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POLLINATION BIOLOGY OF BASAL ANGIOSPERMS (ANITA GRADE)[1]

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The first three branches of the angiosperm phylogenetic tree consist of eight families with ~201 species of plants (the ANITA grade). The oldest flower fossil for the group is dated to the Early Cretaceous (115–125 Mya) and identified to the Nymphaeales. The flowers of extant plants in the ANITA grade are small, and pollen is the edible reward (rarely nectar or starch bodies). Unlike many gymnosperms that secrete "pollination drops," ANITA-grade members examined thus far have a dry-type stigma. Copious secretions of stigmatic fluid are restricted to the Nymphaeales, but this is not nectar. Floral odors, floral thermogenesis (a resource), and colored tepals attract insects in deceit-based pollination syndromes throughout the first three branches of the phylogenetic tree. Self-incompatibility and an extragynoecial compitum occur in some species in the Austrobaileyales. Flies are primary pollinators in six families (10 genera). Beetles are pollinators in five families varying in importance as primary (exclusive) to secondary vectors of pollen. Bees are major pollinators only in the Nymphaeaceae. It is hypothesized that large flowers in Nymphaeaceae are the result of the interaction of heat, floral odors, and colored tepals to trap insects to increase fitness.

Key words: ANITA grade; basal angiosperms; Coleoptera; Diptera; floral deceit; floral thermogenesis; Hymenoptera; pollination biology.

"*Nature will tell you a direct lie if she can.*" —Attributed to Charles Darwin (Lewis and John, 1963, p. 271).

Molecular phylogeny now gives biologists the option of comparing specific lineages of basal angiosperms rather than relying on past dogma that insisted a plant was "primitive" because its flowers possessed or lacked a particular character or suite of characters.

The first three branches of the angiosperm phylogenetic tree, constructed with DNA sequences (coding and noncoding), comprise the ANITA grade. This now includes the Hydatellaceae as the sister group of the Nymphaeales (Qiu et al., 1999, 2000, 2006; Soltis et al., 1999, 2000; Barkman et al., 2000; Graham and Olmstead, 2000; Zanis et al., 2002; Borsch et al., 2003; Friis and Crane, 2007; Saarela et al., 2007). Amborellaceae forms the first branch, Nymphaeales forms the second, and Austrobaileyales is the third and sister to all other flowering plants (Table 1; Fig. 1). Therefore, the term "basal angiosperm" is used here to refer specifically to taxa within the ANITA grade.

The ANITA grade, an amalgam of the lineage names, comprises eight families as follows: Amborellaceae, Hydatellaceae, Cabombaceae, Nymphaeaceae, Austrobaileyaceae, Trimeniaceae, Schisandraceae, and Illiciaceae (Table 1). The 17 genera with ~201 species of flowering plants are distributed from tropical to cold regions of the world (Table 1). Six of the families contain only one or two genera, and two families (Amborellaceae and Austrobaileyaceae) contain only a single species (Table 1).

The oldest unequivocal floral fossil for the taxa, dated to the Early Cretaceous 115–125 Mya, is thought to be related to extant Nymphaeales (Friis et al., 2001). The small fossil flower (3 mm long, 2 mm diameter) shrank during fossilization and was estimated to be about 1 cm in diameter when alive (Friis et al., 2001). Another fossil, *Microvictoria* (Nymphaeaceae) from the Raritan Formation dated to the Turonian (90 Mya), Upper Cretaceous, resembles modern water lilies in the *Victoria*-*Euryale* clade (Gandolfo et al., 2004; Yoo et al., 2005). The precise floral structure of the fossil flower is similar to modern day *Victoria* Lindley, suggesting entrapment of beetle pollinators, indicating that specialized plant–insect associations in the angiosperms were already established at this time (Gandolfo et al., 2004). In a recent study, Ervik and Knudsen (2003) regard pollination of members of the Nymphaeaceae by scarab beetles to be an ancient mutualistic partnership dating back 100 Mya. New data on wind, fly, and bee pollination in ANITA-grade plants, however, suggest we reexamine the hypothesis that beetles pollinated early angiosperms in a "mess and soil" system (Faegri and van der Pijl, 1979).

It is also reasonable to hypothesize that specialized pollination systems between halictid bees, with a lineage extending back 95–100 Mya (Engel, 2001), and *Nuphar*-type flowers is also an old association. These findings suggest insect pollination occurred very early in the first angiosperms. Hu et al. (2008) maintain fossil pollen clumping is evidence for sticky pollen and evolved by the mid-Cretaceous, implying an increase in zoophilous pollination.

This paper presents an overview of reproductive systems, pollination syndromes, and new data were added on floral thermogenesis of ANITA grade plants (Tables 1–3). The literature was searched, and a diagram was constructed to show evolutionary

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TABLE 1. Reproductive traits of ANITA-grade plants.

Taxa	No. species	Flower size	Flower color	Sex	S/I	Reference
First branch terrestrial						
Amborellaceae						
Amborella	1	3–5 mm	Cream	Unisexual, dioecious		Thien et al., 2003
Second branch aquatic						
Hydatellaceae	7					
Hydatella	4	2–4 mm		Unisexual		Saarela et al., 2007
Trithuria	3	2–4 mm		Unisexual, bisexual		Friis and Crane, 2007
Cabombaceae						
Cabomba	5	2.5 cm	White, pink	Bisexual, protogynous		Schneider and Jeter, 1982
Brasenia	1	2.0 cm	Dull purple	Bisexual, protogynous		Cronquist, 1981
Nymphaeaceae						
Nuphar	20	2.5 cm	Yellow	Bisexual, protogynous		Lippok and Renner, 1997; Herring, 2003
Barclaya	4	3.0 cm	Purplish	Bisexual, protogynous		Cronquist, 1981
Ondinea	1	3.5 cm	Purple-red	Bisexual, protogynous		Schneider, 1983
Victoria	2	>50 cm	Red-white	Bisexual, protogynous		Prance and Arias, 1975
Euryale	1	1–2.5 cm	Blue, violet	Bisexual, protogynous		Okada, 1930
Nymphaea	50	>15 cm	Blue, white, yellow, red	Bisexual, protogynous		Meeuse and Schneider, 1979/1980
Third branch terrestrial						
Austrobaileyaceae						
Austrobaileya	1	5 cm	Red, brown, green	Bisexual, protogynous	S/I	Endress, 1980, 2001
Trimeniaceae						
Piptocalyx	12	1–2 cm	White	Unisexual, bisexual		Endress and Sampson, 1983; Philipson, 1993; Endress 1994
Trimenia	1	1–2 cm	White	Unisexual, bisexual	S/I	Endress and Sampson, 1983; Endress, 1994; Bernhardt et al., 2003
Schisandraceae						
Schisandra	25	1–2 cm	Red, yellow	Unisexual, dioecious		Saunders, 2000
Kadsura	22	1–2 cm	Red, yellow	Unisexual, monoecious, dioecious	S/I	Saunders, 1998; Lyew et al., 2007
Illiciaceae						
Illicium	41	1–3 cm	Red, white	Bisexual, protogynous		Smith, 1947; Thien et al., 1983

Notes: S/I = self incompatibility.

trends in the first three branches of the angiosperm phylogenetic tree (Fig. 1). Pollen is the primary food resource for visiting insects in the majority of plants (nectar is rare). The dry stigmas provide no food (droplets) in the woody plants (first and third branches, Tables 1, 3; Fig. 1). The wet stigmas (second branch, Nymphaeaceae) secrete copious amounts of fluid that is not eaten by visiting insects (not a nectar). Floral deceit is common throughout all three lineages and is based on various floral traits, e.g., bright-colored flowers, floral odor, floral heat, host site for egg ovipositing (Fig. 1).

Most of the plants in the ANITA grade have apocarpous flowers or if syncarpous lack a compitum. In syncarpy (united carpels), species of flowering plants typically have a compitum, a zone of tissue in which pollen tubes have the potential to gain entry to several carpels (Carr and Carr, 1961; Endress, 1994; Sheffield et al., 2005). In apocarpy (separate carpels), pollen tubes are restricted to a single carpel. One of the advantages of syncarpy is that it may increase pollen competition for female gametophytes (Endress, 1982; Armbruster et al., 2002). In many apocarpus plants, the extragynoecial compitum gives pollen tubes access to other carpels, thus achieving functional syncarpy (Endress, 1994). Different types of extragynoecial compitums have been described in ANITA-grade plants, e.g., a pool of mucilage in *Austrobaileya scandens* in which pollen tubes can grow and reach neighboring stigmas (Endress, 1994).

This paper begins with important reproductive features of ANITA-grade plants, an analysis of data presented in Tables 1–3. Key features of the various reproductive processes and pollination systems in Fig. 1 are then emphasized in three topics. The first topic, floral deceit and pollination, examines the role of floral resources and the significance of dry and wet stigmas, floral heat, and other factors in the types of floral deceit in aquatic vs. woody plants. The second topic, floral thermogenesis, examines the roles of floral heat in the breeding systems of large (water lilies) and small flowers (*Illicium* and *Kadsura*). A hypothesis is proposed to explain the large flowers in many members of the Nymphaeaceae. The role of the extragynoecial compitum is also explained in this section. The third topic, pollinators, is an analysis of the various insect pollinators emphasizing flies, beetles, and bees. Generalist vs. specialist modes of pollination in the ANITA-grade taxa are presented along with switching of pollinators in species of *Nuphar*. In addition, beetle and bee pollination systems in the ANITA-grade plants are compared with pollination systems in higher taxa. The discussion presents a broad overview of the pollination and reproductive biology found in the first three branches of the flowering plant phylogenetic tree. It focuses on differences between ovule secretions in gymnosperms and dry stigmas, the role of various pollinators, and the significance of syncarpy in angiosperms.

MATERIALS AND METHODS

New data on floral thermogenesis were gathered from *Illicium floridanum* Ellis, and a graph was constructed to show the rhythm of heat production in various parts of the flowers (Fig. 2). Floral temperatures were measured in a population of *I. floridanum* (star anise), a small evergreen shrub with bisexual flowers growing on Morgan's Bluff along the West Pearl River, near Slidell, Louisiana, USA. Floral temperatures were measured for two sets of newly opened flowers labeled diurnal and nocturnal. In the first set (diurnal), 12 newly

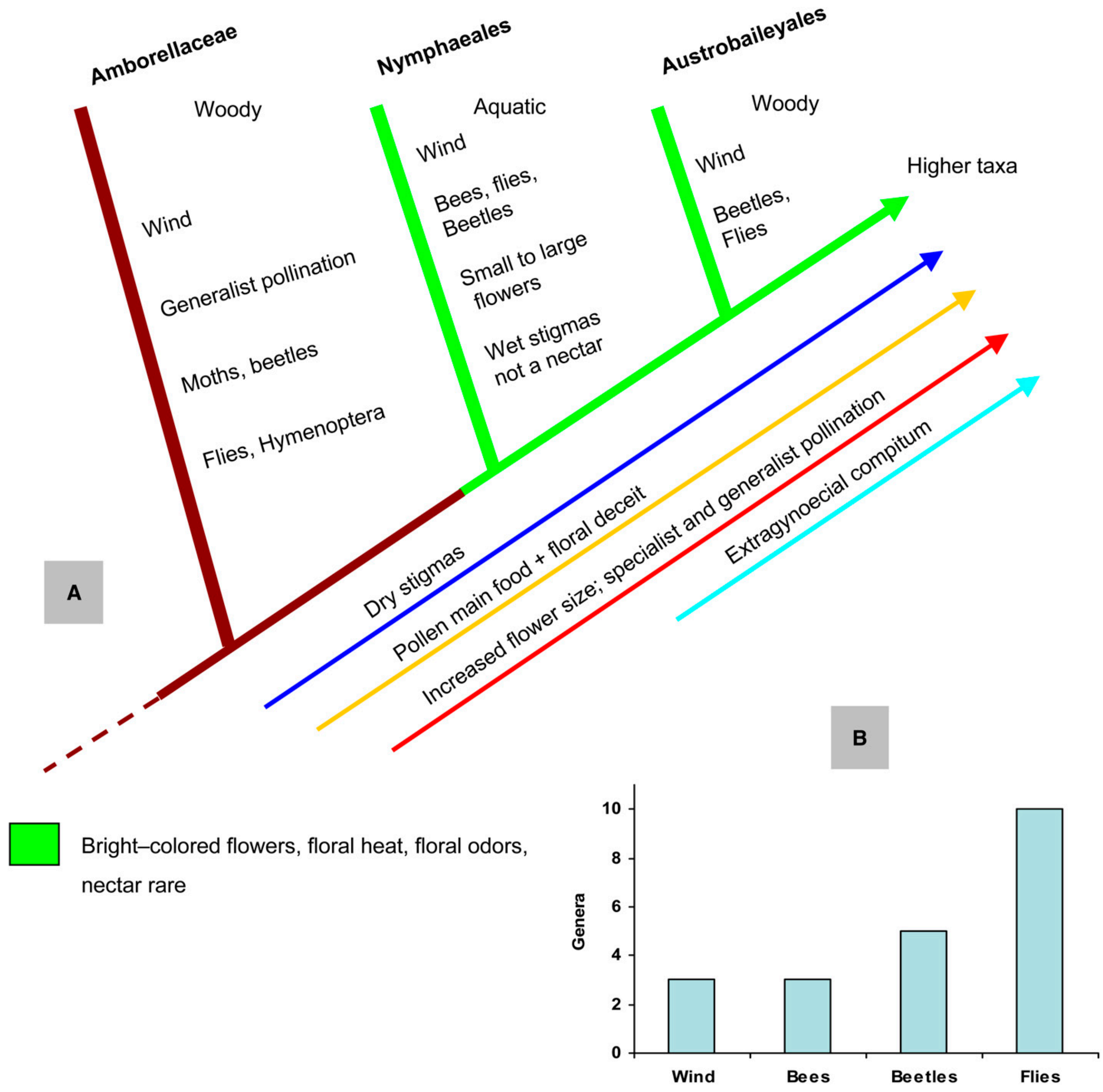

Fig. 1. First three branches of flowering plant phylogenetic tree depicting overall evolutionary trends in floral structure and pollination patterns of various taxa (A, B). Nymphaeales (second branch) differ in many reproductive traits, e.g., possessing wet stigmas and bees as major pollinators (A, B). Pollen is main food for insects and floral deceit mechanisms are prevalent in all three branches of the tree (A, B).

opened flowers on seven plants with curved, papillate stigmas on the same plane as the stamens were labeled with small paper tags. The temperature of the apical residuum, stigma, carpel, and pedicel were measured for each flower. Temperatures were recorded only from the labeled newly opened flowers at four time intervals: at 1050, 1305, 1555, and 2045 hours for 24 h. The second study (nocturnal) measured the temperatures of the same floral parts as listed earlier for nine flowers on seven plants (labeled with paper tags). The nocturnal temperatures were taken at two time intervals: at 2045 and 2300 hours (data not shown). Ambient temperatures were also recorded throughout the measurement periods. In hand-manipulated crosses, Koehl et al., (2004) determined that recurved stigmas were not receptive when upright (90°, Fig. 3), which coincides with anther dehiscence. Thus the temperatures were recorded for flowers with the female phase and portions of the male phase.

Temperatures were recorded using copper-constantan thermocouples (0.3 mm in diameter) connected to a portable, battery-powered, digital thermometer (Omega Engineering, Stamford, Connecticut, USA) accurate to ±0.01°C. Excess temperatures of the apical residuum, carpels, pedicels, and stigmas were compared using one-way analysis of variance. Tukey's Studentized range test was used to separate the means. The SAS System for Windows, version 8 (SAS Institute, 1999) was used to calculate the statistics. In graph construction, the mean excess floral temperatures above ambient temperature were determined as well as the standard error of the mean for the flowers at each time interval.

TABLE 2. Floral thermogenesis in extant angiosperm families.

Taxon	Reference
ANITA grade	
Nymphaeaceae	Schneider and Williamson, 1993
Schisandraceae	Liu et al., 2006; Yuan et al., 2008
Illiciaceae	Dieringer et al., 1999
Eumagnoliids	
Annonaceae	Silberbauer-Gottsberger et al., 2001
Araceae	Seymour et al., 2003
Arecaceae	Ervik and Barfod, 1999
Aristolochiaceae	Vogel, 1990
Cyclanthaceae	Ervik and Barfod, 1999
Magnoliaceae	Dieringer et al., 1999
Eudicots	
Nelumbonaceae	Seymour and Schultze-Motel, 1997
Rafflesiaceae	Patiño et al., 2000

The floral temperatures represent the midpoint of a 40-min interval of recording temperatures of individual flower parts.

RESULTS

Important reproductive features of ANITA grade plants—Reproductive characteristics of members of the ANITA grade are presented in Tables 1 and 3. Data are lacking or scarce for members of the Hydatellaceae, Trimeniaceae, and Illiciaceae. Plants of 10 genera (126 species) bear only bisexual flowers, five genera (63 species) have plants with a mixture of bisexual and unisexual flowers, and two genera (five species) have plants with only unisexual flowers (Tables 1, 3). The flowers in most extant members of the ANITA grade lack a true style.

Flowers vary greatly in size and color (see p. 1113 in Endress, 2001 for colored flower photographs representing plants in each ANITA grade), but overall the reproductive organs are small (Table 1). In the first branch, the flowers of *Amborella* are 3–5 mm in diameter and white to cream in color. Flowers of plants in the Nymphaeales range in size from 2 to 4 mm in Hydatellaceae to 50 cm in *Victoria.* Genera within the Nymphaeaceae s.s. have the broadest range of floral (perianth) pigmentation within the ANITA grade (Table 1). *Nymphaea* s.s. is the only genus within the ANITA-grade plants, containing some species with blue tepals (Fossen et al., 1998; Fossen and Andersen, 1999; Endress, 2001). White tepals within the Nymphaeales often reflect UV patterns unseen by human eyes. Both the nectar producing and peripheral areas on *Cabomba* tepals absorb ultraviolet light, as do the nectarless tepals of some *Nymphaea* spp. (Gottsberger and Gottlieb, 1981; Schneider and Williamson, 1993).

Flowers of *Austrobaileya scandens* C. White (monotypic; Austrobaileyales) are large (5 cm in diameter), but the floral pigmentation pattern may mimic decaying organic matter (yellow, brown; Endress, 2001). The remaining families in the Austrobaileyales have small (1–2 cm in diameter), bright red, orange, white, and yellow flowers (Table 1). In Illiciaceae, species of *Illicium* range in size from 1 to 3 cm in diameter and are usually red or white (Table 1). However, the bright floral colors in species of *Kadsura* and *Schisandra* are similar to those found in higher taxa.

Pollen is the only edible reward consumed by insect pollinators in 13 genera (Table 3). However, while members of the

TABLE 3. Pollination systems in the ANITA grade plants.

Taxa	Floral odor	Floral heat	Pollinators	Floral rewards	Deceit/host	Reference
Amborellaceae						
Amborella			Wind, Coleoptera, Lepidoptera, Hemiptera, Homoptera, Hymenoptera	Pollen	Deceit, host	Thien et al., 2003
Hydatellaceae						
Hydatella						
Trithuria						
Cabombaceae						
Cabomba			Diptera (flies), Hymenoptera	Pollen, nectar		Schneider and Jeter, 1982
Brasenia			Wind, Diptera (flies)	Pollen		Osborn and Schneider, 1988
Nymphaeaceae						
Nuphar	Odor		Coleoptera, Hymenoptera (bees), Diptera (flies)	Pollen, nectar	Deceit, entrapment	Lippok and Renner, 1997
Barclaya	Odor		Diptera (flies)	Pollen		Williamson and Schneider, 1994
Ondinea			Coleoptera, Hymenoptera (bees)	Pollen	Deceit	Schneider, 1983
Victoria	Odor	Heat	Coleoptera, Hymenoptera (bees)	Pollen, carpel appendages	Deceit	Prance and Arias, 1975
Euryale			Aquatic			Kadono and Schneider, 1987
Nymphaea	Odor	Heat	Coleoptera, Hymenoptera (bees), Diptera (flies)	Pollen	Deceit, entrapment	Meeuse and Schneider, 1979/1980; Ervik and Knudson, 2003
Austrobaileyaceae						
Austrobaileya	Odor		Coleoptera, Diptera (flies)	Pollen	Deceit, host	Endress, 1990, 2001
Trimenaceae						
Piptocalyz						
Trimenia	Odor		Wind, Diptera (flies), Hymenoptera (bees)	Pollen	Deceit	Bernhardt et al., 2003
Schisandraceae						
Schisandra	Odor	Heat	Coleoptera, Diptera (flies)	Pollen, nectar	Deceit, host	Liu et al., 2006; Yuan et al., 2007
Kadsura	Odor	Heat	Coleoptera, Diptera (flies)	Pollen, nectar	Deceit	Yuan et al., 2008
Illiciaceae						
Illicium	Odor	Heat	Coleoptera, Diptera (flies), Hemiptera	Pollen, nectar		Thien et al., 1983, 2000; Dieringer et al., 1999

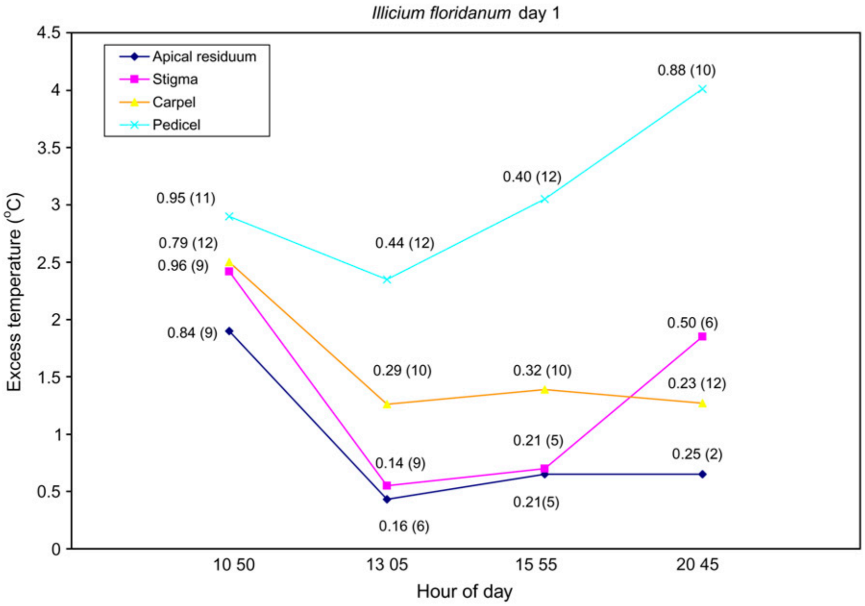

Fig. 2. Mean excess temperature of 12 newly open flowers on seven *Illicium floridanum* plants, measured at four times along West Pearl River in Louisiana. Number at each point represents standard error of mean, and number in parentheses represents number of flowers that had excess temperature at each interval.

ANITA grade also shed their pollen upon anther dehiscence, microscopy fails to show grains encased or united within a dense lipid-rich matrix that promote coherence quite unlike the copious liquid deposits on the exines of several eumagnoliid families including Annonaceae, Magnoliaceae, and Winteraceae (P. Bernhardt, personal observation; Bernhardt and Thien, 1987; Bernhardt et al., 2003; Herring, 2003; Thien et al., 2003). An unusually copious and dense lipid matrix is unnecessary in the Nymphaeaceae because most species produce grains with an echinate exine that would cling to the setal hairs of bees, flies, and anthophilous beetles (Sampson, 2000; Hesse, 2001).

Nectar production in the ANITA grade (Table 3) is detected only in four families (Cabombaceae, Nymphaeaceae, Schisandraceae, and Illiciaceae). Within the Nymphaeales, nectar secretion appears restricted to the genera *Cabomba* and *Nuphar*. Nectar is produced by two auriculate glands (vascular tissue) at the base of the petals in *Cabomba* (Schneider and Jeter, 1982;Vogel, 1998; Endress, 2001). In *Nuphar*, nectar is produced on the reduced tepals (Lippok and Renner, 1997; Zhou and Fu, 2007). Very small *quantities* of "nectar" are secreted at the bases of the tepals in *I. floridanum* (Thien et al., 1983; White and Thien, 1985), *Kadsura longipedunculata* Finet and Gagnepain (Lyew et al., 2007; Yuan et al., 2008) and *Schisandra japonica* Siebold and Zuccarini ex A. Gray (Saunders, 1998). Members of the ANITA grade lack highly differentiated nectar producing glands such as disk nectaries or septal nectaries found in higher taxa (Endress, 2001). The histology and topography of nectar glands in basal monocotyledons appears to be far more variable and differentiated than in the ANITA grade (Smets et al., 1998). Carpel appendages (high in starch) occur in beetle-pollinated species of *Victoria* (Tables 1, 3; Schneider and Williamson, 1993) and may be unique to the ancestral lineage (Gandolfo et al., 2004).

Copious secretions of stigmatic fluid are restricted to the Nymphaeales (Table 3), and the production of a "stigmatic pool" during the protogynous "female phase" is recorded in species of *Nymphaea* and *Ondinea* (Table 3). This fluid is not a nectar because insects do not drink it. Rather, it appears to "wash" pollen off insects that wade through and are trapped in the pool. In contrast, dry stigmas have been reported in four genera (*Amborella*, *Trimenia*, *Kadsura*, and *Illicium*) in the ANITA grade and in such magnoliid families as the Chloran-

Fig. 3. Flower of *Illicium floridanum* (×2). Upright carpels are no longer receptive to pollen. Anthers are just beginning to dehisce (see head of arrow) indicating start of male phase.

thaceae and Saururaceae (Lyew et al., 2007). Consequently, the dry stigma may be regarded as a pleisomorphic character in flowering plants (Bernhardt et al., 2003; Thien et al., 2003; Koehl et al., 2004).

Basal-grade angiosperms with bisexual flowers are uniformly protogynous (Table 1), as are a broader set of early-divergent taxa (Endress, 1980; Endress and Igersheim, 2000; Thien et al., 2000). Whether protogyny was inherited from a gymnosperm-like ancestor or originated de novo in angiosperms, its maintenance in so many early-divergent lineages suggests that avoiding inbreeding was important during the early evolution of bisexual flowers (Lloyd and Webb, 1986).

Stigmatic self-incompatibility has been reported in *Austrobaileya scandens* (Prakash and Alexander, 1984; Endress, 2001) and *Trimenia moorei* (Oliv.) Philipson (Bernhardt et al., 2003). The original report of self-incompatibility in *I. floridanum* (Thien et al., 1983) is now thought to be due to inbreeding depression, although late-acting, postzygotic, ovarian self-incompatibility cannot be ruled out (Koehl et al., 2004).

There are as yet few studies of genetic variation within ANITA-grade taxa, and such studies bear on historical levels of outcrossing, as well as, on pollination ecology. Williams and Kennard (2006) found that a population of *A. scandens* had a low inbreeding coefficient and detected low levels of self-fertilization. Valente (2007) found high within-population vs. among-population genetic variation and a high estimated gene diversity in *Schisandra glabra* (Brickell) Rehder. Using AFLP markers Woods et al. (2005) also found high within-region variation relative to among-region genetic variation in *Nymphaea* using ISSR markers. All three of these patterns of genetic variation are typical of species with predominantly outcrossing mating systems and high levels of pollen and/or seed dispersal (Hamrick and Godt, 1996).

Floral thermogenesis—Floral thermogenesis occurs in the Nymphaeaceae (*Victoria* and *Nymphaea*), Schisandraceae (*Schisandra* and *Kadsura*), and Illiciaceae (*I. floridanum*) (Table 2). Heat production occurs in various floral parts of *I. floridanum* over 24 h (see Material and Methods; Fig. 2). The two sets of floral measurements (diurnal and nocturnal) show a rhythm, in which at 1050 hours the temperatures are high then gradually decline to a low level by 1305 hours, stabilize, then gradually increase reaching high levels until 2045 hours. Then heat production declines, and by 2300 hours, it is low, but by the early morning hours again it gradually increases reaching high levels of heat production by 1050 hours (data not shown).

The various floral parts differ greatly in heat production throughout the rhythm (Fig. 2). In the diurnal set, the pedicel produced the greatest amount of heat of all the floral parts in excess of the ambient temperature (Figs. 2, 4). In the diurnal set, excess temperature of the pedicels was significantly different from that of the apical residua, stigmas, and carpels during the second ($F = 12.25$, root mse = 0.95, df = 47, $P < 0.0001$), third ($F = 21.93$, root mse = 0.94, df = 47, $P < 0.0001$), and fourth ($F = 8.21$, root mse = 1.66, df = 47, $P = 0.0002$) measurement periods. The pedicel is thin (1.7–2.0 mm diameter; Fig. 4) and at the time of heat measurement its length varied from 1.2 to 3.8 cm in length. The pedicel grows throughout the functional life of the flower and, if fertilized the young fruits may produce a pedicel >7 cm in length (Fig. 3). Thus, the pedicel is a "hot rod." In the diurnal set the apical residuum produced the lowest quantity of heat (Fig. 2).

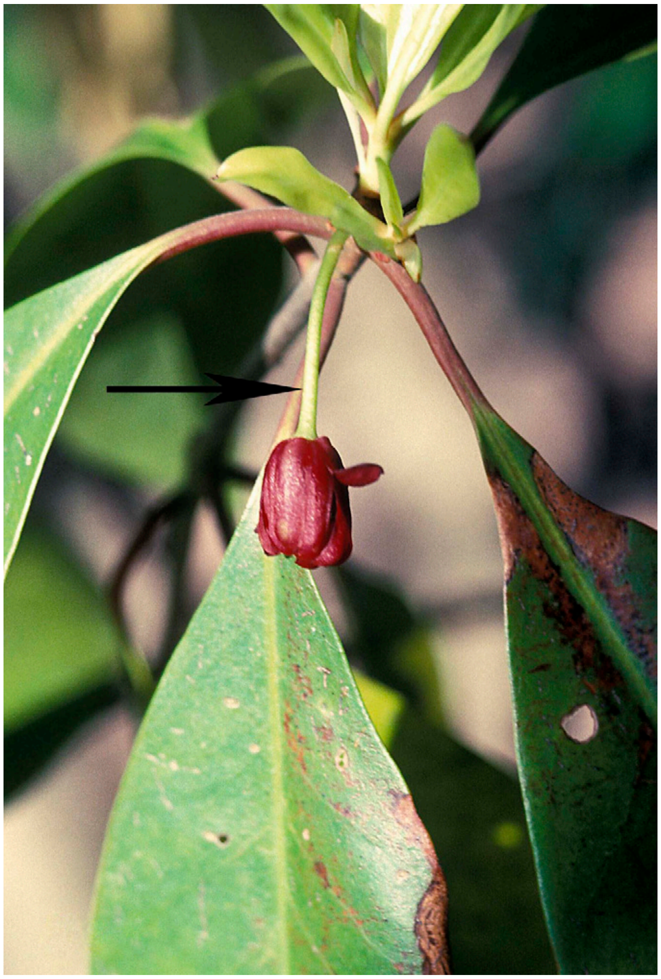

Fig. 4. Opening bud of *Illicium floridanum* (×1), showing pedicel (arrow).

Floral odors—Many plants in the ANITA grade (Nymphaeales and Austrobaileyales) produce floral odors (nine genera, Table 3), but the chemical profiles of floral organs in only a few species have been itemized. Currently, there are no fragrance analyses of pollen in the ANITA grade.

A wide variety of chemicals (30) were detected in the flowers of *Trimenia moorei*, primarily fatty acid derivatives (35.1%), terpenoids (73%), and benzenoids (49.8%) (Bernhardt et al., 2003). The dominant chemicals in the floral odors were 2-phenylethanol and 8-heptadecene that also occur in the flowers of Nymphaeaceae (Knudsen et al., 2006). The chemical 2-phenylethanol is a common component in the floral odor of over 34 genera of flowering plants (Knudsen et al., 2006). The flowers of *Nymphaea lotus* L. produced odors consisting of a mixture of fatty acids derived esters (34%), saturated hydrocarbons (7%), methoxylated benzenoids (47%), and terpenoids (12%) (Ervik and Knudsen, 2003).

The dominant chemical (96.8%) in male and female flowers of *K. longipedunculata* was butanoic acid (Yuan et al., 2008). This compound also occurs in the floral odors of *Gardenia* (Tsuneya et al., 1979), cones of *Picea abies*, *Pinus sylvestris* L., and *Larix sibirica* Ledeb (gymnosperms, Borg-Karlson et al., 1985) and in the flowering plant *Victoria* (Nymphaeaceae, Kite et al., 1991).

Pollinators—Flies (several lineages of lower Diptera) are primary pollinators in six families (10 genera, Fig. 1) in the ANITA grade (Table 3). Beetles are pollinators in five families but primary pollinators in only three genera (*Victoria*, *Nymphaea*, and *Nuphar;* Table 3). Bees are major pollinators only in the Nymphaeaceae but only minor pollinators in *Trimenia* (Trimeniaceae).

Members of the ANITA grade are usually pollinated by diverse insect species; however, in Schisandraceae (*K. longipedunculata* and *Schisandra henryi* Clarke), only a single species of insect pollinates the flowers (Yuan et al., 2007, 2008). Wind/insect pollination occurs in three families (Amborellaceae, Trimeniaceae, and Cabombaceae). Aquatic pollination occurs in members of the Nymphaeaceae (including some members of the Hydatellaceae and *Eurayle*; Table 3). Emergent, bisexual flowering heads occur in some species of *Trithuria* (Hydatellaceae) in Australia (Conn, 1993; Sokoloff et al., 2008). Mechanical autogamy and cleistogamy occurs in some species of *Hydatella*, *Barclaya*, *Nymphaea*, and *Euryale* (Table 3).

In terms of pollination mechanisms and floral structure, *Amborella* and the Austrobaileyales (woody habit) are more alike than members of the Nymphaeales (Fig. 1). In addition, Endress (2001) regards *Amborella* and *Trimenia/Piptocalyx* to be similar in floral structure and also similar to some members of the Chloranthaceae a non-ANITA grade family, but rich in pleisomorphic floral characters. Phylogenetic analysis of traits (mapping) associated with the ecology and physiology of these taxa also supports the relationships based on morphology (Feild et al., 2003; Williams and Friedman, 2004). Endress (2001) regards other groups in the ANITA grade to be more isolated based on floral structure (Cabombaceae, Nymphaeaceae, and Austrobaileyaceae).

FLORAL DECEIT AND POLLINATION

Five floral rewards (brood sites, starchy food bodies, nectar, pollen, and heat as a resource) have been identified in selected flowers belonging to the ANITA grade (Tables 1, 3). Pollen is undoubtedly the primary food resource in species of the ANITA grade in most bisexual and unisexual flowers (Tables 1, 3). Floral deceit in pollination mechanisms is common throughout all three branches of the ANITA grade (Tables 1, 3). A few examples are presented to identify various types of deceit systems operating in extant members of the ANITA grade.

Aquatic plants (Nymphaeales)—In the pollination process (Tables 1, 3), species of *Nuphar*, *Victoria*, *Nymphaea*, and *Ondinea* use floral deceit mechanisms to attract and trap insects. The various pollination mechanisms usually employ a combination of brilliant floral colors, odor, heat, and stigmatic secretions to lure the insects.

In *Nymphaea* (Nymphaeaceae), the diurnal taxa, have large flowers that open and close in successive days (up to 6–7 d) (Valla and Cirino, 1972; Cramer et al., 1975; Meeuse and Schneider, 1979/1980; Schneider, 1982). On the first day, the emergent flowers are female (protogynous), and the upper surface of the bowl-shaped interior of the open flower gradually fills with a large quantity of watery fluid (Meeuse and Schneider, 1979/1980). The stamens and staminodes form a slippery palisade around the stigmatic pool that prevents insects from climbing or crawling out of the flower. The liquid contains about 1% sugar in tropical species and 3% in temperate species of water lilies (Meeuse and Schneider, 1979/1980). A 1% solution of sucrose is below the perception of honeybees.

In diurnal species of water lilies, bees and flies are attracted to the flowers by the brilliant color and floral odors. The nocturnal tropical species attract beetles and have carpel appendages with starch that function as food bodies (Meeuse and Schneider, 1979/1980; Schneider and Williamson, 1993). In water lilies, insects falling into the liquid pool have a tendency to drown, particularly the small-bodied insect visitors (bees, flies) (Meeuse and Schneider, 1979/1980). Besides sugars, the liquid contains many amino acids, B, Ca, K, and Mg, all close to optimal concentrations for pollen germination (Meeuse and Schneider, 1979/1980; Capperino and Schneider, 1985). Surfactants in the stigmatic fluid then wash the pollen off the insects and may also kill them as the air in their trachea is replaced by the watery fluid and they suffocate (facilitated by the surfactants) (Hardman, 1941; Meeuse and Schneider, 1979/1980).

On the second day, the stamens form a cone over the pool of stigmatic fluid, and the anthers commence shedding pollen and gradually open as the stigmatic pool dries. This stage allows insects to pick up pollen and restart the entire pollination process (Meeuse and Schneider, 1979/1980). Floral odor and heat production usually cease or decrease after the first day.

Meeuse and Schneider (1979/1980) regard the entrapment mechanisms to be “exploitative” (not mutualistic) in that many of the pollinators are killed. They regard the process as similar to pollination in species of *Arisaema* (Araceae) in which the pistillate inflorescence lacks an exit and kills flies (pollinators). See Schmucker (1932, 1933, 1934) for an excellent discussion of pollination in *Nymphaea* and Knoch (1899) and Prance and Arias (1975) for pollination in *Victoria*.

Deceit in pollination also occurs in *Ondinea purpurea* den Hartog; the brilliant petals attract insects, and the flowers produce no heat or odor in a mechanism that washes off the pollen without trapping or killing the insects (Kenneally and Schneider, 1983; Schneider, 1983; Schneider et al., 1983). The emergent flowers open and close over 3 days. On the first day of anthesis, the perianth and stamens are reflexed and brilliantly colored. A small cup, formed by the red stigmas, is filled with stigmatic fluid (Schneider, 1983; Schneider et al., 1983). A central pole-shaped structure projects from the center of the cup (about 4–5 mm tall) (Schneider et al., 1983). When insects (small bees) land on the “pole,” they slip and contact the stigmatic pool and pollen (if present) is washed off their bodies, thus pollinating the flower (Kenneally and Schneider, 1983; Schneider et al., 1983).

On the second and third days of anthesis, the stamens move to enclose and conceal the female parts (pole). The bees now land on the dehiscing stamens, no self-pollination occurs because the stigmatic pool has dried and the pollen is now deposited on the foraging bees (Kenneally and Schneider, 1983; Schneider, 1983; Schneider et al., 1983). The system is deceptive because the bees cannot distinguish between male and female phases of the same flower (Schneider et al., 1983), a system known as auto-mimicry.

Terrestrial woody plants and lianas (Amborellaceace and Austrobaileyales)—The dioecious shrubs and small trees of *Amborella trichopoda* Baill. are wind/insect pollinated (Thien et al., 2003). The flowers offer only pollen as the resource for visiting insects. In *A. trichopoda*, the tepals are a dull cream color, and no floral odor or heat has been detected (Endress and Igersheim, 2000; Thien et al., 2003). However, Collett (1999) noted the production of scent at night with accompanying visits by moths (in great number) in plants growing in greenhouses. The female flowers of *A. trichopoda* contain 0–4 staminodes (contain no pollen), are similar in appearance to functional stamens (Endress and Igersheim, 2000; Thien et al., 2003), and appear to be an example of cryptic dioecy, in which the staminodes in female flowers mimic fertile androecia in male flowers (Mayer and Charlesworth, 1991; Thien et al., 2003). No insects were observed at night on the flowers of *A. trichopoda* in situ, and thus all the insects listed as pollinators including Coleoptera, Homoptera, Hemiptera, Microlepidoptera, Hymenoptera, and Diptera were captured throughout the day (Thien et al., 2003).

A free-flowing stigmatic secretion was observed in only three of 1200 female flowers of *A. trichopoda* in nature and in the laboratory (hand cut inflorescences) and in only 30 of ~1000 flowers from Col d'Amieu in New Caledonia (Thien et al., 2003). At Col d'Amieu, the secretions were only apparent after a day of heavy rain. A thin cuticle covered the stigmatic papillae; thus the stigma is regarded as a dry type (Thien et al., 2003), which is important because many workers suggest stigmatic secretions are a source of food for visiting insects (especially flies). The dry-type stigma has now been found in a few other families in the ANITA grade and is considered to be a pleisomorphic character in the flowering plants (Schisandraceae; Lyew et al., 2007).

Floral deceit is also evident in the monoecious and dioecious members of the Schisandraceae (*Schisandra* and *Kadsura*). In *S. glabra* (dioecious), staminodes form a fused "shield" (part receptacle) that produces heat along with floral odor to attract a wide variety of insects to lay eggs on the "shield" and on the gynoecium that also produces odor and heat (Liu et al., 2006). In the process of laying eggs and feeding on pollen, the flowers are pollinated (Liu et al., 2006). Both types of flowers have dull red tepals and droop on long pedicels.

Plants of *K. longipedunculata* (monoecious) in China have red or yellow male flowers (the androecium) and yellow female flowers. All flower types simultaneously produce heat and floral odors (dominated by methyl butyrate) throughout a 4–5 h nocturnal period during which pollination occurs. Pollen is the only food for insects, and the flowers are pollinated by a single species of female *Megommata* (Cecidomyiidae) (Yuan et al., 2008). The floral odor is thought to be the main floral attractant for the insects, and pollen of *K. longipedunculata* occurs in the gut of *Megommata*. Normally, *Megommata* species eat scale insects (Harris, 1968).

The male and female flowers of almost all *Kadsura* and *Schisandra* species have a similar floral structure and produce heat and floral odor. However, the flowers of dioecious *S. henryi* produce no floral odor or heat. Because pollen is the only food for insects, female flowers only mimic the colors of male flowers and offer no edible reward (Yuan et al., 2007). The pollinator is yet another species of *Megommata* (Cecidomyiidae), and only the female fly forages for pollen (Yuan et al., 2007). A small opening formed by the tepals (drum-shaped flower) allows only small insects into the interior of the flower (*Megommata* is 1 mm long; Yuan et al., 2007).

The bisexual flowers of *Austrobaileya scandens* (monotypic), mimic rotting organic matter, produce an odor smelling like rotten fish by stamens and staminodes, and are pollinated by flies (see photograph of fly with pollen, Fig. 1D in Endress, 2001). Fallen flowers were found to contain drosophilid eggs laid in a furrow of the staminodes (Endress, 1984, 2001). However, a survey of fallen flowers from 12 vines from three natural populations (Queensland, Australia) indicated that many fallen flowers never received pollen (20/39 flowers) and the median (± average deviation) pollen load of those that did was 10 ± 27 pollen grains flowers (J. H. Williams, personal observation).

Observations of living flowers on the vine (in midcanopy) indicated that insect visitation during the day was quite rare (two seasons), and beetles were seen dusted with the pollen of the host's flowers (J. H. Williams, personal observation).

FLORAL THERMOGENESIS

Flowers produce heat via specific controlled biochemical reactions (Seymour and Schultze-Motel, 1997; Thien et al., 2000). The flowers of many thermogenic plants also produce strong odors, but simultaneous production of floral odors and heat are not necessarily correlated. Floral thermogenesis was found in only 11 families of extant angiosperms, but three families (five genera) are in the ANITA grade with only two families in the eudicots (Table 2). Production of heat is not restricted to the angiosperms but also occurs in cycads pollinated by beetles and thrips (Norstog, 1987; Tang, 1987; Norstog and Fawcett, 1989; Terry, 2001; Terry et al., 2004; Roemer et al., 2005).

Floral heat production in angiosperm flowers is involved in many aspects of the breeding system, including the following: it ensures protection of flowers during periods of cold temperatures, stabilizes floral development, enhances the evaporation of floral scent, aids germination of pollen, provides an optimum temperature for pollen tube growth, and provides an optimum temperature for development of insect larvae (Ervik and Barfod, 1999).

Heat: Beetles and large flowers—As noted by Seymour and Schultze-Motel (1997), heat is a resource (first proposed by Leick, 1915), one that enhances feeding and mating of insects, conserves energy, and maintains thoracic temperature required to initiate flight. Seymour et al. (2003) measured floral heat in *Philodendron solimoesense* A. C. Sm. (Araceae) in French Guiana and respiration rates of the beetle *Cyclocephala colasi* Endrödi (the pollinator) at ambient temperatures and inside the flower (Gottsberger and Amaral, 1984). The "energy saving factor" (the ratio of excess energy required for activity at ambient temperature to that of required floral temperature) was calculated to be 4.8°C in the evening (when in the flower) and decreased to 2.0°C at dawn (Seymour et al., 2003). The experiment demonstrates that floral heat is a resource for the insects. Floral thermogenesis of flowers in tropical forests is estimated to occur in at least 900 species of plants (e .g., Cyclanthaceae, Annonaceae, Araceae, Arecaceae, Magnoliaceae, and Nymphaeaceae), visited by 220 species of *Cyclocephala* (Schatz, 1990; Gottsberger, 1999; Seymour et al., 2003). Many other species of beetles and flies, however, are also presumed to benefit from the heated flowers.

The experiment of Seymour et al. (2003) can be used to interpret the interplay of floral thermogenesis, odor, and color, in the pollination of *Victoria amazonica* (Poeppig) Sowerby (Nymphaeaceae) in which large beetles are trapped, fed, and released in the Amazon Basin (Prance and Arias, 1975; Schneider, 1976). In the evening of the first day (female stage), the bud opens, and the white flowers produce heat (>11°C above ambient) and a strong odor (smells like butterscotch and pineapple) that attract beetles (>47 beetles/flower; Prance and Arias, 1975). Near dawn, the flowers close and trap the insects, accompanied by a gradual loss of floral heat and odor (Prance and Arias, 1975). During the second day of entrapment, the flowers gradually change color from white to a deep purplish-red via production of anthocyanins (Prance and Arias, 1975). Then in the early evening, the staminodes of the flower open, and the escaping beetles pick up pollen from the dehiscing stamens and usually fly to another first-day white flower of *V. amazonica* because only the white flowers are scented and thermogenic (Prance and Arias, 1975).

When trapped inside the flowers, the beetles (four species of *Cyclocephala* and *Ligyrus*) eat the starchy carpel appendages and presumably mate; it is not known if they eat the pollen (Prance and Arias, 1975). The carpel appendages are composed of 28.7% starch (dry mass) and 5% dextrose and also produce heat (Prance and Arias, 1975; Knoch, 1899).

In a recent study, Seymour and Matthews (2006) analyzed the pattern of anthesis and the role of thermogenesis in the pollination of *Victoria amazonica*. Inside the floral chamber, *Cyclocephala hardyi* Endrödi, the most abundant beetle species trapped inside the floral chamber, competed for mates and ate portions of the stylar processes (starchy appendages, Seymour and Matthews, 2006). Inside the heated chamber, the insects maintained a body temperature of about 31°C (required for flight); stylar processes produced 67% of the heat during the first evening and stamens 84% on the second evening. As a result, the beetles shifted from eating stylar processes to the dehiscing stamens (warmer location), coating them with pollen (Seymour and Matthews, 2006). The authors conclude that floral thermogenesis in *V. amazonica* is an energy reward for the beetles because it maintains their body temperatures at endothermic levels while inside the flowers.

In the population of *V. amazonica*, the larger flowers attract more insects (Prance and Arias, 1975), produce higher temperatures, and presumably generate greater seed production. Therefore, we hypothesize that the large flowers in *Nymphaea* and *Victoria* may be the result of the directional selection of an even greater numbers of beetles crowding into the flowers for heat. This eventually resulted in the evolution of larger flowers with increased seed production. Because no floral compitum has been described to date in either species of *Victoria*, a greater number of beetles would theoretically carry a more genetically diverse range of pollen grains from plant to plant, increasing fitness and flower size over generations.

In *Magnolia tamaulipana* Vasquez-G., some trees produced larger flowers (statistically significant) than other trees in the population (Dieringer et al., 1999). In addition, the major pollinator, *Cyclocephala caelestis* Delgado and Ratcliffe (Dynastinae), preferentially visited the larger flowers at peak thermogenesis when the stigmas were most receptive. The role of heat in the pollination of *V. amazonica* and *M. tamaulipana* coincides with the experiment of Seymour et al. (2003) on *P. solimoesense,* in that heat is a resource for the beetles as they essentially become endothermic within the flower.

Silberbauer-Gottsberger et al. (2001) and Gottsberger (1999) correlated floral thermogenesis with other characters (e.g., large flowers, thick fleshy perianth) associated with beetle pollination in Annonaceae, Araceae, Arecaceae, and Cyclanthaceae to determine the extent of convergent evolution in the animal-pollinated flora of Central Amazonia. Many scientists associate thermogenic plants with large flowers, strong floral odors, and beetle pollination (Silberbauer-Gottsberger et al. (2001).

Heat: Flies and small flowers—It is surprising, however, to find that small, fly-pollinated (sometimes small beetles) unisexual flowers of *Kadsura* and *Schisandra* (Schisandraceae) and small bisexual flowers of *I. floridanum* (Illiciaceae; Dieringer et al., 1999) in the ANITA grade (Tables 1–3) are also thermogenic. In all three genera, the heat-producing parts of the flowers are only 3–8 mm in diameter. The androecial structures of staminate flowers in some *Schisandra* and *Kadsura* species have a wide range of bizarrely shaped structures formed by stamen filaments, staminodes, and receptacle (Smith, 1947; Saunders, 1998, 2000; Liu et al., 2006) that produce heat (Liu et al., 2006).

In *I. floridanum*, pollen tubes from any stigmatic crest may grow between the carpels via an apical residuum (an entragynoecial compitum) to achieve syncarpy (Fig. 2) (Williams et al., 1993; Armbruster et al., 2002) The pollen grains germinate within 1 h of pollination, and the pollen tubes grow to the base of the stigma papillae in 3 h, and enter the substigmatic transmitting tissue within 6 h (Koehl, 2002). The pollen tubes reach the ovary locule within 24 h and enter the micropyle within 48–72 h (Koehl, 2002).

The pollinators are primarily flies (Tables 1, 2) (Thien et al., 1983) that emerge from the forest litter in spring. Observations of *I. floridanum* flowers on cold nights with air temperatures below ~10–15°C, indicate the flowers attract many more insects on these cool nights than on warmer nights (food and heat). Diptera generally have low body temperatures and do not thermoregulate in flight (Heinrich, 1993). Thus we hypothesize that the floral heat also aids growth of the pollen tubes not only in the carpels but also in tissue that connects the carpels. The heated tissue may also function to insure a relative stable temperature for pollen tube growth in which male gametophytes can compete for ovules (a heated race track) to increase fitness.

Thermogenesis, however, in *I. floridanum* does not cease with fertilization, but continues during fruit (seed) development. During development of the fruit, the pedicel produces temperatures 8°C above ambient temperature as do the young fruits (Fig. 4; L. Thien, personal observation). The fruits of *I. floridanum* rapidly expand, and even unfertilized ovules will develop a heated chamber.

An extragynoecial compitum is also present in the female flowers of *K. longipedunculata* in which male and female flowers produce floral odors and heat in a 4-h nocturnal period to attract pollinators (Lyew et al., 2007). The apocarpous carpels are tightly arranged so that only a portion of the stigmatic crest protrudes to capture pollen. Pollen tubes grow extracellularly downward from the stigma (dry type) to the pseudostyle (hidden region) and follow one of two routes. One route leads toward the pseudostyle of a neighboring carpel, and the other leads into the locule of the pollinated carpel. Pollen tubes were not observed to extend beyond an adjacent carpel. Detailed comparisons of the extragynoecial systems in *K. longipedunculata* and *I. floridanum* are presented in Lyew et al. (2007). Friis et al. (2000) noted the presence of an extragynoecial compitum in a putative Illicialean fossil (apocarpous) from the Early Cretaceous mesofossil flora based on interpretation of carpel faces.

THE POLLINATORS

Generalist vs. specialist modes of pollination in the ANITA grade—Tables 1 and 3 show that generalist modes of pollination are currently associated with *A. trichopoda* (a combination of diurnal insects and air currents), the North American *Illicium* spp. (a combination of insects) and *Trimenia moorei* (air currents and a combination of diurnal syrphid flies and bees). In all remaining species studied, we can note a trend toward specialized interactions between their flowers and insects that belong to the same order or genus.

Within the family, Nymphaeaceae, specialized bee- or beetle-pollination systems are found in both *Nymphaea* and *Nuphar* (Nymphaeaceae), but these genera have different commitments to floral presentation within their respective lineages. In most *Nymphaea* spp. studied to date, the inheritance of distinctive suites of floral characters (e.g., floral colors, odors, rhythm of anthesis) determine whether the flower is pollinated primarily by a combination of bees and flies or exclusively by scarab beetles (Table 3). Currently flowers of *Nymphaea lotus* L. are the most important exception to this dichotomy; they are pollinated by both rhinoceros beetles and bees at different times of day (Hirthe and Porembski, 2003).

In contrast, there is no obvious distinctive bifurcation of floral characters in *Nuphar*. The primary attractants, rewards, and flowering periods described in *N. macrophylla* Small, pollinated primarily by beetles in the genus *Donax* (Chrysomelidae; Schneider and Moore, 1977) appear almost identical to floral presentation in four other *Nuphar* species pollinated primarily by small bees (e.g., Halictidae) and various flies (Lippok and Renner, 1997; Zhou and Fu, 2007). E. L. Schneider (Santa Barbara Botanic Garden, personal communication) suggests that pollination systems in *Nuphar* spp. are determined, at least in part, by ambient temperatures, periods of beetle activity and how long *Nuphar* populations stay in flower. Because *N. macrophylla* blooms most of the year at its Texas sites, its flowers are more likely to be visited by *Donax* compared, say, to *N. ozarkana* in bloom for less than six months. Peak flowering in *N. ozarkana* declines after August and stops during the frozen winter, starting again by May in Missouri sites. Consequently, *Donax* spp. are late and relatively infrequent visitors (Herring, 2003).

Japanese populations of *Euryale ferox* Salisb. self-pollinate, although some self-pollination may be accomplished by bees and flies (Kadono and Schneider, 1987). Mechanical self-pollination with cleistogamous flowers continues through most species in the genus *Barclaya*, although *B. rotundifolia* Hotta (Williamson and Schneider, 1994) opens its perianth and receives some visits from flies.

Otherwise, in all remaining, predominantly outcrossing ANITA species studied thus far, the trend is toward a narrow range of pollen vectors. We acknowledge that this observation is probably biased by the fact that these remaining species belong to small (often monotypic) genera or only a few species in a relatively large genus have been studied so far. *Ondinea* (one species) is pollinated only by trigonid bees (Schneider, 1983). *Cabomba* (1/7 species), *Kadsura* (2/22), and *S. henryi* (1/25) appear to be pollinated primarily or exclusively by true flies (Diptera, Table 3). The flowers of *Brasenia* are interpreted as wind-pollinated with some visits by small flies (Osborn and Schneider, 1988).

Pollinators—The majority of insects that effect pollination within the ANITA group eat pollen during the winged phase of their life cycles regardless whether they have suctorial mouthparts, with the probable exception of parasitoid wasps (Thien et al., 2003; Grimaldi and Engel, 2005; Tables 1, 3). The consumption of pollen by the primary pollinators of the ANITA group parallels that of pollen-eating insects that pollinate gymnosperm cones (see reviews in Bernhardt, 2000, and in Terry, 2001) and the "primitive" flowers in other magnoliid families (Bernhardt and Thien, 1987). Indeed, ANITA-grade flowers, magnoliid flowers, and the cones of entomophilous gymnosperms often share the same major groups of pollinators including weevils, true flies, trigonid bees, and moths (Bernhardt and Thien, 1987; Bernhardt, 2000; Terry 2001; Grimaldi and Engel, 2005).

The lineages of insect pollinators of extant basal angiosperms were established by the late Jurassic (Rohdendorf, 1974; Crowson, 1981; Labandeira and Sepkoski, 1993; Farrell, 1998; Ren, 1998; Grimaldi, 1999; Grimaldi and Engel, 2005; Labandeira, 2005). As noted by Labandeira (1998a, b), the pollinating insect lineages established in the Jurassic may have had their mutualisms co-opted by the angiosperms.

Labandeira (2005) classified flowering plant reproductive structures into nine basic types using characters such as size, shape, and thermogenesis. The ANITA-grade taxa were placed in category 2 and characterized as small, bowl-shaped, white to yellowish, actinomorphic flowers with exposed sexual organs (the first category contained Cycadaceae, Ephedraceae, and Gnetaceae). The perianth was composed of separate sepals and petals often clustered in inflorescences. These Early Cretaceous (Hauterivian to Aptian; Late Cretaceous) flowers were probably scented and used deceit mechanisms or produced some sort of liquid nectar (Labandeira, 2005). The dipteran visitors/pollinators were probably members of the Syrphidae and the Muscoidea, especially ancestors of the modern Anthomyiidae, Faniidae, Muscidae, and Lauxaniidae (Labandeira, 2005).

In two recent pollination studies in south central China, flowers of *S. henryi* and *K. longipedunculata* have many characteristics of Labandeira's (2005) proposed category 2 flowers. Both species have small (1–2 cm diameter), bowl-shaped, unisexual flowers. The flowers of *S. henryi* are yellow or orange and red (Yuan et al., 2007) and produce no floral odor or heat, whereas flowers of *K. longipedunculata* produce a strong pineapple-like odor plus heat during a 4-h nocturnal period (Yuan et al., 2008). Both species are pollinated solely by a different species of female pollen-eating *Megommata* sp. (Cecidomyiidae). The gut of each species of insect is filled with either the pollen of *S. henryi* or *K. longipedunculata* (Yuan et al., 2007, 2008). The adult *Megommata* sp. normally prey on scale insects but presumably eat pollen for added protein in reproduction (Yuan et al., 2007, 2008). These two studies are the first reports of pollen-eating in the Cecidomyiidae. Labandeira (2005) indicates that the best direct evidence for food consumption in fossil insects is the contents of the gut. Angiosperm pollen has been found in the guts of modern pollinivorous flies (Wilson and Lieux, 1972; Leereveld, 1982), but not in fossil taxa. However, it occurs in other insect groups from the Middle Carboniferous to Recent (Kukalova-Peck, 1987; Rasnitsyn and Krassilov, 1996; Afonin, 2000; Labandeira, 2005).

For pollinivory by flies, Labandeira (2005) divided feeding types into four basic strategies: (1) direct ingestion of pollen (tubular mouthparts), (2) extraoral digestion by certain Drosophilidae (extraoral mastication and predigestion of molded pollen clumps followed by grain rupture and imbibition of protoplasts), (3) a punch and suck mechanism, (4) collection and transport of pollen along the pseudotracheal channels of muscoid flies.

That pollen is usually the dominant edible reward in flowers of the ANITA group explains why automimicry is documented in *A. trichopoda*, *S. henryi*, and the bee- and fly-pollinated *Nymphaea* and *Ondinea* species (Table 3). Pollen-foraging insects will not visit nectarless, female flowers unless they look and/or smell like male flowers (Bernhardt, 1996). Presumably the bisexual and protogynous flowers of *Nymphaea* and *Ondinea* species also lure prospective bees and/or flies to the female phase flower because it looks and smells like the male phase (stigma receptive/anther dehisced).

The flowers of other members of the ANITA group appear to reward pollinators throughout their floral life span regardless of floral sexuality or protogynous phase. Beetle-pollinated *Victoria* and *Nymphaea* species offer shelter and warmth while the stigmas are receptive but anthers have not dehisced. Female flowers of *Kadsura japonica* (L.), diurnal and female phase flowers of *Nuphar* and *Illicium* species offer nectar. Andromonoecious *Trimenia moorei* lacks nectar, warmth, or a sheltering perianth, but both the small male and bisexual flowers offer copious amounts of pollen.

Bees in the family Apidae (e.g., *Apis*, *Exoneura*, and *Trigona*) are among the many insects (bees, true flies, and beetles) known to pollinate some members of the Nymphaeaceae (Prance and Anderson, 1976; Schneider and Chaney, 1981; Schneider, 1983) and Trimeniaceae (Bernhardt et al., 2003). While apid bees are equipped with elongated, nectar-lapping proboscis, the females that visited ANITA grade flowers foraged for pollen for their offspring or larval siblings and not for true nectar.

In contrast, when bee-pollination was recorded in nectarless *T. moorei* (Bernhardt et al., 2003) and nectariferous *Nuphar* spp. (Lippok and Renner, 1997; Herring, 2003; Zhou and Fu, 2007), the dominant pollen-collecting bees were identified as members of short-tongued families (Halictidae and Colletidae). Pollen load analyses showed that some bees collected on the nectarless flowers of *T. moorei* probably supplemented their diets by foraging on nectar-secreting flowers of co-blooming plants in the families Epacridaceae, Loranthaceae, and Myrtaceae (Bernhardt et al., 2003). Alternating visits to nectarless but pollen-rich flowers with visits to nectar-rich but pollen-poor blossoms during the same foraging bout is a common strategy in many polylectic bees that are the dominant pollinators of nectarless flowers (see review in Bernhardt, 1996). Because *Nuphar* spp. offer nectar, we should therefore predict a higher frequency of some halictid bees foraging exclusively on protogynous *Nuphar* flowers. Provided the bees visit both male and female phase flowers, these foragers will receive both nectar and pollen if they visit more than one *Nuphar* flower during the same foraging bout (Herring, 2003).

Flies—The phylogenetic supertree for Diptera (Yeates and Wiegmann, 2005) includes a number of lower Diptera groups that pollinate extant ANITA-grade plants. The taxa include *Bibionomorpha* (Cecidomyiidae, Mycetophilidae, Sciaridae), Chironomoidea (Ceratopogonidae, Chirononidae), Lauxaniidae, Brachycera, and Ephydridae (Thien et al., 1983). The Bibionidae (lineage) were present throughout the Cretaceous. The Mycetophilidae were present from the Jurassic through the Cretaceous (Crepet et al., 1991; Crepet, 1996). Some members of the Brachycera appeared in the early Jurassic (Crepet et al., 1991).

As noted by Labandeira (2005), it is difficult to determine whether nectarivory or hematophagy was the primitive feeding mode for Diptera. If carbohydrates were needed, they were probably obtained from the sugary secretions of vascular plants, e.g., stigmatic-pollination drops, nectaries, or honey dew. The various modes of pollinivory are derived as shown in Bombyliidae, Syrphidae, and Muscidae (Labandeira, 2005). Labandeira (2005) notes that the Forcipomyiinae (Ceratopogonidae) contained species that used the punch-and-suck method to "eat" pollen (Late Paleocene, 60 Mya).

Beetles—Where does specialized beetle pollination really fit into the hypothetical evolution of early angiosperm reproductive systems? 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 (see Olesen et al., 2007, for a discussion of openness of flowers and visitors in higher taxa). The first flowers received a wide variety of pollen vectors representing several insect orders. While specialized systems, in which the flower is modified to exploit a single order or genus of insects, is common and recurrent in the basal angiosperms, it is of secondary derivation. Based on new evidence, we feel there is no reason to alter this hypothesis considering ongoing analyses of floral biology in the ANITA group. However, we can add that air currents (wind pollination) probably contributed to seed set in early angiosperms based on studies of *Amborella* and *Trimenia* (Tables 1, 2).

Beetle pollination in particular represents a derived, albeit early evolving, syndrome in the ANITA-grade plants. Specialized beetle pollination occurs far more often within various magnoliid lineages compared to the ANITA grade. Beetle pollen vectors of specialized flowers produced by magnoliids (e.g., Annonaceae, Eupomatiaceae, Magnoliaceae, Monimiaceae, and Myristicaceae) represent up to nine families in the order Coleoptera (Cerambycidae, Chrysomelidae, Curculionidae, Mordellidae, Nitiduidae, Oedmeridae, Scarabaeidae, Scraptiidae, and Staphylinidae; Bernhardt, 2000). Within the ANITA group, only three genera within the Nymphaeaceae (*Nymphaea*, *Nuphar*, and *Victoria*) contain species pollinated primarily or exclusively by beetles, and those insects represent only two families in the Coleoptera (Chrysomelidae and Scarabaeidae; Bernhardt et al., 2003). Yes, beetles placed in other families appear to be of some importance in the pollination of female flowers of *A. trichopoda*, but this is plainly a generalist pollination system incorporating wind pollination with a number of unrelated insects including Lepidoptera (Thien et al., 2003), all with short and/or unspecialized mouthparts for pollen consumption.

Both Gandolfo et al. (2004) and Ervik and Knudsen (2003) offer a compelling argument that the pollination of members of the Nymphaeaceae by scarabaeid beetles represents an ancient mutualistic partnership. In comparison, there are only two species in the magnoliid lineage (*Cymbopetalum*; Annonaceae) currently known to be pollinated exclusively by scarabaeids (see Bernhardt, 2000). Specialized beetle-pollination in the magnoliid families is more likely to be dominated by true weevils (Curculionidae). When scarabaeids are found in magnoliid flowers they usually occur in mixed company with other anthophilous beetles representative of at least nine other families in the Order Coleoptera. In fact, modern Mediterranean basin-southern African monocot species and eudicots in the families Droseraceae, Papaveraceae, Ranunculaceae, and Campanulaceae are far more likely to have hairy scarabs as their dominant pollinators compared to eumagnoliids. Convergent evolution of scarab pollination occurs commonly in both tropical forests and Mediterranean-type scrubs or woodlands (Bernhardt, 2000).

Bees—Considering the age of the Nymphaeaceae, some reconstructed fossil flowers appear intermediate between Cabombaceae and Nymphaeaceae (Friis et al., 2001) and also suggest general pollination and/or pollination by small flies as in modern *Cabomba* spp. (Schneider and Jeter, 1982). We must remember, though, that scarab-pollination is not the only specialized trend in modern Nymphaeaceae. First, there is the recurrent evolution of mechanical self-pollination (including cleistogamy) within three genera (described earlier). Of far greater importance, though, is chrysomelid beetle (Schneider and Moore, 1977) vs. bee pollination within the genus *Nuphar* (Table 3). The bee-pollinated species appear dependent on short-tongue bees in the Halictidae, particularly in the genus *Lasioglossum* (Lippok and Renner, 1997; Herring, 2003; Zhou and Fu, 2007). While fossils of *Lasioglossum* are found no earlier than Eocene amber, fossil nests similar to those of modern Halictinae are recorded from the Cenomanian of North America and the Maastrichtian of Uruguay (Elliott and Nations, 1998). Because the halictid lineage is probably 95–100 Myr old, (Engel, 2001) it is reasonable to speculate that specialized pollination systems between solitary bees and the *Nuphar*-type flower is as old as or older than proposed coevolution between scarabaeid lineages and *Victoria* or *Nymphaea* (Gandolfo et al., 2004).

DISCUSSION

Pollination by insects in early nonangiosperm plant taxa is suggested by the presence of fecal pellets in fossil bennettitalean reproductive organs and ephedralean and conifer pollen in the gut contents of fossilized insects (Labandeira, 1997, 1998a; for pollination of Mesozoic gymnosperms, see Labandeira et al., 2007). Pollination of extant nonangiospermous plants include *Gnetum* by moths (Kato and Inoue, 1994), *Ephedra* species by flies (Bino et al., 1984a, b), and cycads by snout weevils (Norstog et al., 1986; Norstog and Fawcett, 1989). In addition, thrips (Thysanoptera) and weevils (Coleoptera) pollinate species of Australian *Macrozamia* cycads in which floral odor and floral heat play roles in the attraction of pollinators (Mound and Terry, 2001; Terry, 2001;Terry et al., 2004, 2005; Roemer et al., 2005). Pollination of *Macrozamia licida* by thrips based on heat and floral odors in a deceit "push-pull" system, was documented by Terry et al. (2007). Fungus gnats (Diptera) pollinate *Zamia pumila* (Breckon and Negrón-Ortíz, 1983).

Several groups of extant flowering plants were analyzed by Hu et al. (2008) including a basal group of 29 families (Amborellaceae to Saururaceae) for modes of pollination. In the basal group of 29 flowering plant families, 86% had species pollinated by insects, 17% by wind, 3% water, and 34% with non-wind-pollinated species had specialized pollination modes (included water and Hymenoptera, Hu et al., 2008). It was noted that general insect pollination occurred initially in the extant families in all groups (with some exceptions).

Our analysis of pollination syndromes (Tables 1–3; Fig. 1) of only ANITA grade plants supports the general pattern described by Hu et al. (2008). Generalist modes of pollination (often combining biotic and abiotic vectors) are currently associated with *Amborella trichopoda*, *Illicium* spp., *Trimenia moorei*, and some species of Schisandraceae. In all remaining families (studied), we note a trend toward specialized interactions between insects and flowers. Combining our analysis with the work of Hu et al. (2008) suggests that the evolution of stamen and carpel architecture provided early angiosperms with a reproductive versatility on a scale that slides between generalist and specialist pollen vectors. Combined with an early trend toward syncarpy (discussed later) this versatility guaranteed higher proportions of fertilized ovules.

Some specialized trends in insect-pollination, e.g., beetles, evolved early (Ervik and Knudsen (2003; Gandolfo et al., 2004). These findings in the ANITA grade suggest insect pollination occurred very early in the first angiosperms. In this regard, however, the Diptera become the strongest candidates as the first pollinators of early angiosperms (Table 3; Labandeira, 2005).

Information on wind, fly, and bee pollination within the ANITA grade suggest we reexamine the hypothesis that beetles pollinated the early angiosperms in a "mess and soil" system (Faegri and van der Pijl, 1979, p. 51). This concept of beetle pollination in basal taxa consists of "—primitive insects messing about in primitive blossoms more or less diffusely covered with pollen on legs and body, some part of which will subsequently touch a stigma" (Faegri and van der Pijl, 1979, p. 51; Crepet et al., 1991). The experimental work of Seymour et al. (2003) with floral thermogenesis and beetles indicates that beetle pollination in the basal angiosperms (*Victoria*, *Magnolia*) is a highly adapted, but specialized type of pollination that appeared in the Cretaceous (Crepet et al., 1991; Gottsberger, 1999; Ervik and Knudsen, 2003; Gandolfo et al., 2004).

The ANITA-grade flower resources—The floral resources in extant members of the ANITA grade are pollen, nectar, starchy food bodies, heat, and brood sites (Tables 1–3).

The pollen, however, lacks a dense, lipid-rich matrix quite unlike the copious lipid deposits on the exines of many taxa above the ANITA grade. Heavily clumped grains would be maladaptive in flowers that alternate between insect and wind pollination. In addition, because microdipterans are the primary pollinators, the sticky grains would probably deter successful flight. In addition to analyzing modes of pollination, Hu et al. (2008) also examined dispersed angiosperm pollen grains and found clumped pollen to be common in the mid-Cretaceous. The study also notes that clusters of pollen grains are rare in wind-pollinated plants and that pollenkitt and other factors cause pollen grains to clump (evidence for early insect pollination in angiosperms).

Nectar—Members of the extant lineages of the Gnetales (Gnetaceae, Ephedraceae, and Welwitschiaceae) secrete pollination drops that attract and are eaten by fluid-feeding flies, moths, bees, beetles, and thrips (Labandeira, 2005; Labandeira et al., 2007). Pollination drops also occur in the cycads (Breckon and Negrón-Ortíz, 1983; Poort et al., 1996; Terry, 2001; Labandeira et al., 2007) and are also eaten by insects. Many conifers also secrete pollination drops (Tomlinson et al., 1991; Owens et al., 1995), but rarely attract insects, even though some flies also eat large quantities of pollen (Burdick, 1961; Holloway, 1976).

Many workers concluded that these "pollination drops" were a precursor to the consumption of stigmatic exudates by small flies in basal angiosperms (Thien et al., 1983; Dilcher, 2000; Labandeira, 2005). However, in the ANITA-grade, taxa in the first diverging lineage (*A. trichopoda*) and third-diverging lineage (Austrobaileyales) possess a dry-type stigma (Heslop-Harrison and Heslop-Harrison, 1970; Mattsson et al., 1974; Heslop-Harrison and Shivanna, 1977; Lloyd and Wells, 1992; Dickinson, 1995; Lyew et al., 2007), that rarely produces secretions. While the stigmas of many species in the Nymphaeaceae secrete copious amounts of stigmatic fluid, these secretions usually drown and/or wash pollen off insects (Table 1) without serving as a nutritive source.

When droplets are produced in the dry-type stigma of *A. trichopoda*, the underlying cuticle is not ruptured (Thien et al., 2003). The dry-type stigma in *Trimenia moorei* produces no nectar as an edible reward (Vogel, 1990, 1998; Bernhardt et al., 2003). In dry-type stigmas, the cuticle layer coats the stigmatic crest and other areas of the carpel, and in *K. longipedunculata* it varies in thickness (Hristova et al., 2005; Lyew et al., 2007).

In small flowers, presumably a wet-type stigma with free-flowing exudates would result in loss of pollen after pollination (pollen in flowing exudate) and in the actual consumption of the exudate (if pollen was present). These may be important factors, particularly in small fly-pollinated flowers with limited pollen production (efficiency of pollination). Flies are the dominant pollinators in most extant ANITA-grade plants studied to date. In *K. longipedunculata* and *henryi*, the only pollinator is only 1 mm in length (*Megommata* sp.), and size may be a factor because the insect might stick to the stigma.

Other key factors: Syncarpy—The fusion of carpels into a unified compound gynoecium is a key innovation and a dominant feature of plant evolution (Stebbins, 1974; Endress, 2001; Armbruster et al., 2002). In the angiosperms above the ANITA grade, 83% of extant species are syncarpous (Endress, 1982), and the condition arose repeatedly in various clades (Armbruster et al., 2002). The advantages of syncarpy include defense of developing seeds, adaptations for fruit dispersal, efficient placement of pollen, and male competition for ovules via the compitum and was first discussed by Endress (1982). In a modeling study of syncarpy in angiosperms, Armbruster et al. (2002) hypothesized the main advantage of syncarpy over apocarpy is to increase offspring quantity and quality. Furthermore, this advantage of syncarpy over apocarpy resulting in increased offspring persisted under conditions of marginal pollination but declined with an increase in pollination (Armbruster et al., 2002). However, offspring quality persisted over a wider range of conditions even under higher rates of pollination (Armbruster et al., 2002).

In the ANITA-grade plants, especially in the Austrobaileyales (Table 1), the extragynoecial compitum evolved in the apocarpous flowers (Fig. 1), allows male gametophytes access to more than one carpel, and the Armbruster et al. (2002) results help explain the importance of the extragynoecial compitum in the ANITA grade (especially with small flies carrying small amounts of pollen). The pooled liquid syndrome in the Nymphaeales is specialized (E. L. Schneider, Santa Barbara Botanic Garden, personal communication). In some species of *Nymphaea*, the pollen germinates in the liquid (pool), and theoretically any given germinated pollen grain could reach several carpels (a mixing bowl) and possibly could be considered an extragynoecial compitum. However, no studies of pollen tube growth relating to the extragynoecial compitum concept have been conducted in the Nymphaeales (E. L. Schneider, personal communication).

It should be noted that pollination and morphological studies of extant ANITA-grade plants have produced a detailed yet broad perspective of pollination and reproduction of plants forming the base of the flowering plant phylogenetic tree. Many of these evolutionary concepts correlate with the plant fossil record, suggesting similar modes of evolution prevailed in the first flowering plants. Studies of the ANITA-grade plants have generated many insights into the evolution of the flowering plants. As stated by Endress (2001, p. 1134), “We are lucky that not only a single clade but a grade consisting of two or three clades has been recognized as the basalmost part of angiosperms. Since this allows parsimony optimization of basal states on cladograms, it can be assumed that states found in more than one clade of the basal grade are likely to be pleisomorphic.”

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