

INVITED REVIEW

The evolution of bat pollination: a phylogenetic perspective

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- **Background** Most tropical and subtropical plants are biotically pollinated, and insects are the major pollinators. A small but ecologically and economically important group of plants classified in 28 orders, 67 families and about 528 species of angiosperms are pollinated by nectar-feeding bats. From a phylogenetic perspective this is a derived pollination mode involving a relatively large and energetically expensive pollinator. Here its ecological and evolutionary consequences are explored.
- **Scope and Conclusions** This review summarizes adaptations in bats and plants that facilitate this interaction and discusses the evolution of bat pollination from a plant phylogenetic perspective. Two families of bats contain specialized flower visitors, one in the Old World and one in the New World. Adaptation to pollination by bats has evolved independently many times from a variety of ancestral conditions, including insect-, bird- and non-volant mammal-pollination. Bat pollination predominates in very few families but is relatively common in certain angiosperm subfamilies and tribes. We propose that flower-visiting bats provide two important benefits to plants: they deposit large amounts of pollen and a variety of pollen genotypes on plant stigmas and, compared with many other pollinators, they are long-distance pollen dispersers. Bat pollination tends to occur in plants that occur in low densities and in lineages producing large flowers. In highly fragmented tropical habitats, nectar bats play an important role in maintaining the genetic continuity of plant populations and thus have considerable conservation value.

Key words: Angiosperms, nectar-feeding bats, plant phylogeny, pollen dispersal, pollination modes.

INTRODUCTION

The floral biology of angiosperms is dominated by biotic pollination, especially in the tropics where up to 99 % of species in some habitats are animal-pollinated (Bawa, 1990). Insects account for most of these interactions, and pollination by vertebrates is relatively uncommon. In a variety of lowland tropical forests, for example, pollination by birds and bats occurs in only 3–11 % of species (Devy and Davidar, 2003). Overall, bird pollination is more common than bat pollination both locally and globally and occurs in nearly 500 genera of plants; bat pollination occurs in approximately 250 genera (Sekercioglu, 2006). At least six families or subfamilies of tropical and subtropical birds are strongly adapted for nectar-feeding. By comparison, only two families of tropical bats contain flower-visitors, and morphologically specialized nectar-feeders are in the minority in both of these families (Fleming and Muchhala, 2008).

Compared with most insects, flower-visiting birds and bats are much larger, have greater energy requirements because of their endothermic metabolism, can carry larger pollen loads, are longer-lived and may be cognitively more sophisticated. Despite the potentially greater costs to plants to attract and reward these larger pollinators, the benefits of vertebrate pollination can be substantial, especially in habitats where insect activity is limited by harsh climatic conditions (e.g. on tropical mountains; Cruden, 1972). Positive aspects of vertebrate pollination include potentially more reliable visitation

and the ability to carry large pollen loads considerable distances. Compared with many insects, birds and bats are excellent in promoting outcrossing, and as a result, most vertebrate-pollinated plants have hermaphroditic breeding systems; very few are dioecious (Renner and Ricklefs, 1995).

This review focuses on the evolution of bat pollination in tropical and subtropical angiosperms. This is to address two fundamental evolutionary questions: what are the causes and what are the consequences of the evolution of this pollination method? Ancillary questions include: (1) how many times during angiosperm history and in what places has bat pollination evolved? (2) What are the phylogenetic consequences of bat pollination? How many higher level taxa (genera, tribes, subfamilies, families, etc.) have evolved in association with bat pollination? And (3) by what phylogenetic routes has bat pollination evolved? How often have bat-pollinated flowers evolved from insect-, bird-, or non-volant mammal-pollinated flowers? Before examining these questions, we provide a brief overview of flower-visiting bats and the basic characteristics of bat pollination. We then examine this pollination mode from a phylogenetic and biogeographical perspective for both plants and bats. Finally, we discuss the various evolutionary routes that have resulted in bat pollination.

FLOWER-VISITING BATS

Only two of the 18 currently recognized families of bats (Simmons, 2005) contain species that are morphologically specialized for nectar-feeding. We discount the

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Mystacinidae, which is endemic to New Zealand and contains one genus, *Mystacina*, that is known to visit terrestrial flowers (Lord, 1991), as being highly evolved for flower-visiting. Insectivory is by far the most common feeding mode in bats and is undoubtedly the ancestral feeding mode in the order Chiroptera (Simmons *et al.*, 2008). The two families that contain nectar-feeding bats (hereafter 'nectar bats') include Pteropodidae (Old World flying foxes and their relatives), which occurs throughout tropical and subtropical regions of Africa including Madagascar, Asia including Indonesia, Australia and Papua New Guinea, and Pacific islands, and Phyllostomidae (American leaf-nosed bats), which inhabits tropical and subtropical regions of the Americas. These two families occur in different suborders of Chiroptera (Yinpterochiroptera and Yangochiroptera for pteropodids and phyllostomids, respectively) and are only distantly related.

The Pteropodidae contains 43 genera and about 186 species (Simmons, 2005), of which only six genera and 15 species, originally grouped together in the subfamily Macroglossinae, are morphologically specialized for flower visiting (Andersen, 1912) (Appendix 1). Molecular phylogenies of bats (Jones *et al.*, 2005; Teeling *et al.*, 2005) suggest that this family is approximately 56 million years old and that its crown group dates from about 26–28 Ma. Its place of origin was tropical Asia (Teeling *et al.*, 2005). Giannini and Simmons' (2005) phylogenetic hypothesis of Pteropodidae implies that frugivory is its basal feeding mode (insectivory is virtually absent in the family) and that specialized nectarivory has evolved independently three times – twice in Asia/Australasia and once relatively recently in Africa – making the Macroglossinae paraphyletic (Kirsch and La Pointe, 1997). In addition to the morphologically specialized species, many primarily frugivorous taxa (e.g. *Pteropus*, *Cynopterus*, *Epomophorus*) are opportunistic flower visitors and pollinators (Baker and Harris, 1957; Ayensu, 1974; Marshall, 1985; Banack, 1998; Elangovan *et al.*, 2000; Campbell *et al.*, 2007) (Appendix 1). The Pteropodidae is unique among bats in that its members do not use ultrasonic echolocation for communication, orientation or foraging. Examples of specialized and opportunistic nectar-feeding pteropodids are shown in Fig. 1.

The New World flower-visiting counterparts of pteropodids are members of a monophyletic clade of Phyllostomidae containing the subfamilies Glossophaginae, Phyllostominae and Brachyphyllinae. We will call this clade 'glossophagines'. In contrast to pteropodids, phyllostomids are echolocating bats whose ancestral feeding mode was insectivory (Ferrarezzi and Gimenez, 1996). Both nectarivory and frugivory are derived feeding modes, and echolocation is used in addition to vision and olfaction to locate food (von Helversen and von Helversen, 1999). The glossophagine clade contains 16 genera and about 38 species (Simmons, 2005) (Appendix 1). The family Phyllostomidae is younger than the Pteropodidae and dates from 39 Ma (Jones *et al.*, 2005; Teeling *et al.*, 2005). Glossophagines are younger still and date from about 12 Ma (Davalos, 2004). In addition to the morphologically specialized glossophagines, a number of frugivorous or omnivorous phyllostomids are opportunistic flower-visitors (Appendix 1). Examples of specialized and opportunistic nectar-feeding phyllostomids are shown in Fig. 1.

As described in detail by Freeman (1995) and others, specialized nectar bats in the two families share a common set of morphological features. These include an elongated rostrum, dentition that is reduced in size and number of teeth, and a long tongue tipped with hair-like papillae which is used to collect nectar rapidly during brief flower visits. Despite sharing these morphological characteristics, pteropodids and phyllostomids differ in several important aspects that affect their interaction with flowers. First, glossophagine bats are significantly smaller than their pteropodid counterparts. Mean glossophagine mass is about 14 g (range 7.5–30 g) compared with 38 g (range 13.2–82.2 g) in pteropodids (Fleming and Muchhala, 2008). Second, the range of rostral and tongue lengths (relative to overall size) of phyllostomids is much greater than that of pteropodids (Muchhala, 2006a; Fleming and Muchhala, 2008). The glossophagine *Anoura fistulata* of the northern Andes, for instance, has the longest tongue (but not the longest rostrum) relative to its body length of any mammal (Muchhala, 2006a). Third, all glossophagine bats typically hover when visiting flowers whereas specialized pteropodids always land on flowers before feeding (Fig. 2). Visits to flowers by members of both families, however, are brief and usually last <2 s (e.g. Horner *et al.*, 1998; von Helversen and Winter, 2003; Srithongchuay *et al.*, 2008). Opportunistic flower visitors in both families are generally larger than specialized flower visitors (up to about 1000 g in pteropodids and 50 g in phyllostomids) and land on flowers rather than hover to feed (Fig. 2). In summary, New World specialized nectar bats are smaller in size with longer tongues and hover whereas their Old World counterparts are larger with shorter tongues and do not hover. Because of these differences, we might expect plants visited by specialized nectar-feeding phyllostomids to produce smaller flowers with smaller nectar volumes per flower than those visited by their pteropodid counterparts (von Helversen, 1993).

The taxonomic richness of flower-visiting bats in both hemispheres varies among regions and within regions with latitude, habitat and elevation (Fleming, 1993, 1995). At the regional level, generic richness, which is used as a surrogate for morphological diversity throughout this review, in Pteropodidae is 12 (including one genus of specialized nectarivore) in Africa, 14 (two) in mainland Asia, nine (two) in Papua New Guinea, five (two) in Australia, and 21 (four) in the islands of south-east Asia and the western Pacific for a total of about 186 species (Nowak, 1994; Simmons, 2005). Generic richness in plant-visiting phyllostomids is 23 (ten specialized) in South America, 21 (11) in Mexico and Central America, and 13 (five) in the West Indies for a total of about 108 species (Nowak, 1994; Simmons, 2005). At the local or community level, species richness in pteropodids averages 2.3 specialized nectar bats ($n = 4$ sites; range, 1–3) whereas it averages 4.4 specialized species in phyllostomids ($n = 14$ sites; range, 2–6; Fleming and Muchhala, 2008). In both families, the number of species of nectar bats per habitat declines steadily with an increase in elevation and includes only one or two species above 2000 m (Heaney *et al.*, 1989; Fleming *et al.*, 2005).

An analysis of community trends in phyllostomid nectar bats with a comparison with their avian analogues, hummingbirds (Fleming *et al.*, 2005), showed that (1) the highest species richness (S) in nectar bats occurs in lowland moist or wet tropical

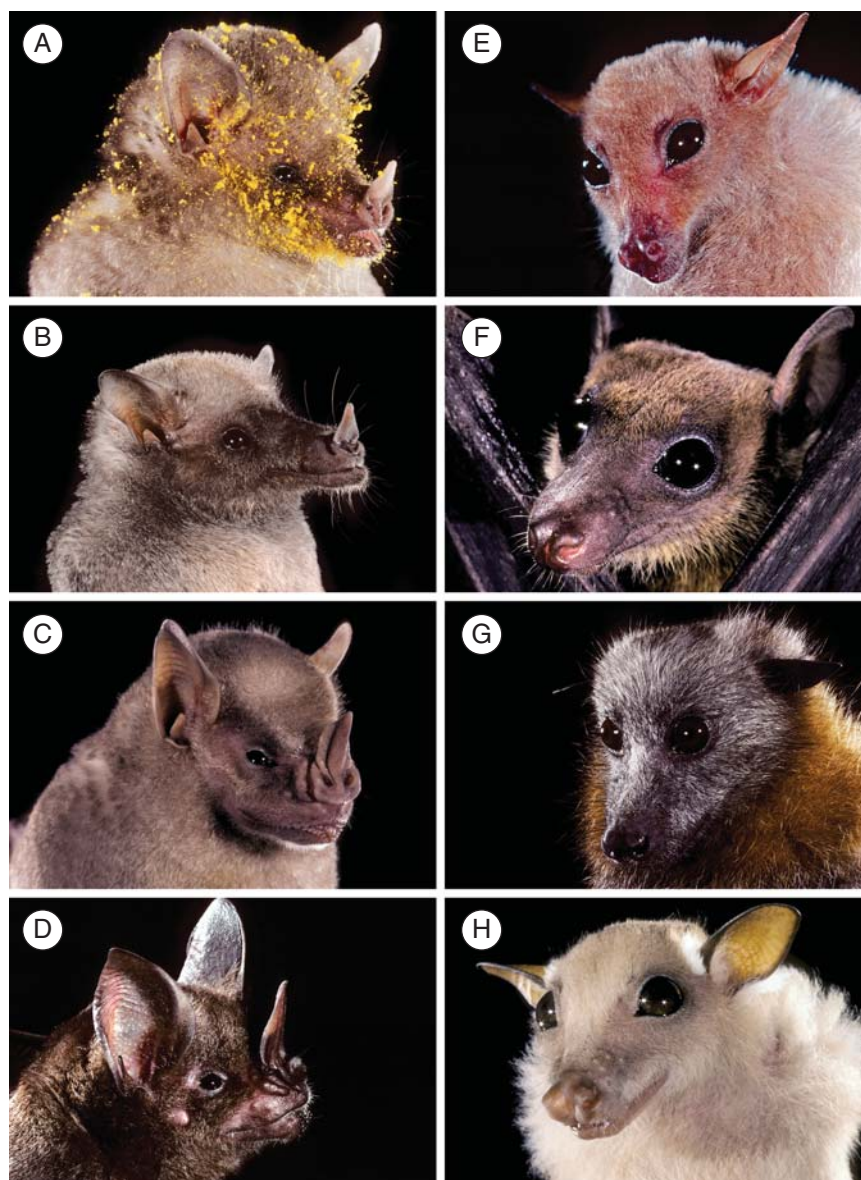


FIG. 1. Portraits of flower-visiting bats. Approximate body masses are in parentheses. (A) *Glossophaga soricina* (10 g), a basal glossophagine; (B) *Choeronycteris mexicana* (16 g), a derived glossophagine; (C) *Artibeus jamaicensis* (45 g) and (D) *Phyllostomus elongatus* (60 g), two opportunistic flower-visiting phyllostomids; (E) *Syconycteris australis* (20 g) and (F) *Eonycteris spelaea* (70 g), two specialized nectarivorous pteropodids; (G) *Pteropus poliocephalus* (750 g) and (H) *Epomophorus gambianus* (100 g), two opportunistic flower-visiting pteropodids. Photo credits: Merlin D. Tuttle, Bat Conservation International.

forests; (2) S increases asymptotically with rainfall with a plateau of about five species at annual rainfall levels of 2500 mm or more; (3) S in communities of both bats and hummingbirds changes seasonally as latitudinal and altitudinal migrants move into and away from particular habitats; (4) species of *Glossophaga* represent the ‘core’ residents in terms of abundance and year-round presence in lowland communities, and species of *Anoura* are ‘core’ residents in montane communities; (5) nectar bats are larger in mass and jaw length in dry habitats than in wet habitats; and (6) average jaw length in nectar bat communities is positively correlated with average corolla length of bat-pollinated flowers in that community – this implies that these bats are generalist (fine-grained) flower

visitors (compared with more specialized (coarse-grained) flower feeding in hummingbirds). Reflecting this last trend, it is common to find several different species of pollen on flower-visiting phyllostomids when captured at night or when pollen on stigmas is identified (e.g. Heithaus *et al.*, 1975; Muchhala *et al.*, 2009). A similar community-level analysis has not been made for pteropodid nectar bats and their Old World avian counterparts [e.g. sunbirds and honeyeaters; but see Fleming and Muchhala (2008) for a global analysis of the evolution of these vertebrates]. Based on their analysis, Fleming and Muchhala (2008) advocated a ‘three-world’ view concerning the evolution of vertebrate pollinators and their food plants – the Neotropics, Africa (including Madagascar) and

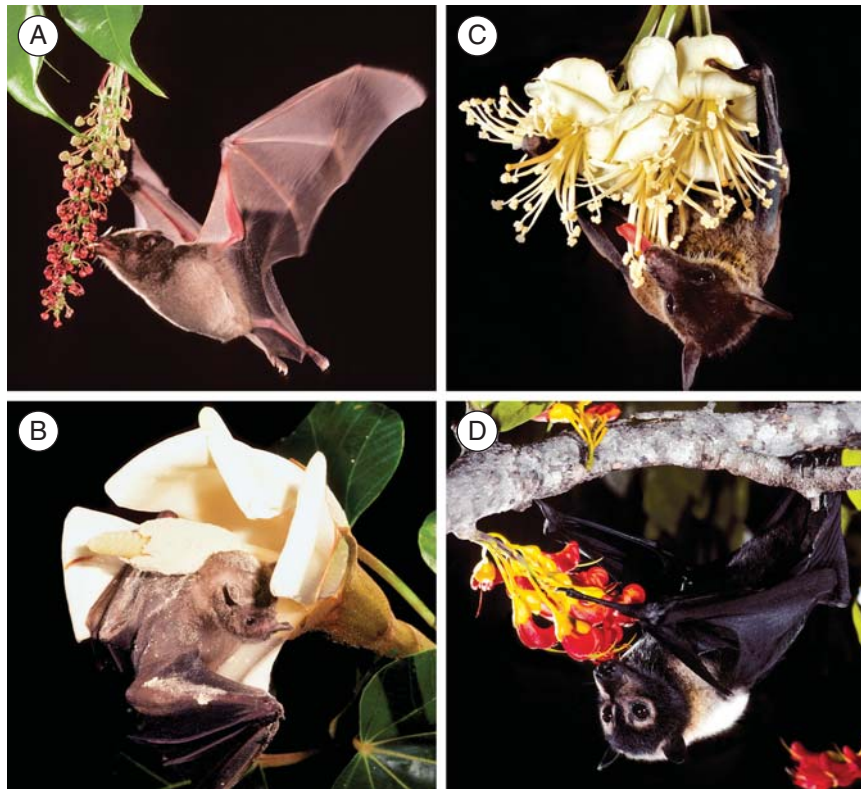


FIG. 2. Nectar-feeding bats visiting flowers. (A) *Glossophaga soricina* at flowers of *Mabea occidentalis* (Euphorbiaceae); (B) *Artibeus jamaicensis* on a flower of *Ochroma pyramidale* (Bombacaceae s.s.); (C) *Eonycteris spelaea* on flowers of *Durio zibethinus* (Bombacaceae s.s.); (D) *Pteropus conspicillatus* at flowers of *Castanospermum australe* (Fabaceae). Photo credits: Merlin D. Tuttle, Bat Conservation International.

Asia/Australasia – rather than a simple New World/Old World dichotomy. This trichotomy is more applicable to nectar-feeding birds than it is to bats, and we will deal only with a New World/Old World comparison in this review.

A particularly important result of the Fleming *et al.* (2005) study and one that was extended to Old World nectarivores as well as New and Old World avian and chiropteran frugivores by Fleming (2005) was the relationship between their species richness and that of their food plants. In the New World, S of both nectar-feeding and frugivorous bats and birds is positively correlated with S of their food plants. Although the intercepts of the regression lines for these relationships differed (higher in frugivores than in nectarivores), the slopes of the two regressions were the same (about 0.38) and indicated that for both groups, the ratio of plant species to animal species is 3 : 1. That is, it takes an average of three species of flowers or fruits to support one species of vertebrate nectarivore or frugivore. Fleming (2005) interpreted this relationship to indicate that resource S controls consumer S in New World nectarivores and frugivores. Interestingly, a similar correlation does not appear to exist in communities of Old World bat and bird nectar-feeders and fruit-eaters. In neither group did the regression coefficient differ from zero, which implies that consumer diversity is not (or is less likely to be) limited by flower or fruit resource diversity. This does not imply, however, that populations of these consumers are not food-limited. A review of data bearing on this issue clearly indicates that populations of vertebrate

nectarivores and frugivores throughout the tropics are often food-limited (T. H. Fleming and W. J. Kress, unpubl. res.).

Finally, species richness of bat-pollinated plants within New and Old World communities is generally similar, averaging 11.9 (range 4–33 species) in the New World and 16.8 (range 4–28) in the Old World (Fleming, 2005). The species richness values of nectar-feeding birds and their food plants are generally higher than those of bats except for Old World flowers in which, on average, bat plants slightly outnumber bird plants at the community level (Fleming, 2005).

BAT FLOWERS AND THE BASICS OF BAT POLLINATION

Bat flowers

Pollination biologists have long recognized a set of plant characteristics (syndromes) that are associated with different kinds of pollinators. The classic characteristics of bat-pollinated flowers (the ‘chiropterophilous syndrome’), as described by Faegri and van der Pijl (1979) and modified by Howe and Westley (1988), include nocturnal anthesis, drab coloration (i.e. white or green), musty smell, flowers often located on branches or tree trunks (cauliflory) or suspended on long stalks (flagelliflory), and tubular or radially symmetrical flowers, often of the ‘shaving brush’ type, that produce relatively large amounts of hexose-rich nectar. Dobat and

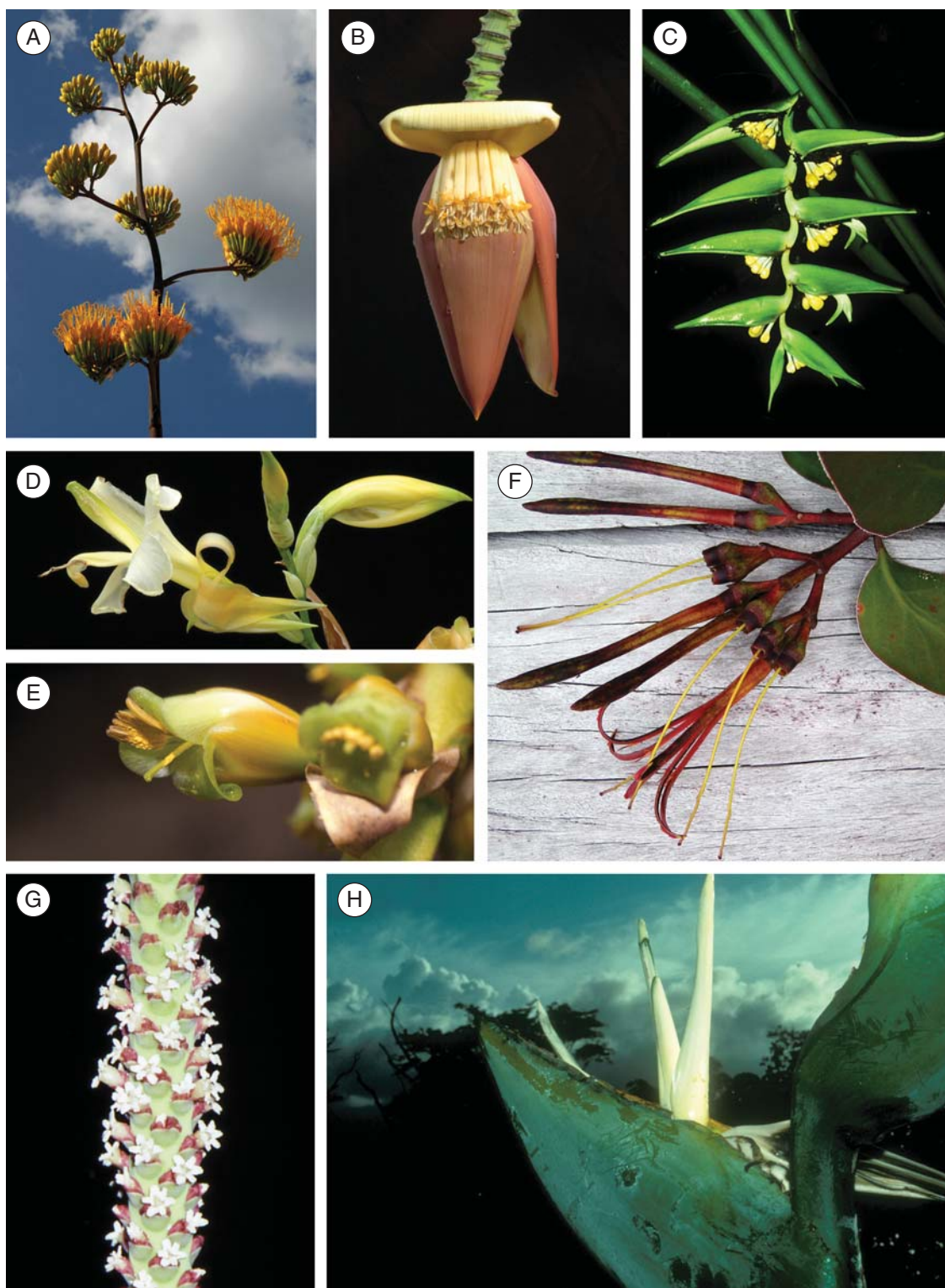


FIG. 3. Bat-pollinated flowers, corolla or perianth length (when known), and their pollinators. (A) *Agave palmeri* (Asparagales: Agavaceae), corolla tube 45–60 mm, glossophagine bats; (B) *Musa acuminata* (Zingiberales: Musaceae), perianth 70 mm, opportunistic and specialized pteropodid bats; (C) *Heliconia solomonensis* (Zingiberales: Heliconiaceae), perianth 45–75 mm, specialized pteropodid bats; (D) *Canna liliiflora* (Zingiberales: Cannaceae), glossophagine bats; (E) *Vriesia* sp. (Poales: Bromeliaceae), glossophagine bats; (F) *Psittacanthus acinarius* (Santalales: Loranthaceae), corolla 50–75 mm, glossophagine bats; (G) *Calyptrogyne ghiesbreghtiana* (Arecales: Arecaceae), rachilla 220 mm, opportunistic phyllostomid bats; (H) *Phenakospermum guyannense* (Zingiberales: Strelitziaceae), perianth up to 280 mm, opportunistic phyllostomid bats. Photo credits: T. Fleming (A), W. J. Kress (B–E, G, H), C. Geiselman (F).

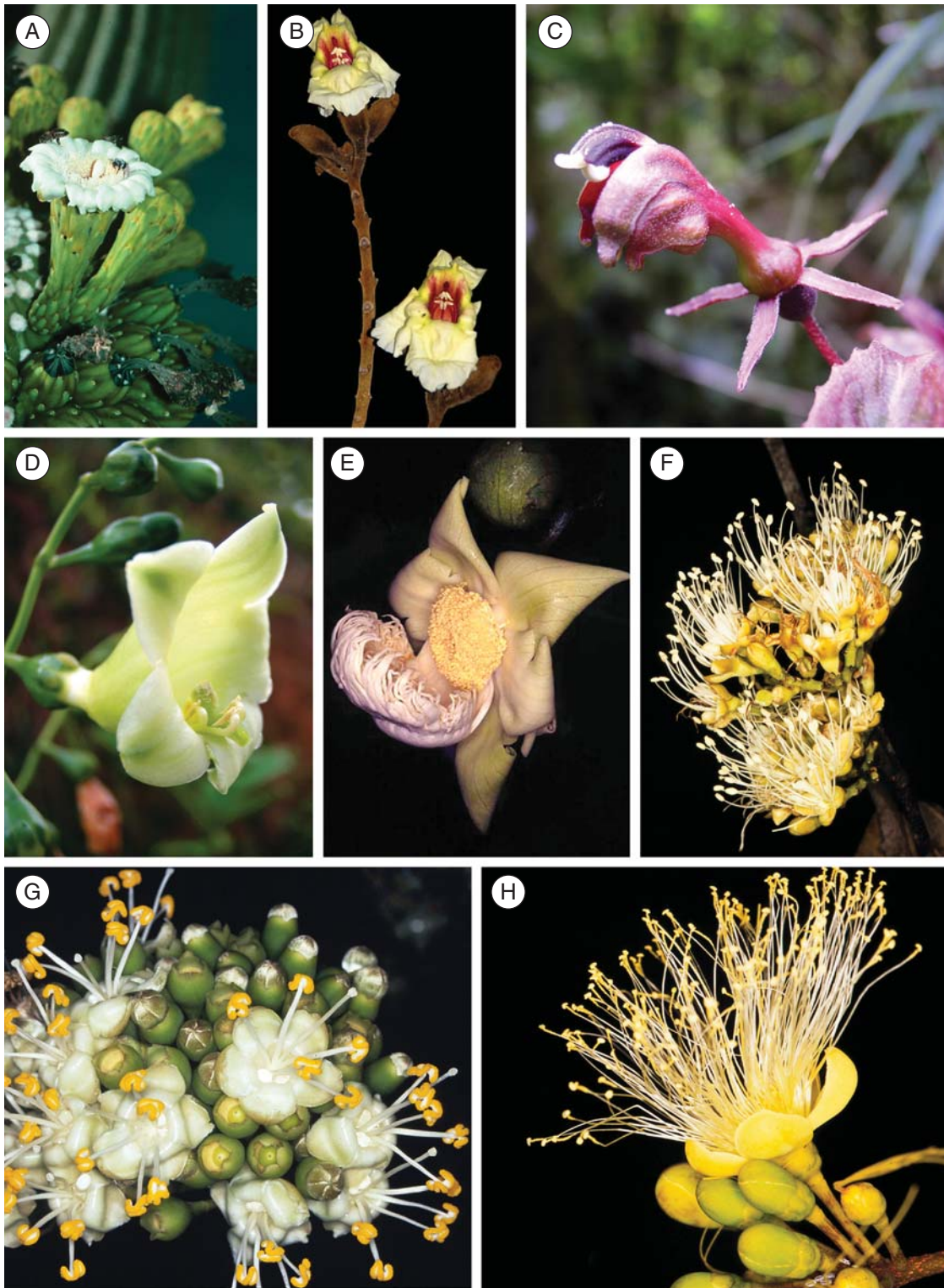


FIG. 4. Bat-pollinated flowers, their corolla or perianth length (when known), and their pollinators. (A) *Carnegiea gigantea* (Caryophyllales: Cactaceae), corolla 112 mm, opportunistic and specialized phyllostomid bats; (B) *Markhamia stipulata* (Lamiales: Bignoniaceae), specialized pteropodid bats; (C) *Burmeistera ceratocarpa* (Asterales: Campanulaceae), corolla 13.2 mm, glossophagine bats; (D) *Chelonanthus alatus* (Gentianales: Gentianaceae), corolla 30–45 mm, glossophagine bats; (E) *Lecythis poiteaui* (Ericales: Lecythidaceae), androecium 50 mm, glossophagine bats; (F) *Hymenaea courbaril* (Fabales: Fabaceae), flower diameter 25 mm, opportunistic and specialized phyllostomid bats; (G) *Ceiba pentandra* (Malvales: Malvaceae), flower diameter 25–35 mm, opportunistic and specialized phyllostomids and pteropodids; (H) *Caryocar glabrum* (Malpighiales: Caryocaraceae), flower diameter 40 mm, opportunistic and specialized phyllostomid bats. Photo credits: T. Fleming (A, B), C. Geiselman (D), S. Mori (E–H), N. Muchhala (C).

Peikert-Holle (1985) profusely illustrate these kinds of flowers, a few of which are shown in Figs 3 and 4.

Knowledge of the characteristics of bat flowers has increased substantially since the review by Faegri and van der Pijl (1979), and we now know that such traits as flower colour are far more variable among bat-pollinated flowers than previously thought (Figs 3 and 4). It remains true, however, that bat flowers occupy a distinct subset of multivariate floral morphological space compared with flowers pollinated by other kinds of animals (Ollerton *et al.*, 2009). Bats, like many other kinds of pollinators, can be opportunistic flower visitors and sometimes visit flowers that do not conform to the classic ‘bat pollination syndrome’ (e.g. bee flowers such as *Thunbergia grandiflora*, hummingbird-pollinated flowers such as *Calliandra laxa*, and hummingbird feeders; Lemke, 1985; T.H. Fleming, pers. obs.). Nonetheless, most kinds of flowers that they visit differ strongly from flowers visited by other kinds of pollinators. Hence, we agree with Fenster *et al.* (2004), among others, that the concept of pollination syndromes has considerable heuristic value and that it should be retained in the pollination literature.

Floral characteristics associated with bat pollination appear to have evolved to attract relatively large, nocturnal, colour-blind, volant pollinators. Advertising their presence with a musty, fetid odour is a common feature among bat flowers. For instance, sulphur-containing compounds, which give some bat flowers their characteristic odour, are uncommon in most floral aromas, but have been isolated multiple times from evolutionarily unrelated bat flowers in the Neotropics (Bestmann *et al.*, 1997; von Helversen *et al.*, 2000). The colour of bat flowers ranges from white, brown and green to pink, fuchsia and yellow (Winter and von Helversen, 2001; von Helversen and Winter, 2003). Although white or light-coloured flowers appear to stand out against foliage or the night sky (Hopkins, 1986), many bat flowers are quite dull in colour, which may function more as a camouflage from other visitors than as a visual cue to bats (Knudsen *et al.*, 2006). Some of this variation may reflect the pollination syndrome from which bat-pollinated species evolved (e.g. red from bird-pollinated and white or yellow from moth-pollinated species; Tripp and Manos, 2008). Finally, some floral advertisements are clearly directed at echolocating bats. The best example is the virgin flower of *Mucuna holtonii* (Fabaceae), which offers an average of five times more nectar than one that has already been visited. These flowers indicate their status by returning echoes over an increased angle of reflectance to echolocating bats (von Helversen and von Helversen, 1999). Bats seem to associate the echoes of virgin flowers with their larger rewards and, when given a choice, were found to visit them significantly more often than opened flowers (von Helversen and Winter, 2003).

While odour, colour and echoes signal the presence of a bat flower, it is ultimately the nutritional reward, including nectar, pollen and edible plant tissues [e.g. in *Freyinetia insignis* (Pandanaeae) and *Calypstrogyne ghiesbreghtiana* (Arecaceae)], that entices bats to visit flowers (van der Pijl, 1956; Gould, 1978; Cunningham, 1995a). In many cases, bat flowers are visited for their nectar and only indirectly for pollen, which is later groomed off the fur following multiple flower visits. Certain glossophagines (e.g. *Anoura geoffroyi*, *Leptonycteris curasoae*) and the pteropodid *Syconycteris*

australis, however, are known to consume and digest the contents of pollen grains, and it is likely that other nectar bats also have this ability (Howell, 1974; Law, 1992; Herrera and Martínez del Río, 1998). In general, chiropterophilous flowers produce more nectar than those in any other syndrome, although the amount varies greatly between species from as little as 10 μ L to as much as 15 mL per flower per night (van der Pijl, 1961; Cruden *et al.*, 1983; Winter and von Helversen, 2001). Plants pollinated by hovering glossophagines, however, can satisfy their pollinators with smaller rewards due to their pollinators’ size and energetic efficiencies in flower detection and acquisition (von Helversen, 1993). In contrast to the large amount produced, most nectar from bat flowers is rather dilute with sugar concentrations ranging from 5 to 29% (von Helversen, 1993). Both nectar amount and its sugar concentration appear to play a role in attracting or deterring bat visits to flowers (Gould, 1978; Sazima and Sazima, 1987). For example, Gottsberger and Silberbauer-Gottsberger (2006) suggested that *Luehea grandiflora* (Malvaceae) is visited exclusively by glossophagines in the cerrado region of Brazil not because it physically excludes opportunistic bats, but because its nectar supply may be insufficient to attract larger bats. In addition to nectar amount and concentration, energy savings associated with the ease in locating and handling conspicuous flowers also factor into determining the net reward of visitation (Heinrich, 1975; Winter and von Helversen, 2001).

Olfactory and visual cues and rewards are responsible for attracting bats to flowers, but it is the flower’s size, shape and durability, its placement on the plant, and time of anthesis that determine whether a bat has access to it and can affect pollination. Compared with many insect- or bird-pollinated flowers (but not hawkmoth flowers), bat-pollinated flowers are often relatively large and robust. The original bat pollination syndrome was based on plants pollinated by large, non-hovering pteropodids and applies less widely to New World plants pollinated by hovering phyllostomids (von Helversen, 1993; von Helversen and Winter, 2003). These plants tend to produce smaller and more delicately built flowers than those visited by pteropodids or opportunistic nectar-feeding phyllostomids (Figs 2–4).

Bat flowers/inflorescences can be roughly divided into three categories based on their shape: (1) ‘shaving-brush’ or ‘stamen ball’ with many projecting stamens (e.g. *Bombax*, *Capparis*, *Eugenia*, *Parkia*); (2) ‘bell-shaped’ with the corolla forming a tube (e.g. *Bauhinia*, *Musa*, *Vriesea*); and (3) ‘cup-shaped’ with an open corolla (e.g. *Carnegiea*, *Caryocar*, *Ceiba*, *Ipomoea*, *Ochroma*) (Baker, 1973; Salas, 1973; von Helversen, 1993; Figs 3 and 4). Similarly, flower shape shows different trends associated with bat visitors. Flowers visited by specialized nectar-feeding phyllostomids are more likely to be tubular in shape and produced by epiphytes and shrubs while flowers visited by pteropodids tend to be produced by trees and of the ‘shaving brush’ type (Fleming and Muchhala, 2008).

Of the five flower characteristics limiting or allowing bat access to flowers, only two appear to be universal or nearly so for all bat flowers. The first is flower/inflorescence placement away from foliage, such as projecting above or below the canopy, emerging from branches or trunk, or borne on deciduous trees after they have dropped their leaves (van der Pijl,

1941, 1956, 1961) (Figs 3 and 4). Both visually orientating and echolocating bats benefit from this arrangement as it allows them easily to find, approach and depart from flowers (von Helversen, 1993). Nocturnal anthesis, the opening of flower buds in the late afternoon or at night, is the second characteristic. The flowers of many bat-pollinated plants open early in the evening and are viable for only one night (Faegri and van der Pijl, 1979). Exceptions include flowers of *Passiflora mucronata*, which do not open until after midnight, and those of *Burmeistera*, which remain open for up to 3 d (Sazima and Sazima, 1978; Muchhala, 2006b). Together, flower placement away from foliage and nocturnal anthesis are the unifying features of the bat pollination syndrome while all other characteristics discussed above, which provide cues and incentives to entice visitation, vary among bat-pollinated species.

Whether or not they are common among all bat flowers or were selected for by bats, many floral characteristics seem to make flowers easier for bats to find as they mirror the sensory abilities of their pollinators. Both pteropodid and phyllostomid bats use a variety of sensory modes, including vision, olfaction and echolocation (phyllostomids only), to locate flowers. Both groups of plant-visiting bats have keen senses of smell and appear to use olfaction for long-distance detection of flowers (Marshall, 1983; von Helversen, 1993). Phyllostomid and pteropodid nectarivores, however, diverge in the chemical components to which they seem most attracted. In captive studies, glossophagines responded most strongly to aromas dominated by dimethyl sulphides while the pteropodid *Cynopterus sphinx* appeared to be more attracted to aromas containing ethyl acetate (von Helversen *et al.*, 2000; Elangovan *et al.*, 2006).

Members of these two families of bats rely on their vision to navigate, communicate with roostmates, detect predators and locate food (Suthers, 1970). Pteropodids, which lack the ability to echolocate (except crudely in *Rousettus*), depend entirely on vision to negotiate their environment and appear to do so quite well even in inclement weather and on moonless nights (Gould, 1978). Visually orientating bats seem capable of discerning white flowers against the dark backdrop of foliage or the night sky (Winter and von Helversen, 2001). Some species of glossophagines appear to recognize patterns, and *Glossophaga soricina* has been shown to detect ultraviolet radiation, which may enable it to locate ultraviolet-reflecting flowers (Suthers, 1970; Winter and von Helversen, 2001; Winter *et al.*, 2003). In addition to sight, nectar-feeding phyllostomids use 'whispering' (low-intensity) echolocation that allows them to navigate in cluttered environments where many of their food plants occur (Winter and von Helversen, 2001). Both flower-visiting pteropodids and phyllostomids undoubtedly rely on their excellent spatial memories to relocate plants they have visited previously, although this ability has only been examined experimentally in glossophagines (Winter and Stich, 2005). This ability probably allows them to minimize search costs, especially when feeding on plants with extended, or 'steady-state' (*sensu* Gentry, 1974), blooming periods (Tschapka and von Helversen, 2007).

Bat roosting and foraging

The roosting and foraging behavior of nectar-feeding bats can affect their interactions with plants and flowers in

a variety of ways. Because they lack the ability to echolocate, most pteropodids roost either gregariously in the foliage of canopy trees or solitarily in understory vegetation rather than in dark caves. Two exceptions are the specialized nectar bat *Eonycteris spelaea*, which roosts in caves in colonies of a few dozen to thousands of individuals in Malaysia (Start and Marshall, 1976), and *Notopterus macdonaldi* of New Caledonia, the Hebrides and Fiji, which forms small colonies in caves. Gregarious bats, including canopy-roosting species of *Pteropus* and *Eidolon* which sometimes live in colonies of hundreds of thousands of bats, and cave-roosting species such as *Eonycteris* forage as much as 50 km away from their day roosts and are potentially long-distance pollen carriers (Gould, 1978; Marshall, 1985). Solitary roosting pteropodids, such as species of *Syconycteris* and *Macroglossus* in Australasia, forage much closer (i.e. hundreds of metres to a few kilometres) to their day roosts and hence are likely to be shorter-distance pollen carriers (Law, 1993; Law and Lean, 1999).

Territorial feeding behaviour, which can strongly limit the distance that pollen moves (e.g. in territorial hummingbirds; Linhart, 1973; Linhart *et al.*, 1987), is known to occur in both gregarious and solitary pteropodids. For example, adult males of *Syconycteris australis* defend feeding territories against juvenile males and females when feeding at *Banksia* flowers in south-eastern Australia (Law, 1996); this probably results in sex- and age-biased pollen movement patterns in this species, but data to support this suggestion are not yet available. Males of *Macroglossus minimus* and *Melonycteris melanops* are thought to defend resource plants against other males (Winkelmann *et al.*, 2003; Bonaccorso *et al.*, 2005). More dramatically, adults of various species of *Pteropus* in Australia and elsewhere set up small feeding territories in the canopies of flowering (and fruiting) trees which they defend against socially subordinate, usually younger, individuals. If allowed to visit flowers, subordinates are more likely to move pollen (and seeds) further away from parent plants than the territory-holders (Richards, 1995; McConkey and Drake, 2006).

In contrast to pteropodids, most flower-visiting phyllostomids roost in relatively small colonies of a few dozen to hundreds of individuals in caves. An exception to this is the migratory bat *Leptonycteris curasoae* (= *yerbabuena*), which lives in large colonies of tens of thousands of individuals in arid and semi-arid parts of Mexico and south-western Arizona. The foraging radius of these colonies can be 30–50 km, and these bats are excellent long-distance pollen movers (Horner *et al.*, 1998; Fleming, 2004). Also in contrast to pteropodids, territorial defence of flowers appears to be uncommon in phyllostomid bats. Instead, like hermit hummingbirds, many species are thought to be trap-liners that each night visit a series of widely spaced flowers, often in the canopy of wet tropical forests (Baker, 1973; Heithaus *et al.*, 1974; Lemke, 1984; Tschapka, 2004). Together, their spatial memory and trapline foraging behaviour enable glossophagines to exploit floral resources that have temporally dynamic availability in spatially predictable feeding sites (Baker, 1973; Gould, 1978; Fleming, 1982; Lemke, 1984, 1985; von Helversen, 1993; Winter and von Helversen, 2001). This behaviour probably results in substantial pollen

movement among plants. For instance, Dick *et al.* (2008) reported that pollen moved about 18 km between individuals in the bat-pollinated *Ceiba pentandra* in Brazilian riverine forest habitat. Among arid-zone columnar cacti, between-population genetic structure, as indicated by Wright's F_{st} index, is lower in bat-pollinated taxa than in insect-pollinated taxa, which implies that bat-mediated gene flow is greater than that mediated by insects (Hamrick *et al.*, 2002). Similarly, low levels of genetic subdivision occur in *Phenakospermum guyanense* (Strelitziaceae), a widespread bat-pollinated Amazonian megaherb (Roesel *et al.*, 1996).

PHYLOGENETIC AND GEOGRAPHICAL DISTRIBUTIONS OF BAT POLLINATION

Phylogenetic distributions

In their review of vertebrate pollination, Fleming and Muchhala (2008, based on data in Dobat and Peikert-Holle, 1985) reported that bat pollination occurs in 58 families of plants in about 24 orders; 43 families contain flowers visited by phyllostomids and 28 by pteropodids. Thirteen of the 58 plant families (28%) are visited by both families of bats. A more complete update of this earlier report (Geiselman *et al.*, 2004, and onwards) indicates that phyllostomids visit 360 species of plants in 159 genera from 44 families; our literature review indicates that pteropodids visit 168 species of plants in 100 genera from 41 families. In total, bat-pollinated plants are found in 67 families in 28 orders of angiosperms (Table 1). Of these families, 26 are exclusively visited by phyllostomids and 23 are exclusively visited by pteropodids; 18 families are visited by both families of bats. Lists of known bat-pollinated species, by family, in the New and Old World are provided in Appendices 2 and 3. In compiling these lists we have attempted to include only those taxa known or strongly suspected to be pollinated by bats. As is the case in much of the pollination literature, however, actual proof of effective pollination by bats is available for only a subset of these taxa.

To examine the evolution of bat pollination from a plant phylogenetic perspective, we mapped 66 of the 67 plant families in Table 1 on a phylogeny organized according to now widely accepted angiosperm relationships (Soltis *et al.*, 2005: appendix; T. H. Fleming and W. F. Kress, unpubl. res.). Only Capparaceae is missing from this phylogeny. For ease of analysis we divided the angiosperm plant families into five major groups, namely basal angiosperms, monocots, basal eudicots, rosids and asterids (Soltis *et al.*, 2005). As van der Pijl (1961) and others have noted, bat pollination is most common in advanced lineages of angiosperms, i.e. in advanced monocots and in the rosids (Fig. 5). Our analysis shows that the distribution of bat-pollinated species at the family level (hereafter referred to simply as 'bat families') is distinctly uneven among the five groups and varies from 6–7% of all families in basal angiosperms and basal eudicots to 17–22% in monocots, rosids and asterids. The average number of genera of bat-pollinated plants per family also varies in these groups (although the differences are not quite statistically significant), but in a different pattern. Few families in the basal eudicots contain bat-pollinated taxa, but in those

families where bat-pollination occurs, it is relatively common. The mean number of bat-pollinated genera per family (median, 1 s.d.) are: basal angiosperms, 1.0 (1.0, 0); monocots, 2.3 (1.0, 2.2); basal eudicots, 8.3 (3.5, 10.5); rosids, 3.9 (1.0, 7.1); and asterids, 3.9 (3.0, 3.4) (Kruskal–Wallis ANOVA based on medians, $W = 8.99$, d.f. = 4, $P = 0.061$). Families with the highest number of bat-pollinated genera include Fabaceae (30 genera, rosids), Cactaceae (24, basal eudicots), Malvaceae (25, rosids) and Bignoniaceae (15, asterids). The number of bat-pollinated genera in two of the three largest groups of angiosperms is correlated with the number of genera per family. Significant positive correlations occur in rosids ($y = -0.38 + 0.045x$, $P < 0.01$) and monocots ($y = 1.45 + 0.035x$, $P < 0.01$), but not in asterids, even after the Asteraceae is removed from the analysis (because of its exceptionally large number of genera) ($y = 3.52 + 0.003x$, $P > 0.50$). Regression coefficients (slopes) were similar in rosids and monocots (about 0.040), and their reciprocal values indicate that about one in every 25 genera in those groups contains a bat-pollinated species.

The proportion of total genera in a family that contains one or more bat-pollinated species varied substantially among the 67 families (Table 1). On average, 15% (range 0.2–100%) of genera in these families contained bat-pollinated species, and the average varied significantly among the five major groups (Kruskal–Wallis ANOVA based on medians, $W = 20.28$, d.f. = 4, $P < 0.001$): basal angiosperms, 1.4% (median 1.4%, 1 s.d. 0.8%); monocots, 44.1% (25.0%, 40.6%); basal eudicots, 9.4% (5.9%, 8.2%); rosids, 9.1% (4.7%, 11.0%) and asterids, 6.4% (4.6%, 7.7%). Ten of the 67 plant families had at least 25% of their genera with one or more bat-pollinated species. These families were concentrated in the monocots, in which seven of 13 families (54%) contained relatively high proportions of bat-pollinated genera. All of these families are small and contain a total of seven or fewer genera (Table 1).

To take into account any phylogenetic bias in these analyses, we mapped the occurrence of bat pollination by order and family within each of the five major groups using Mesquite (version 2.0; Maddison and Maddison, 2007). The number of independent origins of bat pollination in each group at the ordinal and family levels was analysed with the character analysis by parsimony module. By 'independent origin' we mean that the sister-taxon of a bat-pollinated family contained no bat-pollinated species. The converse of 'independent origin' (i.e. non-independent origin) reflects phylogenetic clustering, or the tendency of related groups to contain bat-pollinated taxa. At the ordinal level, bat pollination has originated independently in about half of the orders in which it occurs (14 of 28 orders; Table 2, Fig. 5). At the family level, bat pollination has originated independently in about 77% of the families in which it occurs (i.e. 51 of 66 families; Table 2).

The distribution of bat-pollinated taxa visited by phyllostomids and pteropodids differs at both the ordinal and the family level. Of the 28 orders containing bat families, only eight (29%) contain taxa pollinated by both groups of bats (Table 1, Fig. 5). These orders include Arecales and Zingiberales (monocots); Santalales (basal eudicots); Fabales, Malvales and Myrtales (rosids); and Ericales and

TABLE 1. Summary of families of angiosperms known to produce flowers visited by New World (NW) and Old World (OW) bats

Lineage	Order	Family	Distribution	Total genera	Total species	NW genera	NW spp	OW genera	OW spp.	Total bat genera	Proportion total genera	
Basal angiosperms	Laurales	Lauraceae	Pantropical	50	2500	0	0	1	1	1	0.020	
Monocots	Magnoliales	Annonaceae	Pantropical	129	2220	0	0	1	1	1	0.008	
	Arecales	Arecaceae	Pantropical	189	2361	3	3	4	4	7	0.037	
	Asparagales	Agavaceae	Pantropical	23	637	3	17	0	0	3	0.130	
		Amaryllidaceae	Pantropical	11	146	2	2	0	0	2	0.182	
		Asphodelaceae	Paleotropical	15	785	0	0	1	1	1	0.067	
		Asteliaceae	Southern Hemisphere	4	36	0	0	1	1	1	0.250	
		Xanthorrhoeaceae	Austral	1	30	0	0	1	1	1	1.000	
	Pandanales	Pandanaceae	Paleotropical	4	885	0	0	2	4	2	0.500	
		Velloziaceae	Pantropical	9	240	1	1	0	0	1	0.111	
	Poales	Bromeliaceae	Neotropical	57	1400	6	21	0	0	6	0.105	
	Zingiberales	Cannaceae	Neotropical	1	19	1	1	0	0	1	1.000	
		Heliconiaceae	Neotropical + Pacific	1	150	0	0	1	3	1	1.000	
		Musaceae	Paleotropical	2	35	0	0	2	8	2	1.000	
		Strelitziaceae	Pantropical	3	7	1	1	0	0	1	0.333	
	Basal eudicot	Caryophyllales	Cactaceae	Neotropical	111	1500	26	43	0	0	26	0.234
			Nyctaginaceae	Pantropical	30	395	2	2	0	0	2	0.067
		Proteales	Proteaceae	Pantropical	80	1600	1	1	3	7	4	0.050
Rosid	Santalales	Loranthaceae	Pantropical	68	950	1	1	2	2	3	0.044	
	Brassicales	Capparaceae	Pantropical	16	480	3	8	0	0	3	0.188	
		Salvadoraceae	Paleotropical	3	11	0	0	1	1	1	0.333	
	Celastrales	Celastraceae	Cosmopolitan	89	1300	0	0	1	1	1	0.011	
	Cucurbitales	Cucurbitaceae	Pantropical	118	845	4	5	0	0	4	0.034	
	Fabales	Fabaceae	Cosmopolitan	730	19400	22	59	11	26	29	0.040	
	Geraniales	Geraniaceae	Cosmopolitan	7	805	1	1	0	0	1	0.143	
	Malpighiales	Caryocaraceae	Neotropical	2	21	1	5	0	0	1	0.500	
		Chrysobalanaceae	Pantropical	17	460	2	3	1	3	3	0.176	
		Clusiaceae	Cosmopolitan	27	1050	0	0	1	1	1	0.037	
		Euphorbiaceae	Cosmopolitan	218	5735	3	3	2	2	5	0.023	
		Passifloraceae	Pantropical	16	705	1	5	0	0	1	0.063	
		Rhizophoraceae	Pantropical	16	149	0	0	1	1	1	0.063	
		Salicaceae	Cosmopolitan	55	1010	1	1	1	1	2	0.036	
		Malvales	Malvaceae	Cosmopolitan	243	4225	18	41	7	16	24	0.099
		Myrtales	Combretaceae	Pantropical	14	500	1	1	1	1	2	0.143
			Lythraceae	Cosmopolitan	31	620	1	7	2	4	3	0.097
			Melastomataceae	Pantropical	182	4570	2	2	0	0	2	0.011
			Myrtaceae	Pantropical	131	4620	0	0	8	27	8	0.061
			Onagraceae	Cosmopolitan	22	656	1	1	0	0	1	0.045
	Vochysiaceae		Neotropical, African	7	190	1	1	0	0	1	0.143	
	Oxalidales		Elaeocarpaceae	Pantropical	12	605	0	0	1	3	1	0.083
	Rosales		Moraceae	Pantropical	38	1100	0	0	1	1	1	0.026
			Rhamnaceae	Cosmopolitan	52	925	0	0	1	1	1	0.019
			Rosaceae	Cosmopolitan	90	2520	0	0	1	1	1	0.011
	Sapindales	Anacardiaceae	Pantropical	70	600	0	0	1	1	1	0.014	
		Meliaceae	Pantropical	52	621	0	0	2	2	2	0.038	
Sapindaceae		Pantropical	135	1580	1	1	2	2	3	0.022		
Asterid	Apiales	Araliaceae	Pantropical	43	1450	0	0	1	1	1	0.023	
	Asterales	Asteraceae	Cosmopolitan	1620	23600	3	3	0	0	3	0.002	
		Campanulaceae	Cosmopolitan	84	2380	3	20	1	1	4	0.048	
	Ericales	Ericaceae	Cosmopolitan	126	3995	1	1	0	0	1	0.008	

	Lecythidaceae	Pantropical	25	310	1	3	5	6	0.240
	Marcgraviaceae	Neotropical	7	130	3	17	0	3	0.429
	Polemoniaceae	NW + Eurasia	18	385	1	4	0	1	0.056
	Sapotaceae	Pantropical	53	1100	0	0	7	7	0.132
	Apocynaceae	Cosmopolitan	415	4555	0	0	3	3	0.007
	Gentianaceae	Pantropical	87	1655	4	8	0	4	0.046
	Loganiaceae	Pantropical	13	420	0	0	1	1	0.077
	Rubiaceae	Cosmopolitan	660	11150	3	3	3	6	0.009
	Acanthaceae	Pantropical	229	3500	4	7	1	5	0.022
	Bignoniaceae	Pantropical	110	800	6	14	10	16	0.146
	Gesneriaceae	Pantropical	147	3200	6	20	0	6	0.041
	Lamiaceae	Cosmopolitan	236	7173	2	2	0	2	0.008
	Scrophulariaceae	Cosmopolitan	65	1700	1	1	0	1	0.015
	Verbenaceae	Pantropical	34	1175	2	2	0	2	0.059
	Convolvulaceae	Cosmopolitan	57	1625	1	4	2	3	0.053
	Solanaceae	Cosmopolitan	102	2460	7	13	1	8	0.078
	Boraginaceae	Cosmopolitan	148	2740	1	2	0	1	0.007
		TOTAL			159	360	100	168	

For each family the data include: (1) distribution by major plant lineage and order; (2) geographical distribution; (3) total number of genera and species; (4) number of genera and species pollinated by NW or OW bats; and (5) total number of bat-pollinated genera and proportion of total genera per family that are bat-pollinated. Also indicated in bold type are families that occur on islands that contain bat-pollinated genera and species. Sources of data: major angiosperm lineages from Soltis et al. (2005); the basic list of families and number of New World bat-pollinated genera and species from Geiselman et al. (2004 and onwards); the basic list of families and number of Old World bat-pollinated genera and species comes from numerous literature sources available upon request from the authors; total number of genera and species per family from APG II (2002 and onwards); island bat families from Silva Taboada (1979), Mickleburgh et al. (1992), Gannon et al. (2005) and Marten-Rodriguez et al. (2009).

Gentianales (asterids). Similarly, as indicated above, only 18 of 67 families (27%) with bat-pollinated taxa have representatives in both hemispheres. We estimate that bat pollination has evolved independently in about 85% of these families (Table 3) and is clustered in three families of the Myrtales (Combretaceae, Lythraceae and Onagraceae), although phyllostomid bats are generally minor pollinators in these families (Table 1). Overall, pteropodid and phyllostomid bats basically interact with different orders and families of plants. Rather than being constrained at deep phylogenetic levels such as orders, these interactions have evolved independently many times in different Old and New World plant lineages.

Within each hemisphere bat-pollinated genera can be further subdivided into those visited by specialized or opportunistic nectar-feeding bats. A majority of the 159 genera with bat-pollinated species in the New World have been reported to be visited only by specialized nectar-feeding bats. Species in only 20 genera (13%) have been reported to be visited by opportunistic nectar-feeding phyllostomids. These genera are found in eight families in seven orders and occur in monocots (Arecales, Zingiberales), basal eudicots (Caryophyllales) and asterids (Lamiales); over half of these genera are rosids (Fabales, Malpighiales, Malvales). Opportunistic nectarivores, which land on flowers, are thought to be the main pollinators of species in only four (2.5%) of these genera (*Calypstrogyne ghesbreghtiana*, *Ochroma pyramidale*, *Parkia* spp. and *Phenakospermum guyanense*). In contrast, in the Old World only species in eight genera (8%) from six families (Heliconiaceae, Musaceae, Lythraceae, Myrtaceae, Moraceae and Bignoniaceae) have been reported to be visited solely by specialized nectarivorous bats. These are found among monocots (Zingiberales), rosids (Myrtales, Rosales) and asterids (Lamiales). The remaining 92 genera are visited either by both specialized and opportunistic nectar bats or only by opportunistic nectarivores. Thus, New World bat plants have evolved primarily with specialized nectar feeders whereas Old World bat plants have evolved mostly with opportunistic nectarivores.

It is important to note that analyses conducted at the ordinal and family levels are very ‘coarse’ and should not be interpreted to imply that bat pollination is ancestral in any order or family of angiosperms. As discussed below, the most insightful level of independence in the evolution of bat pollination is at the generic or species level. Bat pollination has seldom evolved at the tribal, subfamily or family level. Phylogenetic clustering (non-independence) at the ordinal and family levels simply indicates that bat pollination shows a tendency to occur in related higher-level taxa. The fact that bat pollination has rarely evolved at higher taxonomic levels (see below) emphasizes the relative recency of this mode of pollination.

Biogeographical, elevational and habitat distributions

Fifty-three of the 67 bat-pollinated families (79%) are either pantropical or cosmopolitan in distribution (Table 1). Seven of the remaining 14 families are endemic to the Neotropics and three are endemic to the Palearctics. Of the 26 ‘exclusive’ phyllostomid families, 19 (73%) have pantropical or cosmopolitan distributions, and the other seven are New World endemics. Similarly, 17 of 23 ‘exclusive’ pteropodid

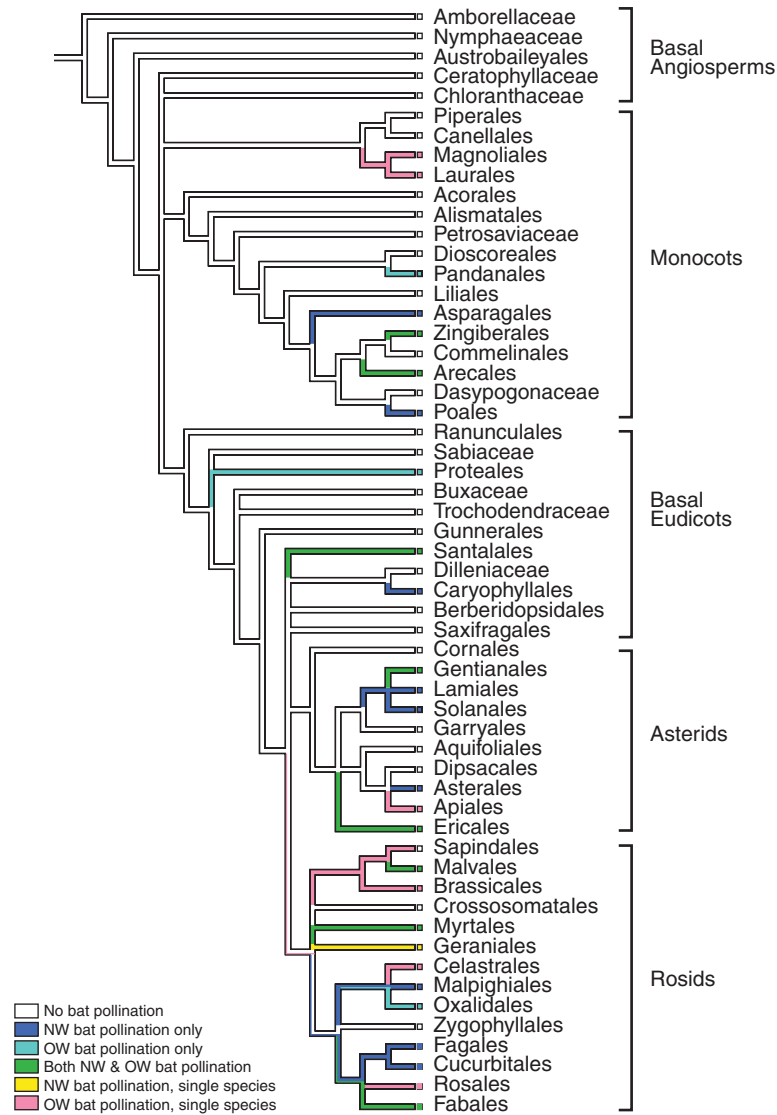


FIG. 5. Cladogram showing the evolutionary relationships of orders of angiosperms and the distribution of families containing bat-pollinated taxa among them. Five types of bat pollination are highlighted: pollination only by New World phyllostomids, pollination only by Old World pteropodids, pollination by both bat families, and single species pollinated either by New World or Old World bats. Cladogram based on Soltis *et al.* (2005).

TABLE 2. Overall distribution of bat pollination among five major lineages of angiosperms by order and family

Lineage	Orders			Families		
	Total	No. with bat-pollinated families	No. of independent origins (%)	Total	No. with bat-pollinated genera	No. of independent origins (%)
Basal angiosperms	9	2	1 (50)	28	2	2 (100)
Monocots	12	5	2 (40)	76	13	9 (69)
Basal eudicots	10	3	3 (100)	63	4	4 (100)
Rosids	14	12	5 (42)	122	26	22 (85)
Asterids	10	6	3 (50)	104	21	14 (67)
Totals	55	28	14 (50)	393	66	51 (77)

Also indicated are the estimated number of independent origins of bat pollination within these lineages by order and family. The phylogenetic hypothesis upon which this summary is based comes from T. H. Fleming and W. J. Kress (unpubl. res.). The number of families recognized in this hypothesis and in Table 1 differ slightly because it does not include Capparaceae.

TABLE 3. Distribution of bat pollination among orders and families of angiosperms by bat family with an estimate of the number of independent origins within plant families

Lineage	Pteropodids		Phyllostomids	
	No. of orders	No. of families (% independent)	No. of orders	No. of families (% independent)
Basal angiosperms	2	2 (100)	0	0
Monocots	3	8 (63)	4	7 (100)
Basal eudicots	2	2 (100)	2	3 (100)
Rosids	7	19 (90)	8	16 (81)
Asterids	3	10 (80)	5	16 (81)
Totals	17	41 (83)	19	42 (86)

This analysis is based on phylogenetic data in T. H. Fleming and W. J. Kress (unpubl. res.), which includes 66 of 67 families in Table 1.

families (74 %) have pantropical or cosmopolitan distributions, and the other six are Old World endemics. Thus, 36 of the 53 broadly distributed plant families that contain bat-pollinated plants (68 %) are pollinated by bats in only one hemisphere whereas only about one-third of them have bat-pollinated species in both hemispheres. This again emphasizes the phylogenetically independent nature of the evolution of bat pollination.

In general, bat pollination is primarily a lowland phenomenon. Very few nectar bats and their food plants occur at elevations above 2000 m. The distribution of bat-pollinated species of the Bromeliaceae, an endemic New World plant family, clearly illustrates this trend. Most bat-pollinated epiphytic bromeliads occur in wet lowland forests in Bolivia and elsewhere in the Neotropics whereas those pollinated by hummingbirds occur at mid- to high elevations; insect-pollinated species occur most frequently in warm, dry regions (Kessler and Krömer, 2000; Tschapka and von Helversen, 2007). Whereas most pteropodid nectar bats and their flowers occur in moist or wet forest habitats, glossophagine nectar bats and their flowers occur in arid as well as in moist and wet habitats. Up to six species of glossophagines, for example, can be found in the tropical dry forests of south-central Mexico (Santos and Arita, 2002), and the morphologically most specialized glossophagines in terms of rostral length and tooth reduction occur in cactus-dominated habitats in the Neotropics (Fleming, 1995; Fleming *et al.*, 2005). Neotropical semi-arid and arid lands are especially rich in bat-pollinated species of Agavaceae, Cactaceae, Fabaceae and Malvaceae (Bombacoideae). No such association between nectar bats and arid habitats occurs in the Old World, although opportunistic Australasian pteropodid flower visitors (e.g. *Pteropus* spp.) are more common in dry eucalypt forests than in wet forests (Richards, 1995; Palmer *et al.*, 2000).

Pteropodid and phyllostomid bats differ fundamentally regarding their occurrence on islands. About 62 % of pteropodid species are island-dwellers whereas only about 12 % of phyllostomid species, including five species of nectar bats in the West Indian endemic subfamily Phyllonycterinae, are restricted to islands (Fleming, 1993; Fleming *et al.*, 2005).

Pteropodids are widely distributed on islands throughout the Old World tropics as far east as the Cook Islands in the Pacific where they often act as ‘keystone’ pollinators and seed dispersers (Cox *et al.*, 1991; Rainey *et al.*, 1995; Banack, 1998). As expected given their wider distribution among islands, island-dwelling pteropodids interact as pollinators with a greater number of plant families than phyllostomids. Pteropodids on islands visit flowers in 21 of 41 (53 %) Old World bat-pollinated families whereas phyllostomids on islands visit flowers in only eight of 44 (18 %) New World bat-pollinated families (Table 1). Plant families pollinated by island pteropodids are concentrated in the rosids; those pollinated by phyllostomids are evenly distributed among monocots, rosids and asterids. About 90 % of these families have pantropical or cosmopolitan distributions. Families with restricted geographical distributions include Cactaceae in the New World and Musaceae and Pandanaceae in the Old World. Most of the flowers visited by bats of both families on islands are produced by trees or tree-like herbs or succulents (e.g. *Heliconia* and *Musa* in south-east Asian islands, Cactaceae in the West Indies). Exceptions include bat-pollinated species of *Gesneria* in the West Indies and three species of *Marcgravia* lianas on Dominica (Zusi and Hamas, 2001; Marten-Rodriguez and Fenster, 2008; Marten-Rodriguez *et al.*, 2009). The predominance of bat-pollinated trees on islands is similar to the mainland situation in the Old World but contrasts with that in the Neotropical mainland where glossophagine bats pollinate many flowers produced by vines and epiphytes as well as trees (Fleming and Muchhala, 2008).

THE PHYLOGENETIC CONSEQUENCES OF BAT POLLINATION

The evolution of bat pollination has made a modest contribution to the overall species and generic diversity of angiosperms. What contribution has bat pollination made at higher taxonomic levels? How many tribes, subfamilies and families are exclusively bat-pollinated, or nearly so? Table 4 summarizes the higher order plant taxa that are associated primarily with bats for pollination. This information is presented at two taxonomic levels, at the family level and within families (i.e. subfamilies or tribes). Among families that are strongly associated with bat pollination, we include two families that have recently been reclassified into larger related families by Angiosperm Phylogeny Group (APG) II: Bombacaceae *sensu stricto* (s.s.; now part of Malvaceae) and Sonneratiaceae s.s. (now part of Lythraceae). We do this because current literature still uses these family names, and not all recent treatments of angiosperm phylogeny (e.g. Heywood *et al.*, 2007) have accepted these reclassifications.

Only two small families with a total of four genera (Caryocaraceae in the Neotropics and the formerly segregated Sonneratiaceae s.s. in the Paleotropics) appear to be either exclusively or primarily bat-pollinated; two others (the formerly segregated Bombacaceae s.s. and the Musaceae) contain genera or species that are primarily bat-pollinated. All four of these families contain species exclusively pollinated by specialized bats in addition to others visited by

TABLE 4. Higher order plant taxa that are associated primarily with bats for pollination

(A) Families strongly associated with pollinating bats		
Family	No. of genera/species in family or subfamily	Estimated age of family
Bombacaceae*	16/120	69–65 Ma
Caryocaraceae	2/25	111–100 Ma
Musaceae*	2/35	Stem = 87 Ma; crown = 61 Ma
Sonneratiaceae	2/8	57 Ma
(B) Families with subfamilies or tribes strongly associated with pollinating bats		
Family and subfamily or tribe	No. of genera/species in family	Estimated age of family
Agavaceae: Agavoideae	23/637 – family	Crown = 13 Ma
Bignoniaceae: 2 of 7 tribes	110/800 – family	49.5 Ma
Cactaceae: Cactoideae, 2+ tribes	92/1250 – subfamily	Crown = 30 Ma
Campanulaceae: Lobelioideae*	29/1200 – subfamily	43–23 Ma
Fabaceae: Mimosoideae, 2 tribes*	82/3275 – subfamily	Crown = 59–39 Ma
Myrtaceae: Leptospermoideae*	131/4620 – family	Stem = 93 Ma
Pandanaceae: Freycinetioideae	4/885 – family	Crown = 51 Ma
Proteaceae: Grevilleoideae*	45/855 – subfamily	Stem = 118 Ma; crown = 82 Ma

Family characteristics include geographical distribution and number of genera/species. Plant data in columns 1 and 2 come from Mabberly (1997) or APG II. Data on estimated ages of families come from APG II, Barker *et al.* (2007) and Ricklefs (2006).

* Bird pollination also occurs in these taxa

both specialized and opportunistic nectar-feeders. Another eight families contain either subfamilies or tribes whose species rely heavily on bats for pollination. Of these families, bat pollination is especially common in Agavaceae and Cactaceae in the New World and Pandanaceae in the Old World. Among the pantropical families, bat pollination is more common in the New World than in the Old World in terms of number of bat-pollinated genera in Bombacaceae *s.s.*, Campanulaceae and Fabaceae whereas it is more common in the Old World than in the New World in Bignoniaceae and Myrtaceae (Table 1). Of the 12 families listed in Table 4, six are either exclusively bat-pollinated or biased toward bat pollination in certain subfamilies or tribes in both hemispheres. Within certain families, therefore, pteropodid and phyllostomid bats appear to have had similar effects on angiosperm diversification. At lower phylogenetic levels (e.g. genera and species), however, phyllostomid-pollinated genera and species outnumber pteropodid-pollinated taxa by factors of 1.6 and 2.1, respectively (Table 1).

The currently estimated ages of plant families or subfamilies that are strongly associated with bat pollination generally pre-date the evolution of nectar-feeding bats (Table 4). Nectar-feeding bats probably evolved in the late Oligocene and Miocene (28–12 Mya), well after most of the families in Table 4 had originated and diversified. Only the New World Agavaceae appears to be approximately coeval with the radiation of glossophagines. Particularly striking are differences in the ages of the four families that are most strongly associated with bat pollination today (Bombacaceae *s.s.*, Caryocaraceae, Musaceae and Sonneratiaceae *s.s.*; Table 4A). Each of these families appears to have evolved in the Late Cretaceous or early Cenozoic, well before the evolution of specialized nectar-feeding bats. This temporal mismatch suggests that stem members of these families were not likely to be bat-pollinated.

EVOLUTIONARY PATHWAYS TO BAT POLLINATION

Bat pollination is clearly a derived condition in most angiosperm lineages. What has been the most common evolutionary route to bat pollination: from insect-, bird- or non-volant mammal-pollinated taxa? Based on the preponderance of insect pollination in angiosperms, it is reasonable to hypothesize that bat pollination evolved most often from insect pollination. If this is true, did bat-pollinated taxa evolve most frequently from diurnally or nocturnally pollinated taxa (e.g. from bee or moth flowers, respectively)? Alternatively, the most common evolutionary route may have been from diurnal bird-pollinated species (e.g. from hummingbird flowers in the New World or from sunbird or honeyeater flowers in the Old World). Finally, as suggested by Sussman and Raven (1978), bat-pollinated flowers may have evolved from flowers pollinated by non-volant mammals such as primates, at least in the Old World.

Answering these questions requires that we have well-resolved, species-level phylogenies onto which pollination systems have been mapped. For particular plant groups in certain regions, this information is available for bird-pollinated plants. For example, within Neotropical *Costus* (Costaceae), hummingbird pollination has evolved independently from euglossine bee pollination at least 12 times, and it has evolved several times from insect pollination in *Iochroma* (Solanaceae) (Kay *et al.*, 2005; Smith *et al.*, 2006). Although not based on well-supported phylogenies, Grant (1994) hypothesized that hummingbird pollination evolved independently numerous times from bee- or moth-pollination in 11 plant families in western North America. Compared with those for birds, the evolutionary transitions to bat pollination are less well known. The best documented cases are summarized in Table 5, but not all of these represent unequivocal

TABLE 5. Examples of the evolution of bat pollination from other pollination modes

Family and genus	Pollination history	Source
(A) Old World examples		
*Bombacaceae, <i>Adansonia</i>	Hawkmoth pollination is ancestral; bat pollination has evolved twice (once in Africa and once in Madagascar)	Baum <i>et al.</i> (1998)
*Bombacaceae, the <i>Cullenia/Durio</i> clade	Vertebrate pollination is probably basal in this clade, derived from insect (beetle) pollination. Bats are major pollinators in <i>Cullenia</i> and <i>Durio</i> ; bees are major pollinators in <i>Boschia</i>	Nyffler and Baum (2001)
*Fabaceae, <i>Parkia</i>	Pollination by nocturnal bees is ancestral; bat pollination evolved in the New World and now occurs in most species	Luckow and Hopkins (1995)
(B) New World examples		
*Acanthaceae, <i>Ruellia</i>	Multiple evolutions of bat pollination from bee (most common), hummingbird, or moth (least common) pollination	Tripp and Manos (2008)
Agavaceae, <i>Agave</i>	Moth pollination is likely to be ancestral in the family; bat pollination is derived in subgenus <i>Agave</i>	Good-Avila <i>et al.</i> (2006)
Bromeliaceae, several genera	Bat-pollinated species probably evolved from either insect or hummingbird pollination	Endress (1994), Benzing (2000)
Cactaceae, tribe Pachycereeae	Bat pollination probably is ancestral among these columnar cacti, but it is ultimately derived from insect (bee) pollination	Anderson (2001), Wallace (2002)
*Campanulaceae, <i>Centropogon</i> and <i>Burmeistera</i>	A clade of bat-pollinated <i>Burmeistera</i> and <i>Centropogon</i> evolved from hummingbird-pollinated <i>Centropogon</i>	Knox <i>et al.</i> (2008)
*Gesneriaceae, <i>Sinningia</i>	Bat pollination evolved independently twice from hummingbird pollination	Perret <i>et al.</i> (2007)
*Gesneriaceae, Gesneriaceae	Bat pollination evolved independently from hummingbird pollination at least five times	Marten-Rodriguez <i>et al.</i> (2009)
*Lecythidaceae, <i>Lecythis</i>	Three bat-pollinated species evolved from euglossine bee pollination	Mori and Boeke (1987), Mori <i>et al.</i> (2007)
Passifloraceae, <i>Passiflora</i>	Bat-pollinated <i>P. trisecta</i> is nested within a lowland clade of bee-pollinated species, not within an Andean hummingbird-pollinated clade	Hansen <i>et al.</i> (2006)
*Polemoniaceae, <i>Cobaea</i>	Three bat-pollinated species have evolved independently twice from hummingbird pollination	Prather (1999)
Strelitziaceae, <i>Phenakospermum</i>	Evolved from arboreal mammal pollination in Africa	Kress <i>et al.</i> (1994)

Asterisks (*) indicate those examples in which evidence for evolutionary transitions appears to be strong; other examples are currently equivocal pending species-level phylogenies.

results because of the absence of species-level phylogenies. All three potential ancestral pollination modes (insects, birds and non-volant mammals) are included in these examples, and generalizations about evolutionary trends are not yet possible. We suspect that bat pollination has evolved most commonly from insect pollination in the Old World [e.g. in the Fabaceae (Mimosoideae) and Myrtaceae]. Flowers pollinated by hawkmoths and beetles also appear to be ancestral to bat flowers in certain Old World taxa. Although we judge that five of the 11 New World examples in Table 5 are equivocal (i.e. the immediate ancestor of bat-pollinated taxa is not clear), there is strong evidence of the evolution of bat flowers from bee, moth and hummingbird flowers in the other six families. It is likely that bat-pollinated taxa have evolved frequently from hummingbird-pollinated taxa in certain New World families of epiphytes (e.g. Bromeliaceae, Gesneriaceae), but strong evidence for this awaits phylogenetic studies, as is the case in the Agavaceae and Cactaceae, in which hummingbird pollination is not likely to be ancestral to bat pollination.

Although bat pollination is usually considered to be a non-reversible evolutionary specialization (Tripp and Manos, 2008), this is not always true. In one case in the primarily neotropical genus *Heliconia*, closely related paleotropical species are pollinated by either small pteropodid bats or by honeyeaters, but not both (Kress, 1985; Pedersen and Kress, 1999). Recent DNA-based phylogenetic work suggests that honeyeater-pollinated species are derived from the bat-pollinated species (Kress and Specht, 2005; L. P.

Lagomarsino, C. D. Specht and W. J. Kress, unpubl. res.). Similarly, a hummingbird-pollinated species of *Burmeistera* is derived from a bat-pollinated ancestor (Knox *et al.*, 2008). Evidence that bat pollination can give rise to more generalized pollination systems involving birds and insects as well as bats comes from studies of saguaro cacti (*Carnegiea gigantea*) in the Sonoran Desert and *Aphelandra acanthus* in the Andes of Ecuador (Fleming *et al.*, 2001; Muchhala *et al.*, 2009). In both of these examples, reduced abundance of bats compared with other potential pollinators is thought to have selected for a change in floral characteristics (e.g. diurnal flower presentation) that favoured non-chiropteran pollinators.

GENERAL DISCUSSION AND CONCLUSIONS

Bat pollination is relatively uncommon in angiosperms compared with bird or insect pollination, and overall, it probably represents a novel (*sensu* 'new') type of pollination mode for these plants. Bat-pollinated taxa occur in at least 67 families and about 250 genera of angiosperms, mostly in advanced evolutionary lineages, particularly in the Zingiberales in monocots and in the rosids among eudicots. The near absence of bat pollination in the basal angiosperms (only two species) is striking. This pollination mode involves relatively large (compared with most insect pollinators), energetically expensive animals that require substantial energetic rewards per flower or inflorescence for attraction. The daily energy budgets of three species of glossophagine bats, for example, are 40–50 kJ whereas those of insects are orders

of magnitude smaller (Horner *et al.*, 1998; Winter and von Helverson, 2001). Bat pollination occurs at night, and the characteristics of bat-pollinated flowers usually differ substantially from those of diurnally pollinated flowers in terms of timing of floral anthesis, flower colour and size, and nectar odour and volume. The structure of bat-pollinated flowers, including methods of flower presentation, often differs substantially from those of their non-bat-pollinated ancestors or sister-species (Faegri and van der Pijl, 1979; Dobat and Peikert-Holle, 1985; Endress, 1994). Differences in the floral morphology and biology of species of *Musa* that are pollinated either by bats or by birds are especially striking. *Musa acuminata*, which is pollinated by the specialized pteropodid *Macroglossus sobrinus*, has pendant inflorescences with dark purple bracts and nocturnal flowers that produce a jelly-like nectar containing 22–25% sugar. In contrast, the diurnal flowers of *M. salaccensis*, which are pollinated by sunbirds, occur on erect inflorescences with pink–purple bracts and produce relatively dilute nectar of 18–21% sugar (Itino *et al.*, 1991).

What are the evolutionary advantages of bat pollination that have led to the independent evolution of this pollination mode in numerous plant lineages? In what ways does bat pollination differ fundamentally from that of insect or bird pollination? We propose that bats differ from insects and birds in at least two ways that affect their effectiveness as pollinators: (1) they often carry large amounts of pollen on their bodies and deposit a large number of pollen grains on stigmas per flower visit and (2) they routinely carry pollen substantial distances among flowers. Muchhala (2006b) compared pollen deposition on flowers of nine species of *Burmeistera* by glossophagine bats and hummingbirds and found that bats deposited about 22 times more pollen on stigmas, on average, than hummingbirds. Likewise, Molina-Freaner *et al.* (2003) reported that the glossophagine bat *Leptonycteris curasoae* deposited a few thousand to over 20000 pollen grains per night on stigmas of the columnar cactus *Pachycereus pringlei*. Deposition of large numbers of pollen grains per stigma can be advantageous to plants for at least two reasons: (1) it ensures that enough pollen is available per flower to fertilize all ovules and (2) it fosters strong pollen–pollen competition for access to ovules.

In addition to depositing large amounts of pollen on plant stigmas, bats also deposit conspecific pollen grains of several different genotypes (i.e. different potential fathers) on stigmas. In bat-pollinated *Pachira quinata*, for instance, the number of pollen fathers in fruits from trees in continuous forest in Costa Rica was 2–3 compared with 1–2 pollen fathers per fruit in trees in forest fragments; levels of biparental inbreeding (i.e. mating between close relatives) were higher in the forest fragment trees than in the continuous forest (Fuchs *et al.*, 2003). Multiple sires per fruit have also been reported in other neotropical bat-pollinated trees, including *Caryocar brasiliense*, *Ceiba pentandra* and *Hymenaea courbaril* (Collevatti *et al.*, 2001; Dunphy *et al.*, 2004; Lobo *et al.*, 2005). Bats also commonly carry more than one species of pollen on their bodies while foraging (e.g. Heithaus *et al.*, 1975; von Helverson and Winter, 2003; Muchhala, 2006b; Muchhala *et al.*, 2009) but whether this interferes significantly with pollination is not currently known. Sympatric species of *Burmeistera* avoid potential

problems associated with heterospecific pollen by placing pollen on different parts of the heads of *Anoura* bats (Muchhala and Potts, 2007; Muchhala, 2008).

In addition to carrying large amounts of pollen of multiple genotypes, bats often move pollen substantial distances between plants, which increases the size of genetic neighbourhoods and reduces levels of genetic subdivision between plant populations. Data summarized in Ward *et al.* (2005), for example, indicate that phyllostomid bats carry pollen substantially longer distances (up to 18 km) within populations of tropical trees than hummingbirds (but not necessarily longer distances than some insects). Bats are particularly effective pollinators for plants that occur at low densities [e.g. in canopy trees in the Bombacaceae s.s., arid-zone columnar cacti (except in the Tehuacan Valley of Mexico where adult cactus densities can exceed 1000 per ha; Valiente-Baunet *et al.*, 1996) and agaves, and epiphytes in general (e.g. Tschapka, 2004)]. Ashton (1998) noted that in Bornean forests, consistently rare species of canopy trees with large fruit such as certain legumes, *Neesia*, *Coelostegia* and *Durio* are pollinated by large, low-fecundity and long-lived animals such as pteropodid bats and *Xylocopa* bees. In the genus *Durio*, species in subgenus *Boscia* are abundant small subcanopy or canopy trees that are pollinated by meliponine bees whereas species in the subgenus *Durio* are low-density canopy trees whose flowers are bat-pollinated. Theoretically, chronically low-density, animal-pollinated plants are expected to provide larger energy rewards per flower to attract pollinators than high-density plants (Heinrich and Raven, 1972). This could pre-adapt some low-density plants for pollination by bats and other long-distance pollinators.

If bats are such good pollinators, why are bat-pollinated flowers not more common among angiosperms? The answer to this question probably involves the costs and benefits of bat pollination to plants relative to those associated with other modes of pollination in addition to phylogenetic constraints such as flower size. Costs involved in bat pollination in terms of resources invested in flowers, inflorescences, nectar and pollen are likely to be substantial. In his survey of nectar production in a Costa Rican dry tropical forest, for example, Opler (1983) showed that floral biomass and nectar volume of bat-pollinated flowers differed from those of flowers pollinated by hummingbirds, bees and butterflies (but not hawkmoths) by several orders of magnitude. Similarly, Fleming (2002) reported that among cactus flowers, bat-pollinated species generally produced 8–20 times more calories of nectar per flower than those pollinated by hawkmoths and hummingbirds. These data suggest that bat flowers are energetically expensive, which probably represents a significant constraint to their evolution when energy for flower production is limited.

A second constraint to the evolution of bat flowers is the general phylogenetic conservatism of flower evolution in angiosperms. Insect pollination is ancestral in many families of angiosperms, and pollination by birds or bats is derived. Unless environmental conditions such as low temperatures in mountains reduce the abundance or reliability of insects (Cruden 1972), selection favouring a shift from insect to vertebrate pollination is not likely to occur. Examples of these kinds of shifts include the preponderance of hummingbird

pollination in Bromeliaceae and many other families in montane regions in South and Central America and the numerous shifts from insect to hummingbird pollination in many lineages of plants in the montane west of North America (Grant, 1994; Kessler and Krömer, 2000; Luteyn, 2002). Furthermore, given that bat-pollinated flowers tend to be larger and energetically more expensive than bird flowers, which reflects the generally larger size of nectar-feeding bats compared with nectar-feeding birds worldwide (Fleming and Muchhala, 2008), selection is more likely to favour the evolution of bird flowers than bat flowers in most situations favouring a shift from insect to vertebrate pollination. In support of this, many more angiosperm families contain bird-pollinated genera and species than bat-pollinated taxa (Fleming and Muchhala, 2008). In the end, although floral and pollinator conservatism probably prevails in angiosperms, the evolution of pollination systems can also be opportunistic so that many plant families have evolved derived modes of pollination involving vertebrates. Although birds appear to be the vertebrates of choice as pollinators for many plant families, probably because of their abundance, diversity and generally small size, bats clearly offer some advantages as pollinators. As a result, bat pollination has evolved numerous times across angiosperm phylogeny.

Besides its evolutionary implications, long-distance pollination by bats also has important conservation implications. Human disturbance in the tropics and elsewhere often fragments plant populations and increases the distance between conspecifics. Without long-distance pollinators, plants with self-compatible or mixed mating systems are likely to experience higher rates of self-fertilization within habitat fragments than plants in continuous forests. Isolated self-incompatible plants (the most common mating system in tropical plants; Bawa, 1992) will fare even worse because they require pollen from another plant to set any fruit and seeds at all. Studies of canopy trees in continuous and fragmented forests in Brazil, Costa Rica, Mexico and Puerto Rico provide support for these generalizations (Gribel *et al.*, 1999; Collevatti *et al.*, 2001; Fuchs *et al.*, 2003; Quesada *et al.*, 2003; Dunphy *et al.*, 2004). Thus, bat pollination, along with pollination by other kinds of long-distance pollinators, can serve to ‘rescue’ plants from some of the adverse effects of habitat fragmentation.

About 85 % of the cases of bat pollination appear to have evolved independently at the level of angiosperm family. A particularly striking example of this pattern is the occurrence of bat-pollinated flowers in only one hemisphere or the other in many pantropically distributed plant families. An exception to this pattern occurs in the monocot order Zingiberales in which bat pollination is widespread among related families. The common occurrence of bat pollination in the monocots, and especially the Zingiberales, may be due to the concentration of many of these taxa in the tropics, particularly the large succulent and/or arborescent species in which bat pollination almost exclusively occurs. Of the seven families of monocots in which more than a single species is bat-pollinated (Table 1), all are exclusively tropical in distribution. In addition, many of these same taxa have large flowers (Strelitziaceae) and/or large floral displays (Agavaceae, Arecaceae, Pandanaceae) in closely related taxa that are bird- or insect-pollinated. In the Zingiberales, bat

pollination is concentrated in the tropical genera with large, accessible flowers that produce copious amounts of nectar and pollen (i.e. *Musa*, *Ensete*, *Phenakospermum*, *Heliconia*), all adaptations for visitation by large pollinators. Bat pollination is rare or absent in the ‘ginger families’ with more restrictive floral morphology, reduced stamen numbers and smaller nectaries (i.e. Zingiberaceae, Costaceae, Marantaceae, and Cannaceae; Kress and Specht, 2005). This same pattern – the evolution of bat pollination in large-flowered plant lineages – may also be found in the tropical Bombacaceae *s.s.*, Bromeliaceae, Gesneriaceae, Malvaceae and possibly Bignoniaceae (Table 5).

Bat pollination occurs in about twice as many genera and species in the New World than in the Old World, despite the fact that pteropodid bats, including specialized nectar-feeders, are likely to be significantly older evolutionarily than specialized nectar-feeding phyllostomids. One reason for this is that the neotropical angiosperm flora is much richer in species, genera and families than are the floras of Africa, Asia and Australasia (Whitmore, 1998; Morley, 2000). But this explanation only begs the question, why is the neotropical flora richer than those in other tropical areas? Gentry’s (1982) widely cited explanation for this emphasized the importance of Andean orogeny as a generator of exceptional plant species diversity, particularly among understory shrubs, epiphytes and palmettos of Gondwanan ancestry. Andean-associated families such as Bromeliaceae, Campanulaceae, Cactaceae, Gesneriaceae, Marcgraviaceae and Solanaceae are relatively rich in bat-pollinated genera and/or species. Only bat-pollinated canopy trees in the Bombacaceae *s.s.* and Fabaceae are not strongly associated with the Andes. Interestingly, whereas hummingbirds have radiated extensively in the Andes (Bleiweiss, 1998a, b; McGuire *et al.*, 2007), the same is not true for glossophagine bats in which species of only 1–2 genera (e.g. *Anoura* and *Platalina*) occur at mid- to high elevations (Koopman, 1981). All hummingbirds have the capacity to undergo torpor while glossophagine bats do not (McNab, 2002; but see Kelm and von Helversen, 2007). The ability to undergo torpor and to reduce energy demands significantly while still maintaining high body temperatures when active has enabled hummingbirds to radiate extensively under conditions of low ambient temperatures and flowers that offer low energetic rewards in the Andes (Altshuler *et al.*, 2004). The inability to undergo torpor has probably constrained the radiation of glossophagine bats in montane environments.

Another reason for the higher diversity of bat-pollinated plants in the Neotropics than in the Paleotropics probably reflects the small size and hovering ability of glossophagines. Large, non-hovering pteropodids and their New World counterparts, non-glossophagine phyllostomid bats, often visit large, sturdily built flowers many of which are exerted well away from foliage on erect stalks or long pendants (Figs 2–4). In contrast, small hovering glossophagines often visit small, delicate flowers that may or may not be exerted well away from foliage. The ability to hover has allowed these bats to interact with small flowers produced by a wider range of growth habits, including epiphytes and shrubs that produce small flowers as well as large-flowered canopy trees, than pteropodids (Fleming and Muchhala, 2008). We assume that it is cheaper for plants to produce small flowers than

large flowers. If this is true, then it should be easier for selection to modify insect-pollinated flowers to attract small hovering glossophagines than to attract larger non-hovering phyllostomids or pteropodids. The presence of small hovering bats (and birds) in the New World has thus expanded the range of possible pollinator niches for neotropical plants. The absence of such vertebrate pollinators in the Old World has probably constrained the range of vertebrate pollination niches in angiosperms there.

Finally, we note that while the overall species richness of bat-pollinated plants is relatively modest, the ecological and economic importance of these plants is considerable. From an ecological perspective, bat-pollinated plants are conspicuous members of various New World habitats, including deserts and other arid to semi-arid habitats (e.g. columnar cacti and paniculate agaves) and dry and wet tropical forests (e.g. canopy trees of the Bombacaceae *s.s.*). Similarly, members of the Bombacaceae *s.s.* are conspicuous members of certain African and Madagascan habitats, and species of *Sonneratia* are important members of south-east Asian mangrove communities. From an economic perspective, many of these same taxa or their cultivated relatives have considerable monetary value. For example, fruits of bat-pollinated columnar cacti are widely harvested in many parts of the Americas (Yetman 2007), and tequila, which is derived from *Agave tequilana*, is a major cultural icon and agricultural industry in Mexico. *Ceiba pentandra* is an important source of fibre worldwide, and species of neotropical *Ochroma* are renowned for their lightweight wood. In south-east Asia, economically important fruits come from bat-pollinated *Durio zibethinus* and two species of *Parkia*, and bat-pollinated species of *Eucalyptus* are important timber trees in Australia (Fujita and Tuttle, 1991). Although domestic bananas (*Musa* species) produce fruit parthenocarpically, their wild relatives are bat-pollinated (and dispersed).

In conclusion, bat pollination has evolved independently in many advanced orders and families of angiosperms. It is particularly common in lowland habitats throughout the tropics but is also common in arid tropical and subtropical habitats in the New World, particularly in the Agavaceae and Cactaceae. As noted above, a number of ecologically or commercially important tropical trees, especially those in the Bombacaceae *s.s.*, as well as many large herbaceous or arborescent plants in the monocot order Zingiberales are bat-pollinated. In the New World tropics, many epiphytes in the Bromeliaceae, Cactaceae and Gesneriaceae rely on bats for pollination. The evolution of bat-pollinated lineages probably began in the Miocene, well after the first appearance of families that currently contain many such lineages. Bat pollination is thus derived in most plant groups, and its evolution has entailed significant changes in the timing of anthesis, morphology, biochemistry and physiology of flowers. We propose that bat pollination has been particularly likely to evolve in plants that occur in chronically low densities and that from a conservation viewpoint it is a particularly valuable adaptation in landscapes in which plant populations have recently become fragmented owing to habitat destruction. The loss of nectar-feeding bats in tropical and subtropical habitats would probably have profound ecological and evolutionary effects on their food plants and on the plant communities in which they occur.

CODA: WHERE DO WE GO FROM HERE?

Our knowledge about the occurrence of bat pollination in tropical and subtropical plants has increased substantially in the past few decades but there is still much more to be learned on both sides of this fascinating mutualism. On the bat side, we need more studies on the foraging behaviour (foraging routes and food choices) of flower-visiting bats. Do these bats forage in an energetically efficient manner, as predicted by optimal foraging theory? Do they routinely rely on spatial memory to locate flowering plants? To what extent do foraging decisions made by bats conflict with the reproductive interests of plants? As one example, the foraging behaviour of the arid-zone phyllostomid *Leptonycteris curasoae* appears to be energetically suboptimal because it involves long commute flights from day roosts (up to 30+ km) and large, overlapping foraging areas (up to 2.5+ km²) containing much more energy and pollen from cactus flowers than is needed to support one or more individuals (Horner *et al.*, 1998). Why is this? From the perspective of cactus flowers pollinated by this bat, this behaviour is beneficial because it provides great mobility for pollen and genes within and between populations (Hamrick *et al.*, 2002). These strong-flying bats are therefore excellent out-crossers (Molina-Freaner *et al.*, 2003). But we do not yet know whether all or most nectar-feeding bats are excellent out-crossers because the genetic consequences of bat pollination have rarely been documented, especially in the Old World tropics. Available data on the foraging behaviour of specialized pteropodid bats (e.g. *Syconycteris australis*, *Macroglossus minimus*, *Eonycteris spelaea* and *Melonycteris melanops*) suggest that, except for *E. spelaea*, these bats are short-distance commuters that feed in small home ranges of less than 10 ha (Winkelman *et al.*, 2000, 2003; Bonaccorso *et al.*, 2005). They are not likely to provide nearly as much long-distance mobility for pollen and genes as does *L. curasoae* or their opportunistic pteropodid relatives, but genetic studies to document this are lacking.

On the plant side, we need more information about ecological conditions that favour evolutionary switches from insect- or bird-pollination to bat-pollination. Analysis of the geographical distributions of different pollination syndromes in Bromeliaceae (Kessler and Krömer, 2000) begins to provide this kind of information, but similar studies of other plant groups are needed. In addition, more detailed information is needed about why bats are favoured as pollinators in some habitats and not others. What is it about the population and behavioural ecology of nectar-feeding bats that makes them 'attractive' pollinators for particular plants in particular habitats? Pollinator 'reliability' is often mentioned as a necessary condition for the evolution of specialized pollination systems (e.g. Valiente-Banuet *et al.*, 1996; Waser *et al.*, 1996), but how do we operationally define the 'reliability' of nectar bats? Finally, we need more studies of pairs of plant species where one is bat-pollinated and the other is not to understand patterns, and ultimately the mechanisms, of character change. What is involved in the switch from diurnal to nocturnal flower anthesis? In the evolution of large corollas and nectaries? In the production of strong floral scents featuring sulphur compounds (in the New World)? Etc. It should be clear from this review that we know a lot about the natural history and

phylogenetic and biogeographical distributions of nectar-feeding bats and their food plants. We now need to dig deeper into this mutualism to understand how and why it has evolved.

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APPENDIX 1

Number of nectar-feeding bats in two families. Indicated first are morphologically specialized genera (number of species in parentheses) in bold type followed by genera of opportunistic flower visitors from which pollen has been collected. Taxonomy follows Simmons (2005).

Family Pteropodidae: ***Eonycteris* (3)**, ***Macroglossus* (2)**, ***Megaloglossus* (1)**, ***Melonycteris* (3)**, ***Notopteris* (2)** and ***Syconycteris* (3)**; *Balionycteris*, *Cynopterus*, *Eidolon*, *Epomophorus*, *Epomops*, *Lissonycteris*, *Micropteropus*, *Myonycteris*, *Nanonycteris*, *Pteropus* and *Rousettus*,

Family Phyllostomidae: ***Anoura* (5)**, ***Brachyphylla* (2)**, ***Choeroniscus* (3)**, ***Choeronycteris* (1)**, ***Erophylla* (2)**, ***Glossophaga* (5)**, ***Hylonycteris* (1)**, ***Leptonycteris* (3)**, ***Lichonycteris* (1)**, ***Lionycteris* (1)**, ***Lonchophylla* (7)**, ***Monophyllus* (2)**, ***Musonycteris* (1)**, ***Phyllonycteris* (3)**, ***Platalina* (1)** and ***Scleronycteris* (1)**; *Ametrida*, *Artibeus*, *Carollia*, *Chiroderma*, *Glyphonycteris*, *Micronycteris*, *Phyllostomus*, *Platyrrhinus*, *Rhinophylla*, *Sturnira*, *Trinycteris*, *Uroderma* and *Vampyressa*.

APPENDIX 2

New World bat-pollinated species listed by plant family

(1) This list excludes species reported to be visited by bats in the New World that are introduced from the Old World (*Bombax*, *Durio*, *Kigelia*, *Mahduca*, *Musa*, *Thespesia*, *Thunbergia*, *Zingiber*); visited by bats for fruit, not nectar/pollen (*Anacardium*, *Brosimum*, *Carica*, *Chrysophyllum*, *Eugenia*, *Manilkara*, *Muntingia*, *Solanum*, *Symphonia*, *Syzygium*); known to be pollinated by wind (*Acalypha*, *Alnus*, *Celtis*, *Pinus*, *Quercus*) or small insects (*Aristolochia*, *Berberis*, *Bursera*, *Theobroma*); or where bat-pollination seems very doubtful (*Clusia*, *Vanilla*).

(2) Inclusion in this table does not indicate that bats pollinate all listed species throughout their ranges.

(3) Plant families follow the Angiosperm Phylogeny Group system. Species names correspond to those accepted in the Missouri Botanical Garden's VAST (VAscular Tropicos – <http://mobot.mobot.org/W3T/Search/vast.html>) nomenclatural database or found in the International Plant Name Index (IPNI; <http://www.ipni.org>). The references to all other name changes are provided in the footnotes. Genus sp. is only included when no other species represents the genus.

(4) Information gathered from the Database of Neotropical Bat/Plant Interactions (Geiselman *et al.*, 2004 onwards).

ACANTHACEAE

Harpochilus neesianus
Louleridium chartaceum
Louleridium donnell-smithii
Ruellia eurycodon
Ruellia exostemma
Ruellia malaca
Trichanthera gigantea
AGAVACEAE
Agave angustifolia
Agave cocui
Agave colimana
Agave deserti
Agave desmettiana
Agave grisea
Agave havardiana
Agave macroacantha
Agave neomexicana
Agave palmeri
Agave parryi
*Agave salmiana*¹
Agave schottii
Agave shawii
Agave tequilana
Hesperaloe sp.
Manfreda brachystachys

AMARYLLIDACEAE

Eustephia sp.
*Hippeastrum calyptratum*²
ARECACEAE
Calyptrogyne ghiesbreghtiana
Coccothrinax sp.
Roystonea regia
ASTERACEAE
Cirsium subcoriaceum
Gongylolepis jauaensis
Wunderlichia cruelsiana
BIGNONIACEAE
Adenocalymna dichilum
*Amphitecna isthmica*³
*Amphitecna kennedyae*⁴
*Amphitecna latifolia*⁵
*Amphitecna spathicalyx*⁶
*Crescentia alata*⁷
Crescentia amazonica
Crescentia cujete
Cydista diversifolia
Parmentiera cereifera
Parmentiera edulis
Parmentiera macrophylla
Tabebuia obtusifolia
Tabebuia platyantha

BORAGINACEAE

Cordia alliodora
Cordia gerascanthus
BROMELIACEAE⁸
Encholirium glaziovii
Guzmania calothyrsa
Guzmania danielii
Guzmania killipiana
Guzmania morreniana
Guzmania retusa
Guzmania sphaeroidea
Pitcairnia brongniartiana
Pitcairnia trianae
Puya ferruginea
Vriesea bituminosa
Vriesea gigantea
Vriesea longicaulis
Vriesea longiscapa
Vriesea morrenii
*Vriesea platynema*⁸
*Vriesea sazimae*²
*Werauhia gladioliflora*⁹
*Werauhia kupperiana*¹⁰
*Werauhia ororiensis*¹¹
*Werauhia rugosa*¹²

CACTACEAE

*Browningia riosaniensis*¹³
Carnegiea gigantea
*Cephalocereus columna-trajani*¹⁴
Cereus hexagonus
*Dendrocereus nudiflorus*¹⁵
Echinocactus sp.
Harrisia sp.
Hylocereus undatus
Lemaireocereus sp.
Leptocereus arboreus
Leptocereus santamarinae
Leptocereus wrightii
Machaerocereus sp.
Marginatocereus marginatus
*Monvillea smithiana*¹⁶
Myrtillocactus sp.
*Neobuxbaumia euphorbioides*¹⁷
Neobuxbaumia macrocephala
Neobuxbaumia tetetzo
Opuntia sp.
Pachycereus pecten-aboriginum
Pachycereus pringlei
Pachycereus weberi
Pilosocereus catingicola
*Pilosocereus chrysacanthus*¹⁸
*Pilosocereus lanuginosus*¹⁹
*Pilosocereus leucocephalus*²⁰
*Pilosocereus moritzianus*²¹
*Pilosocereus tillianus*²
Platyopuntia sp.
*Pterocereus gaumeri*²²
Samaipaticereus corroanus
Selenicereus sp.
*Stenocereus griseus*²³
Stenocereus queretaroensis
Stenocereus stellatus
*Stenocereus thurberi*²⁴
Subpilocereus horrispinus
Subpilocereus ottonis
*Subpilocereus repandus*²⁵
Weberbauerocereus weberbaueri
Weberocereus trichophorus
Weberocereus tunilla

CAMPANULACEAE

Burmeistera borjensis
Burmeistera ceratocarpa
Burmeistera cyclostigmata
Burmeistera cilindrocarpa
Burmeistera fusco-apicata
Burmeistera lutosa
Burmeistera multiflora
Burmeistera smaragdi
Burmeistera sodiroana
Burmeistera succulenta
Burmeistera tenuiflora
Burmeistera truncata
Centropogon mandonis
Centropogon nigricans
Centropogon smithii

Siphocampylus corynoides
Siphocampylus foetidus
Siphocampylus giganteus
Siphocampylus sulfureus
Siphocampylus tunicatus

CANNACEAE

*Canna liliiflora*²⁶

CAPPARACEAE

Capparis flexuosa
Capparis hastata
Capparis scabrida
Cleome anomala
Cleome arborea
Cleome moritziana
Cleome viridiflora
*Crateva tapia*²⁷

CARYOCARACEAE

Caryocar brasiliense
Caryocar coriaceum
Caryocar costaricense
Caryocar nuciferum
Caryocar villosum

CHRYSOBALANACEAE

Couepia dolichopoda
Couepia longipendula
Hirtella sp.

COMBRETACEAE

Combretum sp.

CONVOLVULACEAE

Ipomoea ampullacea
*Ipomoea neei*²⁸
*Ipomoea wolcottiana*²⁹

CUCURBITACEAE

Calycophysum pedunculatum
*Calycophysum spectabile*³⁰
Cayaponia sp.
Cucurbita argyrosperma
Lagenaria siceraria

ERICACEAE

Arbutus sp.

EUPHORBACEAE

Croton sp.
Hura crepitans
Mabea occidentalis

FABACEAE

Acacia farnesiana
Albizzia occidentalis
Alexa grandiflora
Bauhinia angulicaulis
Bauhinia glabra
*Bauhinia multinervia*³¹
Bauhinia pauletia
*Bauhinia rufa*³²
Bauhinia siqueiraei
*Bauhinia unguolata*³³
Browneopsis cauliflora
Browneopsis disepala
Browneopsis macrofoliolata
Browneopsis ucayalina
Caesalpinia bahamensis

Caesalpinia vesicaria
*Calliandra calothyrsus*³⁴
Calliandra formosa
*Calliandra grandiflora*³⁵
*Calliandra tweediei*³⁶
Conzattia sp.
Dichrostachys cinerea
Elizabetha leiogyne
Elizabetha paraensis
Elizabetha speciosa
Eperua falcata
Eperua leucantha
*Eperua stipulata*³⁷
*Erythrina fusca*³⁸
Hymenaea courbaril
Hymenaea stigonocarpa
Inga bahiensis
Inga cayennensis
Inga marginata
Inga sessilis
Inga spectabilis
Inga vera
Jacqueshuberia purpurea
Jacqueshuberia quinquangulata
Lonchocarpus sp.
Lysiloma latisiliquum
Mimosa lewisii
*Mucuna holtonii*³⁹
Mucuna mutisiana
Mucuna pruriens
Mucuna rostrata
Mucuna sloanei
*Mucuna urens*⁴⁰
Ormosia sp.
Parkia cachimboensis
Parkia decussata
*Parkia discolor*⁴¹
Parkia gigantocarpa
Parkia igneiflora
*Parkia nitida*⁴²
*Parkia panurensis*⁴³
Parkia pendula
Parkia platycephala
Peltophorum adnatum

GENTIANACEAE

*Chelonanthus alatus*⁴⁴
Gentiana sp.
Macrocarpaea duquei
Macrocarpaea glabra
*Macrocarpaea macrophylla*⁴⁵
Macrocarpaea polyantha
*Macrocarpaea quelchii*⁴⁶
Symbolanthus latifolius

GERANIACEAE

Geranium sp.

GESNERIACEAE

Drymonia sp.
Gesneria alpina
Gesneria calycina
Gesneria calycosa

<i>Gesneria clandestina</i>	<i>Chiranthodendron pentadactylon</i>	<i>Mirabilis longiflora</i>
<i>Gesneria exserta</i>	<i>Eriotheca pentaphylla</i>	ONAGRACEAE
<i>Gesneria fruticososa</i>	<i>Helicteres baruensis</i>	<i>Oenothera</i> sp.
<i>Gesneria gloxinoides</i>	<i>Helicteres rekoii</i>	PASSIFLORACEAE
<i>Gesneria onychocalyx</i>	<i>Hibiscus clypeatus</i>	<i>Passiflora galbana</i>
<i>Gesneria pedunculosa</i>	<i>Hibiscus elatus</i>	<i>Passiflora mucronata</i>
<i>Gesneria pumila</i>	<i>Luehea alternifolia</i> ⁵⁶	<i>Passiflora penduliflora</i>
<i>Gesneria shaferi</i>	<i>Luehea candida</i>	<i>Passiflora recurva</i>
<i>Gesneria viridiflora</i>	<i>Luehea grandiflora</i>	<i>Passiflora ovalis</i> ⁶³
<i>Kohleria tigridia</i> ⁴⁷	<i>Luehea paniculata</i>	POLEMONIACEAE
<i>Paliavana prasinata</i>	<i>Matisia bracteolosa</i>	<i>Cobaea aschersoniana</i>
<i>Paliavana sericiflora</i>	<i>Matisia cordata</i>	<i>Cobaea gracilis</i> ⁶⁴
<i>Paliavana werdermannii</i>	<i>Ochroma pyramidale</i> ⁵⁷	<i>Cobaea scandens</i>
<i>Rhytidophyllum grande</i>	<i>Pachira aquatica</i>	<i>Cobaea trianae</i>
<i>Rhytidophyllum tomentosum</i>	<i>Pachira quinata</i> ⁵⁸	PROTEACEAE
<i>Sinningia brasiliensis</i> ⁴⁸	<i>Pseudobombax ellipticum</i>	<i>Roupala</i> sp.
LAMIACEAE	<i>Pseudobombax grandiflorum</i>	RUBIACEAE
<i>Catopheria chiapensis</i>	<i>Pseudobombax longiflorum</i>	<i>Condaminea corymbosa</i>
<i>Salvia</i> sp.	<i>Pseudobombax septenatum</i>	<i>Hillia illustris</i>
LECYTHIDACEAE	<i>Quararibea asterolepis</i>	<i>Palicourea</i> sp.
<i>Lecythis barnebyi</i>	<i>Quararibea gomeziana</i>	SALICACEAE
<i>Lecythis brancoensis</i>	<i>Quararibea ochrocalyx</i>	<i>Salix</i> sp.
<i>Lecythis poiteaui</i>	<i>Quararibea parvifolia</i>	SAPINDACEAE
LORANTHACEAE	<i>Quararibea pendula</i>	<i>Cupania</i> sp.
<i>Psittacanthus acinarius</i>	<i>Wercklea insignis</i>	SCROPHULARIACEAE
LYTHRACEAE	<i>Wercklea lutea</i> ⁵⁹	<i>Eremogeton grandiflorus</i>
<i>Lafoensia acuminata</i> ⁴⁹	MARCGRAVIACEAE	SOLANACEAE
<i>Lafoensia densiflora</i>	<i>Marcgravia brownei</i>	<i>Datura innoxia</i>
<i>Lafoensia glyptocarpa</i>	<i>Marcgravia comosa</i>	<i>Dyssochroma viridiflora</i>
<i>Lafoensia pacari</i>	<i>Marcgravia coriacea</i> ⁶⁰	<i>Juanulloa verrucosa</i> ⁶⁵
<i>Lafoensia puniceifolia</i>	<i>Marcgravia dressleri</i>	<i>Merinthopodium dressleri</i> ⁶⁶
<i>Lafoensia replicata</i> ⁵⁰	<i>Marcgravia evenia</i> ²	<i>Merinthopodium neuranthum</i> ⁶⁷
<i>Lafoensia vandelliana</i>	<i>Marcgravia helverseniana</i>	<i>Merinthopodium pendulum</i> ⁶⁸
MALVACEAE	<i>Marcgravia longifolia</i>	<i>Merinthopodium vogelii</i> ⁶⁹
<i>Abutilon bedfordianum</i>	<i>Marcgravia mexicana</i>	<i>Nicotiana otophora</i>
<i>Abutilon niveum</i>	<i>Marcgravia myriostigma</i>	<i>Nicotiana tomentosa</i>
<i>Abutilon pedrae-brancae</i>	<i>Marcgravia nepenthoides</i>	<i>Solandra guerrerensis</i>
<i>Abutilon peltatum</i>	<i>Marcgravia nervosa</i>	<i>Solandra maxima</i>
<i>Abutilon regnellii</i>	<i>Marcgravia pittieri</i>	<i>Trianaea nobilis</i>
<i>Abutilon rufinerve</i>	<i>Marcgravia polyantha</i>	<i>Trianaea speciosa</i> ⁷⁰
<i>Anoda</i> sp.	<i>Marcgravia serrae</i>	STRELITZIACEAE
<i>Anotea flavida</i> ⁵¹	<i>Marcgravia trinitatis</i> ⁶¹	<i>Phenakospermum guyannense</i>
<i>Bakeridesia</i> sp. ⁵²	<i>Marcgraviastrum macrocarpum</i>	VELLOZIACEAE
<i>Berrya cubensis</i> ⁵³	<i>Norantea</i> sp.	<i>Barbacenia rubro-virens</i>
<i>Bombacopsis squamigera</i>	MELASTOMATAACEAE	VERBENACEAE
<i>Ceiba aesculifolia</i> ⁵⁴	<i>Meriania pichinchensis</i>	<i>Citharexylum</i> sp.
<i>Ceiba pentandra</i>	<i>Purpurella grossa</i> ⁶²	<i>Lantana</i> sp.
<i>Ceiba speciosa</i> ⁵⁵	NYCTAGINACEAE	VOCHYSIACEAE
<i>Ceiba trichistandra</i>	<i>Bougainvillea spectabilis</i>	<i>Vochysia</i> sp.

¹Cited as *Manfreda saliana* by Eguiarte *et al.* (1987), but must refer to *Agave saliana*. ²Not recognized by Tropicos but is by Index Kewensis. ³*Dendrosicus isthmicus* = basionym. ⁴*Dendrosicus kennedyi* = basionym. ⁵Synonym of *Dendrosicus latifolius* and *Enallagma latifolia*. ⁶*Dendrosicus spathicalyx* = basionym. ⁷Synonym of *Parmentiera alata*. ⁸Cited as *Vriesea moehringiana* by Dobat and Peikert-Holle (1985), but must refer to *V. platynema*. ⁹Synonym of *Vriesea gladioliflora*. ¹⁰*Vriesea kupperiana* = basionym. ¹¹Synonym of *Thecophyllum irazuense* and *Vriesea irazuense*. ¹²Synonym of *Vriesea rugosa*. ¹³*Rauhocereus riosaniensis* = basionym. ¹⁴Synonym of *Cephalocereus hoppenstedtii*. ¹⁵Cited as *Acanthocereus nudiflorus* by Simmons and Wetterer (2002), but must refer to *Dendrocereus nudiflorus*. ¹⁶*Cephalocereus smithiana* = basionym. ¹⁷Synonym of *Cephalocereus euphorbioides*. ¹⁸Synonym of *Cephalocereus chrysacanthus*. ¹⁹Synonym of *Pilocereus lanuginosus*. ²⁰Synonym of *Cephalocereus leucocephalus*, *C. palmeri* and *C. sartorianus*. ²¹Synonym of *Cephalocereus moritzianus*. ²²Synonym of *Pachycereus gaumeri*. ²³Synonym of *Cereus griseus*, *Lemaireocereus griseus* and *Ritterocereus griseus*. ²⁴Synonym of *Lemaireocereus thurberi*. ²⁵Synonym of *Cereus atroviridis*, *C. grenadensis*, *C. repandus* and *Samaipaticereus peruvianus*. ²⁶Synonym of *Canna brittonii*. ²⁷Synonym of *Crateva benthamii*. ²⁸Synonym of *Ipomoea peduncularis*. ²⁹Synonym of *Ipomoea arborecens*. ³⁰Synonym of *Edmondia spectabilis* (Asteraceae). ³¹Synonym of *Bauhinia megalandra*. ³²Synonym of *Bauhinia holophylla*. ³³Synonym of *Bauhinia macrostachya*. ³⁴Synonym of *Calliandra confusa*. ³⁵Synonym of *Calliandra anomala*.

³⁶Synonym of *Calliandra guildingii*. ³⁷Synonym of *Eperua schomburgkiana*. ³⁸Synonym of *Erythrina glauca*. ³⁹Synonym of *Mucuna andreana*. ⁴⁰Synonym of *Mucuna altissima*. ⁴¹Synonym of *Parkia auriculata*. ⁴²Synonym of *Parkia alliadora*, *P. inundabilis* and *P. oppositifolia*. ⁴³Synonym of *Parkia pectinata*. ⁴⁴Synonym of *Irlbachia alata*, *Lisianthus alatus*, *L. cheloniodes* and *L. viridiflorus*. Struwe et al. (2002) determined that the accepted name is *Chelonanthus alatus*. ⁴⁵Synonym of *Lisianthus macrophyllus* and *Macrocarpaea valerioi*. ⁴⁶*Lisianthus quelchii* = basionym. ⁴⁷Synonym of *Capanea grandiflora*, *C. oerstedii* and *C. picturata*. ⁴⁸Synonym of *Lietzia brasiliensis*. ⁴⁹Synonym of *Lafoensia speciosa*. ⁵⁰Could be a subspecies of *Lafoensia vandelliana*. ⁵¹Synonym of *Malvaviscus acerifolius*. ⁵²Cited as *Bakeridesia paulistana* by Dobat and Peikert-Holle (1985), but this name is not recognized by Tropicos or IPNI. ⁵³Synonym of *Carpodiptera cubensis*. ⁵⁴Synonym of *Ceiba acuminata* and *C. grandiflora*. ⁵⁵Synonym of *Chorisia speciosa*. ⁵⁶Synonym of *Luehea speciosa*. ⁵⁷Synonym of *Ochroma lagopus*. ⁵⁸Synonym of *Bombacopsis fendleri* and *B. quinata*. ⁵⁹Synonym of *Hibiscus luteus*. ⁶⁰Synonym of *Marcgravia cuyuniensis*. ⁶¹Synonym of *Marcgravia rectiflora*. ⁶²*Purpurella* included in *Tibouchina* by Renner (1989). ⁶³Synonym of *Tetrastylis ovalis* (Feuille and MacDougal, 2007). ⁶⁴Synonym of *Cobaea panamensis*. ⁶⁵Synonym of *Markea verrucosa* (Knapp et al., 1997). ⁶⁶*Merinthopodium* is a synonym of *Markea* (Knapp et al., 1997). ⁶⁷Synonym of *Markea campanulata*, *M. internexa* and *M. neurantha* (Knapp et al., 1997). ⁶⁸Synonym of *Markea pendula* (Knapp et al., 1997). ⁶⁹Synonym of *Markea vogelii* (Knapp et al., 1997). ⁷⁰Synonym of *Trianaea spectabilis* (Knapp et al., 1997).

APPENDIX 3

Old World Bat-pollinated species listed by plant family

(1) This list excludes species visited by bats for fruit, not nectar/pollen (*Calophyllum*, *Carica*, *Cerbera*, *Chlorophora*, *Mammea*, *Mangifera*, *Morus*, *Palaquium hispidum*, *Syzygium inophylloides*, *Terminalia*); those known to be pollinated by small insects (*Arenga*, *Celtis*, *Cocos*, *Diospyrus*, *Elaeagnus*, *Rhaphiolepis*, *Tamarix*, *Trema*) or wind (*Casuarina*, *Dendrocnidne*, *Pipturus*, *Tamarix*); those introduced in areas where bats have been recorded visiting them (*Agave*, *Callistemon citrinus*, *Ceiba*, *Crescentia*, *Hevea*, *Ochroma*, *Pachira*, *Parmentiera*, *Ravenala madagascariensis*, *Samanea saman*); or those whose flowers are destroyed instead of pollinating by bats (*Eria obusta*, *Eucalyptus* spp.). (See footnote †, below table.)

(2) Inclusion in this appendix does not indicate that bats pollinate all listed species throughout their ranges.

(3) Plant families follow the Angiosperm Phylogeny Group system. Species names correspond to those accepted in the Missouri Botanical Garden's VAST (VAScular Tropicos) nomenclatural database or the International Plant Name Index. Genus sp. is only included when no other species represents the genus.

ACANTHACEAE

Avicennia sp.^T

ANACARDIACEAE

Rhus taitensis^{T, E}

ANNONACEAE

Cananga odorata^{D, E}

APOCYNACEAE

Alstonia actinophylla^T

Cerbera oppositifolia^{*I, S}

Neisosperma sp.^D

ARALIACEAE

Polyscias samoensis^E

ARECACEAE

Areca sp.^{*I, S}

Livistona chinensis^T

Carpentaria acuminata^T

Gulubia sp.^T

ASPHODELACEAE

Aloe dolomitica^{I, S, T}

ASTELIACEAE

Collospermum samoense^T

BIGNONIACEAE

Fernandoa sp.^I

Haplophragma adenophyllum^{I, AA}

Heterophragma roxburghii^{I, I, T}

Kigelia africana^{2, A, C, I, Z, AA}

Markhamia stipulata^{3, D, Z, AA}

Nyctocalos sp.^{*G, I, S}

Oroxylum indicum^{G, I, K, S, T, Y, Z, AA}

Pajanelia longifolia^{4, I, Y, Z}

Spathodea campanulata^{A, E, I, T}

Stereospermum xylocarpum^{5, I, T}

CAMPANULACEAE

Lobelia sp.^T

CELASTRACEAE

Cassine sp.^T

CHRYSOBALANACEAE

Maranthes aubrevillei^{T, U}

Maranthes corymbosa^W

Maranthes polyantra^{6, I, P, T}

CLUSIACEAE

Pentadesma butyrace^{T, U}

COMBRETACEAE

Lumnitzera littorea^T

CONVOLVULACEAE

Erycibe micrantha^{7, I, AA}

Ipomoea albivenia^{*I, S, AA}

ELAEOCARPACEAE

Elaeocarpus rarotongensis^{I, T}

Elaeocarpus tonganus^E

Elaeocarpus ulianus^E

EUPHORBIACEAE

Glochidion ramiflorum^{E, I, T}

Macaranga tanarius^T

FABACEAE

Bauhinia hookeri^{8, I, S}

Castanospermum australe^{*I, S, T, X}

Cynometra sp.^T

Daniellia oliveri^{I, S, U, Z}

Erythrina fusca^T

Erythrina variegata^{9*E, I, S}

Inocarpus sp.^{*I, T}

Intsia bijuga^T

Mucuna flagellipes^{I, T}

Mucuna gigantea^{I, T, AA}

Mucuna junghuhniana^{I, AA}

Mucuna macropoda^N

Mucuna monosperma^{I, AA}

Mucuna pruriens^{Z, AA}

Mucuna reticulata^{I, AA}

Parkia bicolor^{I, L, N, T}

Parkia biglandulosa^F

Parkia biglobosa^{C, D, F, N}

Parkia clappertoniana^{A, B, C, I, T}

Parkia filicoidea^{I, N}

Parkia javanica^{I, M, Y}

Parkia singularis^{I, Y}

Parkia speciosa^{C, K, M, N, Y, AA}

Parkia timoriana^{10, I, N, T, AA}

Erythrophleum sp.^T

Sesbania formosa^D

HELICONIACEAE

Heliconia indica^Z

Heliconia papuana^Z

Heliconia solomonensis^{O, T}

LAURACEAE

Neolitsea sp.^T

LECYTHIDACEAE

Abdulmajidia sp.^V

Barringtonia asiatica^{11, E, I, T, Z}

Careya arborea^{*G, S}

Foetidia mauritiana^{*I}

Planchonia careya^T

LOGANIACEAE*Fagraea* sp.^{12, S, T}**LORANTHACEAE***Amyema* sp.^T*Loranthus* sp.^{*I, S, T, X}**LYTHRACEAE***Duabanga grandiflora*^{13, I, T, Y, Z}*Duabanga moluccana*^{I, X, AA}*Sonneratia alba*^{14, I, T, Y, Z, AA}*Sonneratia apetala*^{15, I, Y, Z}**MALVACEAE***Adansonia digitata*^{A, C, I, P, T, Z, AA}*Adansonia gibbosa*^{16, I, AA}*Adansonia grandidieri*^{D, Z}*Adansonia madagascariensis*^{AA}*Bombax buonopozense*^T*Bombax ceiba*^{17, I, T, Z, AA}*Bombax valetonii*^{I, Y, AA}*Ceiba pentandra*^{A, B, C, E, I, J, Y, Z, AA}*Cullenia excelsa*^I*Dombeya* sp.^{AA}*Durio carinatus*^I*Durio graveolens*^{I, Y, Z}*Durio kutejensis*^{I, Z, AA}*Durio malaccensis*^D*Durio zibethinus*^{I, K, Y, Z, AA}*Kostermansia* sp.^S**MELIACEAE***Azadirachta indica*^{18, A, I, T}*Dysoxylum gaudichaudianum*^T**MORACEAE***Artocarpus* sp.^{*I, T, Y}**MUSACEAE***Ensete glaucum*^I*Ensete ventricosum*^I*Musa acuminata*^{19, I, K, BB}*Musa balbisiana*^I*Musa coccinea*^{AA}*Musa itinerans*^R*Musa paradisica*^{I, AA}*Musa textilis*^{I, T, AA}**MYRTACEAE***Angophora costata*^{*I, T}*Angophora subvelutina*^{*I, X}*Angophora woodsiana*^{20, *I, X}*Callistemon pachyphyllus*^{*I, T}*Callistemon salignus*^{*I, S}*Leptospermum* sp.^{*I, S, T}*Lophostemon confertus*^T*Lophostemon grandiflorus*^T*Lophostemon lactifluus*^T*Melaleuca argentea*^{*T}*Melaleuca cajuputi*^{*T}*Melaleuca dealbata*^{*T}*Melaleuca leucadendra*^{21, *I, T}*Melaleuca nervosa*^{*T}*Melaleuca quinquenervia*^{*I, T}*Metrosideros vera*^{*I}*Metrosideros villosa*^{*T}*Syncarpia glomulifera*^{22, *I, T, X}*Syncarpia hillii*^{*I, T}*Syzygium corniflorum*^{*I}*Syzygium cumini*^{23, T, AA}*Syzygium dealatum*^{*E}*Syzygium jambos*^{*I, T}*Syzygium malaccense*^{24, E, T, AA}*Syzygium richii*^{*E, T}*Syzygium samarangense*^{25, I, T, AA}*Syzygium tierneyanum*^{*I}**PANDANACEAE***Freycinetia insignis*^{I, AA}*Freycinetia reineckei*^E*Pandanus fragrans*^T*Pandanus tectorius*^{E, T}**PROTEACEAE***Banksia integrifolia*^{I, Q, T, X}*Banksia robur*^T*Banksia serrata*^{26, T, X}*Grevillea pteridifolia*^T*Grevillea robusta*^{I, T}*Protea elliotii*^{I, P, T}**RHAMNACEAE***Alphitonia* sp.^E**RHIZOPHORACEAE***Rhizophora* sp.^{*I, S, T}**ROSACEAE***Eriobotrya* sp.^T**RUBIACEAE***Aidia* sp.^T*Guettarda speciosa*^{E, T}*Neonauclea forsteri*^{E, T}**SALICACEAE***Populus* sp.^T**SALVADORACEAE***Salvadora persica*^T**SAPINDACEAE***Diploglottis cunninghamii*^T*Tristiropsis* sp.^T**SAPOTACEAE***Madhuca beccarii*^{27, G}*Madhuca indica*^{28, F, G, I, T, AA}*Madhuca macrophylla*^{AA}*Manilkara hexandra*^{29, I, S, T}*Palaquium gutta*^{30, I, AA}*Palaquium obovatum*^M*Palaquium quercifolium*^{*I, S, AA}*Palaquium stehlinii*^E*Payena macrophylla*^I*Planchonella samoensis*^E*Planchonella torricellensis*^{*I, S, T}*Tieghemella heckelii*^{31, H, AA}*Vitellaria* sp.^T**SOLANACEAE***Physalis* sp.^T**XANTHORRHOACEAE***Xanthorrhoea* sp.^T

*Indicates where authors have doubted if bat visitation affects pollination.

¹Synonym of *Heterophragma quadriloculare*. ²Synonym of *Kigelia aethiopica* and *K. pinnata*. ³Synonym of *Dolichandrone cauda-felina* and *D. stipulata*. ⁴Synonym of *Pajanelia multijuga*. ⁵*Stereospermum* is a synonym of *Rademachera*. ⁶Synonym of *Parinari polyandra*. ⁷Synonym of *Erycibe ramiflora*. ⁸Synonym of *Lysiphyllum hookeri*. ⁹Synonym of *Erythrina lithosperma*. ¹⁰Synonym of *Parkia roxburghii*. ¹¹Synonym of *Barringtonia racemosa*. ¹²Cited as *Fagraea baterialana* but no species name in Tropicos and IPNI. ¹³Synonym of *Duabanga sonneratioides*. ¹⁴Synonym of *Sonneratia acida* and *S. caseolaris*. ¹⁵Synonym of *Sonneratia ovata*. ¹⁶Synonym of *Adansonia gregorii*. ¹⁷Synonym of *Bombax malabaricum*; *Bombax* is a synonym of *Gossampinus*. ¹⁸Synonym of *Melia azadirachta*. ¹⁹Includes subspecies *Musa banksii* and *M. truncata*; synonym of *Musa halabanensis* and *M. malaccensis*. ²⁰Basionym of *Angophora floribunda* and *A. lanceolata*. ²¹Synonym of *Melaleuca viridiflora*. ²²Synonym of *Syncarpia laurifolia*. ²³Synonym of *Eugenia cumini*. ²⁴Synonym of *Eugenia malaccensis*. ²⁵Synonym of *Eugenia javanica*. ²⁶Synonym of *Banksia aemula*. ²⁷Synonym of *Ganua beccarii*. ²⁸Synonym of *Bassia latifolia* and *Illipe*. ²⁹Synonym of *Mimusops hexandra*. ³⁰Synonym of *Dichopsis gutta*. ³¹Synonym of *Dumoria heckelii*.

References: ^AAyensu (1974);

^BBaker (1973); ^CBaker & Harris (1957); ^DBaker *et al.* (1998); ^EBanack (1998 and references therein); ^FBhat (1994); ^GCorlett (2004); ^HCunningham (1995b); ^IDobat & Peikert-Holle (1985 and references therein); ^JElmqvist *et al.* (1992); ^KGould (1978); ^LGrünmeier (1990); ^MHodgkison *et al.* (2004b); ^NHopkins (1983, 1984, 1993) ^{BB}Itino *et al.* (1991); ^OKress (1985); ^PLack (1978); ^QLaw (1992); ^RLiu *et al.* (2002); ^SMarshall (1983, 1985); ^TMickelburgh *et al.* (1992 and references therein); ^UPettersson *et al.* (2004); ^VPrance & Mori (2004); ^WPrance & White (1988); ^XRatcliffe (1932); ^YStart & Marshall (1976); ^ZStroo (2000); ^{AA}van der Pijl (1941; 1956; 1961)

[†]References used to determine legitimate pollinators of excluded species: Andersson (1998); Calley *et al.* (1993); Friis (1993); Gaskin (2003); Henderson (2002); Johnson & Wilson (1993); Nyhagen *et al.* (2005); Pennington (2004); Stevens (2007); Todzia (1993).