

Review

The evolution of floral biology in basal angiosperms

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In basal angiosperms (including ANITA grade, magnoliids, Choranthaceae, Ceratophyllaceae) almost all bisexual flowers are dichogamous (with male and female functions more or less separated in time), and nearly 100 per cent of those are protogynous (with female function before male function). Movements of floral parts and differential early abscission of stamens in the male phase are variously associated with protogyny. Evolution of synchronous dichogamy based on the day/night rhythm and anthesis lasting 2 days is common. In a few clades in Magnoliales and Laurales heterodichogamy has also evolved. Beetles, flies and thrips are the major pollinators, with various degrees of specialization up to large beetles and special flies in some large-flowered Nymphaeaceae, Magnoliaceae, Annonaceae and Aristolochiaceae. Unusual structural specializations are involved in floral biological adaptations (calyptas, inner staminodes, synandria and food bodies, and secretory structures on tepals, stamens and staminodes). Numerous specializations that are common in monocots and eudicots are absent in basal angiosperms. Several families are poorly known in their floral biology.

Keywords: basal angiosperms; floral biology; floral structure; flower evolution; pollination biology

1. INTRODUCTION

The evolution of sexual diversity in angiosperms, including pollination and mating biology, exhibits some basic principles (Barrett 2008). Floral evolution proceeds along certain trajectories shaped by organizational and architectural traits. In different major angiosperm groups they are different in detail, depending on their structural idiosyncrasies. In the current circumscription the angiosperms include two large clades, the monocots and eudicots, a basal grade of three small clades (*Amborella*, Nymphaeales, Austrobaileyales), and a clade of moderate size, the magnoliids. The relationships between monocots, eudicots and magnoliids and two additional, isolated families, Chloranthaceae and Ceratophyllaceae, are unsettled (Soltis *et al.* 2005). In ‘basal angiosperms’ I am including here all groups that are not monocots or eudicots, in total 30 families (7% of the angiosperm families). This review shows traits that are characteristic for basal angiosperms. Is their success in basal angiosperms enabled by special structural conditions that are not present in other angiosperms? Conversely, it also asks why certain trajectories that are common in other angiosperms are less abundant or lacking in basal angiosperms. Some repeated patterns became apparent through the data mining in the vast original literature.

2. DICHOGAMY, FLORAL ORGAN MOVEMENTS AND DIFFERENTIAL STAMEN ABCISSION

(a) *Dichogamy*

It has long been known that in basal angiosperms bisexual flowers tend to be protogynous (Gottsberger *et al.* 1980; Endress 1984a, 1990, 2001; Lloyd & Webb 1986; Bernhardt & Thien 1987). In fact, this has become even more clear in more recent studies. Of the 23 families with at least partly bisexual flowers, 21 are protogynous judging from a check of the original literature for 176 species; the dichogamy patterns of the other two (Gomortegaceae and Hernandiaceae) are unknown. Adichogamy has only been reported for three derived beetle-pollinated *Nymphaea* species (Prance & Anderson 1976; Wiersema 1988; Borsch *et al.* 2008) and for *Piper regnelli* (de Figueiredo & Sazima 2000). The problem here is that beetle-pollinated flowers sometimes open only incompletely in the first phase of anthesis, and thus the early functional female phase may just not have been noticed properly. There are only three reports of protandrous flowers: *Peperomia magnoliifolia* (Vogel 1998), *Piper xylosteoides* (de Figueiredo & Sazima 2000) and *Magnolia delavayi* (Johnstone 1955); the third case is, however, dubious. Thus dichogamy in basal angiosperms is almost 100 per cent protogyny. Protogyny appears to be the ancestral condition in angiosperms. In contrast, in the angiosperms as a whole, protandry is even considerably more common than protogyny (Lloyd & Webb 1986). Why is this so? Is it an organizational feature that is stable for deeply rooted genetic reasons? Or is

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it constrained by a specific floral architecture, which does not easily allow protandry in basal angiosperms? In protandrous flowers the anthers move out of the way of approaching pollinators at the end of the male phase. This is efficient when stamen filaments can bend away from the floral centre and/or anthers can efficiently abscise and fall out of the flower (Lloyd & Webb 1986). For this, relatively long slender stamen filaments or a constriction on top of the filament are necessary. In monosymmetric flowers, a long style can add to these movements. All these features are almost absent in basal angiosperms, in which short and stout filaments, lack of an abrupt transition from filament to anther, and short styles are characteristic. Protogyny is common together with wind, beetle, fly and thrips pollination, especially also in refuge, trap and brood blossoms (Lloyd & Webb 1986). In contrast, protandry is predominant in bee- and butterfly-pollinated flowers. The former agents (except for wind) are common in basal angiosperms, whereas the latter play a minor or no role. In protogynous flowers of some basal angiosperms the male phase overlaps with part of the female phase. More conspicuous are those not uncommon cases in which there is an inactive phase intercalated between the female and male phase. This is found, e.g. in Degeneriaceae (Miller 1989), Eupomatiaceae (Endress 1984a), some Annonaceae (e.g. *Bocageopsis*, Webber & Gottsberger 1995; *Uvaria*, Nagamitsu & Inoue 1997), Lauraceae (Stout 1927; Kubitzki 1982; Kubitzki & Kurz 1984) and Aristolochiaceae (*Aristolochia tagala*, Murugan *et al.* 2006). Why this is so will be explained in §3.

(b) *Floral organ movements*

The different phases of anthesis are often accompanied by conspicuous movements of floral organs and abscission of certain parts. A common theme is that the stigma becomes hidden at the end of the female phase, which happens in different ways. The most radical method is that the flowers close after the female phase and open again in the male phase. This is known from a number of families (also related to day–night rhythm), such as Cabombaceae (Osborn & Schneider 1988), Nymphaeaceae (Heslop-Harrison 1955a,b; Valla & Cirino 1972; Prance & Arias 1975; Prance & Anderson 1976; Schneider & Chaney 1981), some Magnoliaceae (Heiser 1962; McDaniel 1966; Thien 1974; Kikuzawa & Mizui 1990), Annonaceae (Silberbauer-Gottsberger *et al.* 2003; Ratnayake *et al.* 2006, 2007), and Winteraceae (Thien 1980; Thien *et al.* 1985). Austrobaileyaceae and a number of families in Magnoliales and Laurales have an unusual kind of organ, inner staminodes that cover the stigma at the end of the female phase in some groups such as Degeneriaceae, Himantandraceae, Eupomatiaceae, Calycanthaceae and Atherospermataceae (Endress 1984b, 1992; Staedler *et al.* 2009). Another means of covering the stigmas is by the (extrorse) stamens, which bend over the stigmatic disc in some Nymphaeaceae (e.g. *Nymphaea*, Schmucker 1932; van der Velde 1986; Hirthe & Porembski 2003), or by the gynostemium in

Aristolochia (Aristolochiaceae) (Petch 1924). In some Canellaceae the androecial tube elongates and covers the stigma with its upper part (Kubitzki 1993). The stigmas themselves may bend over the floral centre or become appressed to each other or to the dorsal side of the other carpels and so become hidden (Nymphaeaceae, Hirthe & Porembski 2003; Illiciaceae, Thien *et al.* 1983; Magnoliaceae, Thien 1974). Even more dramatic are flowers in Annonaceae, in which the stigmas abscise and fall off at the end of the female phase (e.g. *Annona* species, Gottsberger 1989a; *Monodora*, Lamoureux 1975; *Popowia*, Momose *et al.* 1998).

(c) *Differential abscission of stamens in the male phase of anthesis*

In Magnoliales there is another unusual theme with variations: The stamens abscise early, before pollen has been transferred to pollinators. In Magnoliaceae the stamens tend to fall into the bowl-shaped perianth and pollen is taken from there by the pollinators (Heiser 1962; Thien 1974; Gibbs *et al.* 1977). In some West Indian *Magnolia* species, however, the long tips of the abscised stamens are held in the slits between the carpels and are so presented like little flags (Howard 1948). Another variation is common in Annonaceae. The abscised stamens remain loosely held by the extended thickening spirals of the tracheids of their own vascular bundle (Endress 1985). This loosening is necessary, because in the female phase, the stamens are densely arranged and form a firm platform with a tanniferous or even woody surface, apparently as a protection against chewing/destructive beetles (figures, e.g. in Endress 2008b). Stamen abscission in the male phase is especially impressive in Eupomatiaceae. Here all the stamens and inner staminodes form a massive synandrium, which abscises and falls to the ground in the male phase at night (Endress 1984a). From there beetles reach new flowers that open early in the next morning. Their larvae develop in the starchy tissues of the synandrium on the ground (Armstrong & Irvine 1990). There are other flowers in which massive, basally united parts abscise and may have a similar function, either the entire flowers (Degeneriaceae, Miller 1989) or the unified perianth (among Annonaceae, in *Annona* and *Melodorum* species, Gottsberger 1989a; Silberbauer-Gottsberger *et al.* 2003). Outside of the Magnoliales, the submerged water plants of Ceratophyllaceae, which have underwater pollination, exhibit an unusual behaviour. The stamens (which probably represent unistaminate flowers; Endress 2004) detach from the plant; they ascend to the water surface and release pollen, which reaches stigmas in the water (Ludwig 1881).

3. SYNCHRONOUS DICHOGAMY AND HETERODICHOGAMY

(a) *Synchronous dichogamy*

The conspicuous behaviour of the flowers of some basal angiosperms, for instance, the apparent intercalation of an inactive phase between the female and male phase, is best seen in the context of

synchronization of flowering within a population or species. Such synchrony, combined with dichogamy, results in synchronous dichogamy. In some taxa the synchrony is pronounced and very obvious. It uses the daily rhythm of light and darkness as a framework. The most common pattern is anthesis over 2 days, beginning in the morning of the first day with the female phase and continuing in the morning of the second day with the male phase. A variant is nocturnal flowering, in which anthesis begins in the evening of the first day. Less common is anthesis compressed into a single day, with the female phase in the morning and the male phase in the afternoon. Anthesis duration of more than 2 days also occurs, more commonly in temperate than in tropical regions. Anthesis may also become slower at the end of the flowering period or under adverse weather conditions (e.g. Wells & Lloyd 1991). Pollination is with pollen from flowers in the male stage visited earlier, and thus with some probability from other individuals. Summarizing, what is needed as a basis for synchronous dichogamy is (i) a fixed sequence and timing of the phases during anthesis for each individual flower, and (ii) a synchronization of all flowers in a population, regulated primarily by the day–night rhythm of light. The physiological mechanism of this behaviour, however, has not been studied in any of the basal angiosperms. Synchronous dichogamy (at the individual and population level) is known from Eupomatiaceae (Endress 1984a), several Annonaceae (*Guatteria*, Webber 2002; *Polyalthia*, Rogstad 1994, now *Maasia*, Mols *et al.* 2008; *Rollinia*, Murray & Johnson 1987) and *Canella* of Canellaceae (Wilson 1982). Loose synchronization was reported from *Pseudowintera* of Winteraceae (Wells & Lloyd 1991). As a more simple system, daily synchrony also occurs in dioecious plants between unisexual flowers, such as in *Myristica insipida* (Armstrong 1997). At the population level synchronous dichogamy appears also to be present in Nymphaeaceae, in which an individual often has a single open flower at any given time.

(b) *Heterodichogamy*

Rarely, synchronization is even more intricate, as is found in heterodichogamy. Heterodichogamy is a special case of synchronized dichogamy, in which there are two morphs of individuals with reciprocal flowering behaviour. They commonly occur in equal proportions, which suggests a simple genetic dimorphism (Renner 2001). Heterodichogamy is known from only a few taxa in angiosperms (Renner 2001). One of the first studied cases was in basal angiosperms: avocado (*Persea americana*) in Lauraceae (Stout 1927). In avocado the flowers of some individuals (morph A) begin anthesis in the morning (they are functionally female in the morning and male in the afternoon), whereas the flowers of morph B begin anthesis in the afternoon (they are functionally female in the afternoon and, after a resting phase during the night, male the next morning). The result is that in a population there are functionally female and male flowers available for cross-pollination every morning and every afternoon. An interesting detail is that the

individual flowers of morph B have a longer lifespan than those of morph A, because they have a functionless phase during the night. Kubitzki (1982) and Kubitzki & Kurz (1984) later found this kind of heterodichogamy in several other Lauraceae and assumed that it is probably widespread in those Lauraceae with bisexual flowers. As early as 1910, Wester mentioned that in *Annona squamosa* (Annonaceae) certain trees constantly shed pollen in the morning, others in the afternoon (Wester 1910). This may be another candidate for the same mechanism, but appears not to have been studied in detail. Another mode of heterodichogamy, this one based on unisexual flowers, was found in *Hernandia* (Hernandiaceae, also in Laurales) (Endress & Lorence 2004). These trees are monoecious. In morph A only female flowers are open in the morning, and only male flowers in the afternoon. In morph B it is the other way round. This kind of heterodichogamy is otherwise unknown in the angiosperms.

A potential evolutionary pathway from synchronous dichogamy to heterodichogamy can be seen in cases like *Eupomatia laurina* (Eupomatiaceae) (Endress 1984a) or *Rollinia jimenezii* (Annonaceae) (Murray & Johnson 1987), in which the flowering programme of an individual flower is restricted to 24 h and each individual tends to open several flowers every second day and have a flowerless day in between. Some of the individuals will then flower on the flowerless days of the other individuals. In both cases this pattern is not absolute. In Laurales it would be intriguing to know whether there is an evolutionary connection between the bisexual-flower heterodichogamy in Lauraceae and the unisexual-flower heterodichogamy in Hernandiaceae. The study of Hernandiaceae with bisexual flowers and of Lauraceae with unisexual flowers may help to resolve this question.

4. POLLINATION SYSTEMS

The importance of beetle and fly pollination in basal angiosperms has been pointed out repeatedly: beetle pollination since Diels (1916) and Grant (1950), later elaborated especially by Gottsberger (1970, 1974, 1989a,b), and fly-pollination especially since Schneider & Jeter (1982) and Thien *et al.* (2000, 2009). Nectar is not common in flowers of basal angiosperms and, if present, is not produced in large amounts. Thus other rewards, such as pollen, food tissues, warmth, shelter and brood sites appear to play a relatively important role in pollination biology (e.g. Thien *et al.* 2000; Sakai 2002; Bolin *et al.* 2009). Cases of narrowly specialized pollination are in general better studied than cases with different pollination agents.

(a) *Beetles*

Beetle pollination by large beetles (*Cyclocephala*, scarabaeids) is prominent in large-flowered Nymphaeaceae (*Nymphaea* p.p., Victoria, Valla & Cirino 1972; Prance & Arias 1975; Prance 1980), some Annonaceae (*Annona*, *Rollinia*, Gottsberger 1989a,b) and some Magnoliaceae (*Magnolia tamaulipana*, Dieringer *et al.* 1999). These flowers are typically

nocturnal, have a strong fruity odour, are thermogenic, are large, robust, have a large chamber in which pollinators may gather, and are self-compatible (Gottsberger 1989a,b; Dieringer *et al.* 1999; Davis *et al.* 2008). These three groups emerge as peaks from a more general systematic substratum of beetle pollination, which is present in Nymphaeaceae, in all families of Magnoliales (the pollinators of Himantandraceae are unknown, but are also likely beetles), Calycanthaceae, some Winteraceae, and Hydnoraceae. In these families a diversity of groups of smaller beetles are involved (especially chrysomelids, curculionids, nitidulids, staphylinids and tenebrionids). Many of these flowers have food tissues consumed by the beetles (Nymphaeaceae on carpel tips, Hirthe & Porembski 2003; Himantandraceae, Eupomatiaceae and Annonaceae on inner staminodes or inner tepals, Endress 1984b; Calycanthaceae on inner tepal and stamen tips, Rickson 1979; Staedler *et al.* 2007; and Winteraceae on tepals, Thien *et al.* 1990).

(b) *Flies and other diptera*

Fly pollination occurs especially in Cabombaceae, in all families of Austrobaileyales, some Annonaceae, some Monimiaceae and Lauraceae, some Winteraceae, Saururaceae, some Piperaceae, and is most prominent in Aristolochiaceae, in which some carrion-mimicking sapromyiophilous flowers have become giant (*Aristolochia grandiflora*, more than 1 m long; Davis *et al.* 2008). A special group of Diptera, gall midges (cecidomyiids), were found to be the exclusive pollinators of Siparunaceae (Feil 1992) and some Schisandraceae (Yuan *et al.* 2007, 2008). They have also been found in flowers of other families, such as Amborellaceae (Thien *et al.* 2003), Illiciaceae (Thien *et al.* 1983), Piperaceae (Ollerton 1996), Aristolochiaceae (Ollerton 1996) and some Hydnoraceae (Visser 1989), where they might contribute to pollination.

(c) *Thrips*

Thrips have been underestimated as pollinators, as they may be destructive in flowers when present in large numbers or are simply overlooked (Grinfel'd 1975; Kirk 1984). Flowers pollinated by thrips are often white or cream, are scented and present pollen at night (Kirk 1988); they are concave and have narrow entrances or narrow clefts at the base as hiding places and brood places. As thrips eat not only pollen and nectar but also floral tissues, thrips flowers, even if small, may have a certain internal robustness. Such flowers are sometimes also visited and pollinated by small beetles (staphylinids) (e.g. Kirk 1985; Momose *et al.* 1998; Luo & Li 1999; Jürgens *et al.* 2000). A number of basal angiosperms are known to be pollinated exclusively or mainly by thrips, such as *Chloranthus* species (Chloranthaceae) (Ma *et al.* 1997; Luo & Li 1999), some Myristicaceae (Bawa *et al.* 1985; Armstrong 1997), species of several genera of Annonaceae (*Bocageopsis*, *Deeringothamus*, *Oxandra*, *Popowia*, *Trigynaea*, *Xylophia*; Webber & Gottsberger 1995; Momose *et al.* 1998; Gottsberger 1999; Norman 2003; Silberbauer-Gottsberger *et al.* 2003), *Idiospermum* of Calycanthaceae (Worboys &

Jackes 2005), genera of Monimiaceae (*Mollinedia*, Gottsberger 1977; Mound & Marullo 1996; *Wilkiea*, Williams *et al.* 2001), perhaps some Siparunaceae (Feil 1992), and some Winteraceae (*Drimys*, Gottsberger *et al.* 1980; *Pseudowintera*, Norton 1984; *Zygogynum*, Thien 1980; Pellmyr *et al.* 1990).

(d) *Bees*

In contrast to other angiosperms, bee pollination is conspicuously rare in the basal groups. Genera or families with predominantly bee pollination (mainly by small bees, such as *Trigona* and relatives) are day-flowering *Nymphaea* species (Prance & Anderson 1976; Schneider 1982a,b), some Magnoliaceae (Carpenter & Guard 1950; Huang *et al.* 1999), a few Annonaceae (Silberbauer-Gottsberger *et al.* 2003), some Lauraceae (Stout 1927; Kubitzki & Kurz 1984; Forfang & Olesen 1998), and some Piperaceae (Semple 1974). An unexpected specialization is perfume flowers pollinated by male euglossine bees known from two species of *Unonopsis* (Annonaceae), secreting perfume on the inner tepals (Carvalho & Webber 2000; Teichert *et al.* 2009).

(e) *Wind and water*

Abiotic pollination is also uncommon in basal angiosperms. Nowhere is wind pollination well developed, perhaps with two exceptions. One is *Hedyosmum* (Chloranthaceae), in which some species have large, flexible male catkins and relatively large anthers, large amounts of dry pollen and large stigmas (Endress 1987). The other exception is the water plant *Brasenia* (Cabombaceae), which also has an increased stigma surface (Osborn & Schneider 1988; Endress 2005). In Chloranthaceae, *Ascarina* is also probably largely wind-pollinated. In other groups, wind pollination may be partly shared with modes of biotic pollination and adaptation to it is less obvious (Amborellaceae, Thien *et al.* 2003, 2009; Trimeniaceae, Philipson 1993b; Bernhardt *et al.* 2003; exceptionally Winteraceae, Anderson *et al.* 2001; Saururaceae, Thien *et al.* 1994; a few Piperaceae, de Figueiredo & Sazima 2000, 2006; Lactoridaceae, Bernardello *et al.* 1999; Anderson *et al.* 2001). Water pollination is conspicuously specialized in the submerged Ceratophyllaceae. Whether Hydatellaceae (Nymphaeales) are pollinated in the air or in the water is still unknown. The tender stigmatic hairs (Rudall *et al.* 2007) suggest at least a moist environment.

5. UNUSUAL FLORAL STRUCTURAL SPECIALIZATIONS AND THEIR RELATIONS TO FLORAL BIOLOGY

The following floral structural specializations of basal angiosperms are either rare in angiosperms as a whole or have sometimes been overlooked in basal angiosperms.

(a) *Calyptra*

A calyptra is a compact floral envelope that abscises at a certain point of development. It is present in flowers of Magnoliales, such as Magnoliaceae,

Himantandraceae, Eupomatiaceae and exceptionally in Annonaceae (Endress 1977, 2003; Kim *et al.* 2005), and among Laurales in many Monimiaceae (e.g. Endress 1980a). In Magnoliales it is morphologically based on an elaborate single bract, and in Monimiaceae on united tepals. Whether in the Annonaceae *Letestudoxa* and *Duguetia spixiana* the calyptra consists of the completely united outer tepals as suggested by Le Thomas (1969) and Maas *et al.* (2003) still needs critical developmental study, especially as in *Duguetia lanceolata* an envelope is formed by the bract that precedes the floral organs and could represent an incipient calyptra (Endress 1977). In Magnoliales the calyptra falls off when the flower opens. In contrast, in Monimiaceae the calyptra falls only *after* anthesis, whereas at anthesis an opening forms on top of the calyptra through which pollination takes place (Endress 1980a).

(b) Atepalous and unistaminate flowers

In basal angiosperms there are several atepalous taxa, Hydatellaceae (Nymphaeales, Saarela *et al.* 2007; Rudall *et al.* 2007), Ceratophyllaceae and Chloranthaceae (except female *Hedyosmum*) (Endress 1987), among Magnoliales: Eupomatiaceae and Himantandraceae, and among Piperales: Saururaceae and Piperaceae. Bud protection is performed by bracts: either the floral-subtending bract (in Chloranthaceae, Saururaceae and Piperaceae) (von Balthazar & Endress 1999; Endress 2004, 2008b) or flower-preceding bracts, such as in the water plants Hydatellaceae (Rudall *et al.* 2007) and Ceratophyllaceae (Endress 2001), and in Himantandraceae and Eupomatiaceae (Endress 1977, 2003). A combination of atepalous and unistaminate flowers occurs in three unrelated families: Hydatellaceae (Rudall *et al.* 2007), Chloranthaceae (*Ascarina* s.p., *Hedyosmum*, *Sarcandra*) (Endress 1987), and probably *Ceratophyllaceae* (Endress 2004; Endress & Doyle 2009). In Hydatellaceae and Ceratophyllaceae, which are both water plants, this reflects a repeated trend of floral reduction in a number of water plants also including monocots and eudicots (Endress & Doyle 2009).

(c) Syntepaly

In basal angiosperms there are many taxa with at least basally united tepals. Syntepaly is diverse and is involved in floral biology in various ways. *Amborella*, *Cabomba* and *Hedyosmum* are syntepalous (Endress 2008a). In many magnoliids the outermost two to three tepals are united, more rarely only the inner tepals. Among Magnoliales, Myristicaceae have only three tepals, which are united, often forming a narrow floral entrance, and restrict floral access to small insects (Armstrong & Irvine 1989); in Degeneriaceae the outer three tepals are basally united; in Annonaceae the outer three tepals are united in many genera, or the inner three or six are united (*Annona*, *Cardiopetalum*, *Disepalum*, *Hexalobus*, *Hornschuchia*, *Isolona*, *Monodora*, *Rollinia*; van Heusden 1992). Among Laurales, in Monimiaceae the united tepals form a floral cup with an often narrow entrance (Endress 1980a); in Hernandiaceae

Gyrocarpous has partially united tepals (Kubitzki 1969). Among Canellales, in *Cinnamosma* (Canelaceae) the inner three to six tepals are united into a bell-shaped structure (Kubitzki 1993) and in Winteraceae the outer two or three tepals are commonly united (Vink 1970). In Piperales, syntepaly is most pronounced in the kettle trap flowers of *Aristolochia* (González & Stevenson 2000) and Hydnoraceae.

(d) Secretory structures on (inner) tepals or stamens

The inner surface of inner tepals is a hot spot area of reward production, especially in Annonaceae. Nectaries, food bodies, osmophores or perfume glands are variously formed there and tend to occur in collateral pairs (e.g. Kessler 1988; van Heusden 1992; Teichert *et al.* 2009). This is also true for the paired nectaries in *Cabomba* (Cabombaceae), whereas in *Chimonanthus* (Calycanthaceae) nectar is secreted by numerous nectarioles on the same site, and in *Nuphar* (Nymphaeaceae) the single nectary is on the dorsal side of the 'petals' (Vogel 1998; Endress 2008a). In five families of Laurales (Gomortegaceae, Atherospermataceae, Monimiaceae, Hernandiaceae, Lauraceae) nectaries are formed in collateral pairs at stamen filaments and staminodes (Sampson 1969; Schodde 1969; Endress 1980b; Buzgo *et al.* 2007; Rohwer 2009; Staedler & Endress 2009). The inner side of the simple perianth of some *Aristolochia* species contains nectaries and osmophores (Vogel 1998) and that of some *Hydnora* species osmophores (Bolin *et al.* 2009).

(e) Inner staminodes

Inner staminodes are present in Austrobaileyaceae (Endress 1984b), among Magnoliales in Degeneriaceae (Thien 1980), Himantandraceae (Endress 1984b), Eupomatiaceae (Endress 1984a) and *Anaxagorea* of Annonaceae (Scharaschkin & Doyle 2006), and among Laurales probably in all families, except perhaps for Siparunaceae (Calycanthaceae, Staedler *et al.* 2007, 2009; Gomortegaceae, Staedler & Endress 2009; Atherospermataceae, Schodde 1969; *Hortonia* of Monimiaceae, Endress 1980b; Lauraceae, Rohwer 2009; Hernandiaceae, Endress & Lorence 2004). In some families of both Magnoliales and Laurales they function in herkogamy by covering the stigmas in the male phase; in families of Laurales they bear nectaries, and in families of Magnoliales other secretory structures, which make the bodies of pollinators sticky and/or are eaten by them.

(f) Synandry

An androecium with united stamens is present in a number of families of basal angiosperms and is variously involved in floral biology (see also Endress 1990). In Schisandraceae, in the thermogenic flowers of *Kadsura pedunculata* (Yuan *et al.* 2008) the synandrium may contribute to temperature elevation. In *Chloranthus* (Chloranthaceae) it may play a role in thrips pollination in forming clefts between the anthers and sheltering the gynoecium. In Eupomatiaceae it functions as a food substrate for the larvae of the

pollinator when it lies on the ground (Armstrong & Irvine 1990). The function of the completely united androecium in Myristicaceae, Canellaceae, some Lauraceae (*Gamanthera*, *Pleurothyrium*; van der Werff & Endress 1991; van der Werff 1993), and the partially united androecium in Hydnoraceae is probably unknown.

(g) *Floral cup and inferior ovary*

A floral cup is formed in several basal angiosperms. With this floral architecture the gynoecium is more or less hidden from destructive flower visitors (Grant 1950). A similar protection is achieved by an inferior ovary. A floral cup is present in *Amborella* and in most Laurales; a partial cup is formed by the androecium around the ovaries in Himantandraceae and some Annonaceae, such as *Crematosperma*, *Fusaea*, *Guatteria*, *Xylopia* (Endress 1977; van Heusden 1992). An inferior ovary is present in *Hedyosmum* (Chloranthaceae), among Magnoliales in Eupomatiaceae, among Laurales in Gomortegaceae, a few Monimiaceae, Hernandiaceae and some Lauraceae, and among Piperales in Aristolochiaceae (Endress 1977; Igersheim & Endress 1998; González & Stevenson 2000) and Hydnoraceae.

(h) *Syncarpy and functional convergences (compitum, partial compitum, extragynoecial compitum, hyperstigma)*

Syncarpy with congenitally united carpels and a normal, **internal compitum** is rare in basal angiosperms (Endress 1982; Endress & Igersheim 2000a). It occurs in a few Annonaceae (*Isolona*, *Monodora*; Deroin 1985, 1991), in Canellaceae, *Takhtajania* of Winteraceae (Endress *et al.* 2000), Piperaceae, Saururaceae and Aristolochiaceae (Igersheim & Endress 1998). However, partial and extragynoecial compita are widespread, which may partly provide regular pollen tube distribution and centralized pollen tube selection (Endress 1982; Armbruster *et al.* 2002). A **partial compitum** is present when the inner space of groups of carpels (not of all carpels of a gynoecium) are confluent. It has been recorded from Eupomatiaceae (Endress 1977, 1984a), *Cananga* (Annonaceae; Deroin 1988, 1997), *Pseudowintera* and *Zygogynum* (Winteraceae; Sampson & Kaplan 1970; Vink 1985). An **extragynoecial compitum**, in which the apocarpous carpels have contiguous secretory stigmas that allow crossing of pollen tubes between carpels, is common in all three orders of the basalmost angiosperms (also in *Amborella*, in contrast to Thien *et al.* 2009; Endress 1982; Williams *et al.* 1993; Endress & Igersheim 2000a,b; Williams 2009). Among Magnoliales it occurs in Himantandraceae and many Annonaceae (e.g. *Annona*, *Rollinia*, *Hexalobus*, *Uvaria*, *Neostenanthera*, *Boutiquea* (Endress 1982; Deroin 1991; Briechle-Mäck 1994) and among Laurales in Calycanthaceae (Staedler *et al.* 2009), Siparunaceae (Renner *et al.* 1997), and some Monimiaceae (Endress 1980a; Endress & Lorence 1983). A unique invention in Monimiaceae is a **hyperstigma**, in which the carpels are enclosed in a floral cup and communicate with the outer world via

a narrow pore. Pollen is received and germinates at this pore by a secretion from highly reduced, minute tepals, and pollen tubes grow through a lining of secretion into the floral cup, where they reach the stigmas of the carpels (Endress 1980a). Thus the receptive structure (hyperstigma) is not part of the gynoecium. A hyperstigma is known from the species of five genera of Monimiaceae (*Faika*, *Hennecartia*, *Kibara*, *Tambourissa*, *Wilkiea*; Endress 1980a; Philipson 1993a). Interestingly, these genera do not form a clade. Thus hyperstigmas either have evolved more than once or there were reversals.

6. LACKING SPECIALIZATIONS

Some floral biological specializations that are common in angiosperms are lacking in basal angiosperms. This is, in part, related to the weak or non-existent synorganization of floral organs (Endress 2006). Lacking are floral tubes that can easily evolve various proportions, in spite of syntepaly (except for *Aristolochia*), long, slender stamen filaments (the stamens of *Brasenia* in Cabombaceae and *Saururus* in Saururaceae come closest; Osborn & Schneider 1988; Thien *et al.* 1994), and long styles (except Calycanthaceae and Atherospermataceae, in which they are thin and weak and are postgenitally connected; Staedler *et al.* 2009). This may also be related to a relatively slow pollen tube growth in basal angiosperms (Williams 2008). The latter three features are dependent on well-developed intercalary meristems. Because of short stamen filaments and styles, heterostyly and protandry are lacking. Elaborate syncarpy with internal compitum is almost absent, except for the taxa mentioned in §5. Elaborate monosymmetric flowers are absent, except for *Aristolochia*, in which monosymmetry is needed for the curved floral tube, which is a constituent part of the kettle-trap fly flowers. Disc nectaries and septal nectaries are lacking, and if nectar is produced at all, then it is not in large amounts. Bird, mammal, butterfly and sphingid pollination are lacking, and with them also bright red flowers, concomitant with the lack of floral tubes and extensive nectar production. Bee pollination is not common; blue flowers only occur in some Nymphaeaceae (Gottsberger & Gottlieb 1981), and bright yellow flowers are also not common. Among the clades adapted to bee pollination, buzz pollination is absent, and concomitantly also poricidal anthers, postgenitally united anthers, *Solanum* type flowers and heteranthery. Elaborate anemophily is not common (occurring in *Brasenia*, *Hedyosmum* and probably *Ascarina*), and appears to be absent in magnoliids (except for some *Piper* species; de Figueiredo & Sazima 2000).

7. EVOLUTION OF FLORAL BIOLOGY

There are features that are invariant (e.g. protogyny) and features that are absent (see §6) in basal angiosperms, but other features are diverse or variable at various systematic levels. On the basis of stable protogyny, synchronous protogyny evolved especially in Nymphaeaceae and several magnoliids (Magnoliales,

Laurales, Canellales), and heterodichogamy in some Magnoliales and Laurales. In the basalmost angiosperms (ANITA grade) with small flowers, dipteran pollination alone or combined with micropterigid-moth and wind pollination is predominant, whereas specialized wind/water pollination and bee pollination are of minor importance (Endress 2001; Hu *et al.* 2008; Thien *et al.* 2009). Only in derived groups of Nymphaeaceae with enlarged flowers is more specialized beetle pollination present. In magnoliids there are several evolutionary lines with specialized beetle and fly pollination, also thrips pollination plays a role, whereas bee pollination is also not predominant, and wind pollination is almost lacking. Specialized beetle and fly pollination is often combined with extensive floral thermogenesis and sometimes floral gigantism (Nymphaeaceae, Annonaceae, Magnoliaceae, Aristolochiaceae). However, weak thermogenesis and its use as an energy reward are also present in a number of less specialized fly flowers in the ANITA grade (Thien *et al.* 2000, 2009) and was probably the precursor of large and hot flowers. A number of floral structural oddities are involved in floral biological specializations but did not lead to large radiations in basal angiosperms and were largely lost or never evolved to a noticeable extent in the more evolutionarily successful angiosperm clades eudicots and monocots, such as inner staminodes, external compitum and hyperstigma.

8. OUTLOOK

Only relatively few taxa have been studied more broadly, especially in Nymphaeaceae, Magnoliaceae, Eupomatiaceae, Annonaceae, Lauraceae (with bisexual flowers), Winteraceae and Aristolochiaceae. Many groups are still completely unknown in their floral biology, such as Gomortegaceae and most Hernandiaceae, or are poorly known, such as Hydatellaceae, Himantandraceae, Atherospermataceae, Lauraceae with unisexual flowers, and Canellaceae. In those that have been studied, many aspects cannot be easily compared as many authors with different foci and at different times were involved. Many taxa are difficult to study because they are large trees (e.g. Myristicaceae, Himantandraceae, many Lauraceae). Floral secretions or tissues as pollinator awards, especially at the inner tepals and stamens are only poorly known. A study of the molecular developmental genetics of the specially odd, exclusive features would be of interest for the elucidation of their origin. There is a widely open field for future studies.

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