenous with regard to their size, residence time in a flower and behavior during a flower visit. Some flies just take-up pollen or nectar, while others, such as cecidomyiid flies

may use flowers as breeding places (e.g., in Schisandraceae, Siparunaceae); some species of the Schisandraceae have even heated flowers, and thus provide conditions for larval development assuring the future generation of their pollinators. Thrips seem to prefer semi-closed flowers or flowers that have a cup-like receptacle and they often breed inside the flowers they pollinate. In *Mollinedia* (Monimiaceae) species of Phlaeothripidae even puncture closed buds with their ovipositor and deposit eggs into the closed flower interior. Euglossine bees that pollinate Araceae and Annonaceae while collecting perfume at their inflorescences or flowers are a very specialized bee group and certainly late-comers in the evolutionary history of bees (Roubik & Hanson 2004). The only representatives of Lepidoptera known to act as pollinators in basal angiosperms are micropterigid moths in species of *Zygogynum* (Winteraceae), where they are co-pollinators of otherwise cantharophilous species. Beetles as pollinators are also a diversified group. There are many small beetles; several belong to early divergent groups and others belong to more recent groups. Large scarab beetles of the subfamilies Dynastinae, Rutelinae, Cetoniinae or Trichiinae are late-comers among beetles and originated during the Tertiary. These scarab beetle-pollinated lines occur convergently in the Nymphaeaceae, Araceae, Magnoliaceae and Annonaceae. The highly specialized and late-divergent mode of scarab beetle pollination and the euglossine bee pollination mode in Araceae and Annonaceae show that basal angiosperms in spite of their early origin have lineages which were apparently flexible enough to radiate into sophisticated and modern ecological niches.

Finally, a last example is given to illustrate the complexity and difficulty of classifying generalist and specialist pollination. The most early divergent genus of Annonaceae, *Anaxagorea*, was mentioned above as pollinated by small nitidulid beetles of the genus *Colopterus*, and therefore was defined to exhibit specialist beetle pollination. A closer look in different species in the Amazon and the Brazilian Atlantic forests has revealed that the pollinators of each of these *Anaxagorea* species consists of three to six different *Colopterus* species (Webber 1996, Braun & Gottsberger 2011, 2012). *Colopterus* beetles are also not host-specific and visit flowers of up to three sympatric genera of Annonaceae in Central Amazonia (Webber 1996). They are probably independent of floral resources for survival, as they regularly forage on decaying fruits (Gottsberger 1970, Williams & de Salles 1986). Thus, *Colopterus* beetles appear to be generalists and also the cantharophily of *Anaxagorea* is a kind of generalistic beetle pollination, nevertheless by our classification *Anaxagorea* was classified to have specialist pollination. When we compare the pollination of *Anaxagorea* with e.g. any *Annona* species pollinated by dynastid scarab beetles, then the latter are real specialists, because each species of *Annona* usually attracts only one species of *Cyclocephala*. *Cyclocephala* and other flower-visiting Cyclocephalini species seem to have a strong link to the flowers they visit, because the adult beetles seem to feed exclusively on tissue and pollen of the flowers that attract them and also because the scent of these flowers not only attracts but stimulates them to settle and to initiate mating. For those beetles, the flower is not only the place for nourishment but also a rendezvous and mating place and thus essential for their proper reproduction. Thus again, the terms generalist and specialist pollination are only the extremes of a continuum between broader and more narrow interrelationships of pollinators and their respective flowers.

Acknowledgements

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