Nocturnal pollination of *Parkia velutina* by *Megalopta* bees in Amazonia and its possible significance in the evolution of chiropterophily

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ABSTRACT. Canopy observations of the rain forest tree *Parkia velutina* (Leguminosae: Mimosoideae) in Amazonian Brazil indicate that it is pollinated by night-flying bees. The small red flowers are organized into spherical heads; they open in the late afternoon and attract *Megalopta* bees (Halictidae: Augochlorini) which forage for pollen after dark. In contrast to the numerous bat-pollinated species of *Parkia,* no nectar was detected. Nocturnal melittophily is proposed as a possible intermediate stage in the evolution of chiropterophily from diurnal ento-mophily in *Parkia.*

RESUMO. Observações realizadas na copa de *Parkia velutina* (Leguminosae: Mimosoideae), uma árvore de mata pluvial na Amazônia brasileira, indicam que ela é polinizada por abelhas noturnas. As flores são vermelhas e pequenas e estão organizadas em capitulos esféricos. Antese ocorre no final da tarde e as flores atraem abelhas *Megalopta* (Halictidae: Augochlorini) que forageiam por pólen depois de escurecer. Ao contrário das várias espécies de *Parkia* polinizadas por morcegos, esta espécie não produz néctar. O presente trabalho propõe que melito-filia noturna possa representar um estágio intermediário na evolução de quiropter-ofilia para entomofilia diurna no gênero *Parkia*.

KEY WORDS: Amazonia, Augochlorini, bat-pollination, bee-pollination, Halicti-dae, Leguminosae, *Megalopta,* melittophily, *Parkia,* nocturnal pollination

INTRODUCTION

The pantropical genus *Parkia* R.Br. (Leguminosae: Mimosoideae) is largely but not exclusively chiropterophilous. Although bat-pollination has been demon-strated in SE Asia (van der Pijl 1936), Africa (Baker & Harris 1957, Grünmeier

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1990) and South America (de Carvalho 1960, Hopkins 1984, Vogel 1968–69), Baker & Harris (1957) suggested that the neotropical *Parkia ulei* (Harms) Kuhlm. was entomophilous because it has a very different suite of floral characters from the chiropterophilous species. Its small yellow flower-heads, or capitula, resemble those of some other entomophilous mimosoids such as *Mimosa, Leucaena* and some species of *Acacia,* and they are borne in much branched inflorescences. In the chiropterophilous species the capitula are much larger and typically borne on long, pendent peduncles arranged in little-branched inflorescences. Brief observations at a large tree of *P. ulei* in the botanical gardens at the Museu Goeldi, Belém, Brazil, in 1979 indicated that meliponine bees were its likely pollinators though the flower-heads were visited by a range of diurnal insects (Hopkins 1981, 1984).

Parkia is divided into three taxonomic sections (Hopkins 1986) whose characters are summarized in Table 1. Together with two other neotropical species, *Parkia velutina* Benoist and *P. multijuga* Benth., *P. ulei* belongs to section *Sphaeroparkia* while all known chiropterophilous species belong to either sect. *Platyparkia,* which is also neotropical, or to sect. *Parkia,* which is pantropical. The sections differ from one another in numerous characters but an obvious difference is in the presence and location of specialized nectar-secreting flowers. In the two bat-pollinated sections these nectariferous flowers are located either towards the base of the capitulum (sect. *Parkia)* or around the apex (sect. *Platyparkia),* while in sect. *Sphaeroparkia* they are absent (see Hopkins 1984, figure 1). Since nectar is a major food source for bats which visit *Parkia,* chiropterophilous capitula being capable of producing 5–12 ml per night (Grünmeier 1990), the absence of nectariferous flowers in sect. *Sphaeroparkia* suggests that bats are unlikely to be the pollinators of any of this group of species.

Parkia velutina, P. multijuga and *P. ulei* differ slightly from one another in the characters associated with their pollination syndromes, such as the size and colour of the capitula and the structure and position of the inflorescence axes. Crepuscular and nocturnal observations of *P. multijuga* in Brazil in 1979 were

Table 1. Characters of the three taxonomic sections of *Parkia*.

	Taxonomic section		
	Parkia	*Platyparkia*	*Sphaeroparkia*
Characters			
Number of species	*c*. 28	3	3
Distribution	Pantropical	Neotropical	Neotropical
Shape of capitula	Clavate, pyriform or biglobose	Oblate	Spherical
Disposition of capitula	Pendent or rarely erect	Pendent	Neither pendent nor erect
Length of peduncles	Usually long	Long	Short
Nectariferous flowers?	Between fertile and staminodial flowers	Around apex of capitulum	None
Staminodial flowers?	At base of capitulum	None	None
Pollinators	Pteropodid bats – palaeotropics; Phyllostomid bats – neotropics	Phyllostomid bats	Insects

Figure 1. *Parkia velutina* and its pollinators. (a) Flowering branch showing inflorescences proximal to the leaves (voucher *Nascimento & Silva 608)*. (b) Capitulum with two *Megalopta* bees. Photographs by M.J.G. Hopkins.

inconclusive but suggested that diurnal entomophily was unlikely to provide a complete explanation for this species (Hopkins 1984, and see below). Here we report on observations of floral visitors at *Parkia velutina* in Amazonian Brazil that demonstrate a third pollination mechanism in *Parkia,* distinct from both chiropterophily and diurnal melittophily.

STUDY PLANTS

Parkia velutina is a large tree found in *terra firme* forest, up to 420 m altitude, often near rivers and streams (Hopkins 1986). It has a wide but discontinuous distribution in Amazonian Brazil and Peru, French Guiana, eastern Venezuela and

Colombia west of the Andes. The crown has a rather distinctive appearance with clusters of large, bipinnate leaves at the ends of thickened twigs (Figure 1a). Herbarium material shows that the flowers are clustered into ball-like capitula that are borne on peduncles up to 4 cm long. The number of capitula per inflorescence is usually up to *c.* 15, their peduncles arising from an unbranched axis inserted proximally to the leaves (Figure 1a, and see Hopkins 1986, figure 24), so that the flower-heads are somewhat concealed by the foliage and not exposed around the edge of the crown as is typical in many species of *Parkia*. The capitula open acropetally along each inflorescence axis so that usually there is no more than a single capitulum at anthesis per inflorescence at any time.

Individual flowers are small and tubular, with the corolla exserted beyond the calyx and the anthers shortly exserted beyond the mouth of the corolla, so that a flower-head at anthesis resembles a ball of anthers (Figure 1b). In bisexual flowers, the style projects beyond the corolla, and the stigma is small and terminal. A survey of herbarium material at the Royal Botanic Gardens, Kew showed that functionally male flowers, in which the gynoecium is reduced or usually completely absent, occur frequently; however, the distribution of male and hermaphrodite flowers in the same or different capitula was not determined. The fruits are large, tardily dehiscent pods, up to 50 cm long, with rather ligneous valves. They contain up to 36 seeds, each *c.* 2 cm long and weighing 0.60–0.72 g. Seed dispersal probably involves monkeys but we know of no actual data.

MATERIALS AND METHODS

On 18 October 1994, a flowering tree of *Parkia velutina c.* 30 m high was found on the edge of *igarapé* Acará, Reserva Ducke, near Manaus, Central Amazonian Brazil (voucher *J.R. Nascimento & C.F. Silva 608*, deposited at the Instituto Nacional de Pesquisas da Amazônia, Manaus [INPA] and K, MG, MY, SP, RB, U). The capitula in the material collected were unexpectedly found to be fully open at 21h00, suggesting nocturnal, not diurnal, anthesis. The tree was climbed again the following day, nocturnal anthesis was confirmed, and observations of visitors were made. Further observations, photographs and collection of visitors were made between 16h30 and 20h15 on 26 October 1994. The tree was climbed using jumar clamps and a fixed rope, and observations were made in the crown, at a height of 20–25 m. The bees were identified to genus by F. Peralta, INPA.

OBSERVATIONS

Floral biology
The spherical capitula were *c.* 4 cm diameter, each composed of about 430 tightly packed flowers (counts of 349, 418, 420, 458, 461, 462). The overall colour at anthesis was bright red, including the filaments and anthers (Figure 1b), and bright yellow pollen was visible on dehiscence of the anthers. A

minute, caducous, greenish-white, spherical gland, which falls around the time of anther dehiscence, occurs at the apex of each anther. The flowers produced no detectable nectar. The scent was strong, somewhat sweet to sickly or musty, and unpleasant to humans. A single stigma was noted on one of the capitula from the original collection but all the capitula observed closely in the crown on subsequent nights consisted entirely of male flowers. The tree had up to about 50 capitula at anthesis on the nights when observations were made and it was reaching the end of its flowering period. The tree showed no sign of setting fruit, all flowers dropping within 2 d of opening.

Floral cycle

16h30   Flowers start to open; pollen polyads visible as the anthers dehisce longitudinally.
18h00   Dusk. Anthesis more or less complete, odour becoming stronger. A few insects seen to visit flowers, including wasps and very small Diptera.
18h50   Odour strongest. Visits by bees begin.
19h00–19h45   Bee visits numerous, *c*. 100 bees estimated to be in tree crown at any time.
20h00   Most of pollen removed. Bee activity sporadic.
Dawn (04h30–06h00) Flowers beginning to drop.

Behaviour of visitors

The bees collected all belonged to a single species of *Megalopta* Smith (Figure 1b) (vouchers deposited at INPA). They hovered briefly about 2 cm from a capitulum, then landed and immediately started moving quickly through the projecting anthers using their fore and mid legs. As they walked, they waggled their abdomens from side to side, while their hind legs moved backwards and forwards, apparently combing pollen from the anthers. The hind legs and lower abdomen rapidly became coated with a thick layer of pollen. The bees were in constant motion while on the capitula and did not stop to probe the flowers. They typically visited a capitulum for about 4 to 5 s (range 2 to 16 s). It was not possible to follow individual bees to see if they left the tree, but many perched on leaves within the crown, and the sporadic activity after about 19h45 was probably due to their being disturbed by the observer. They flew readily to light, and were very easy to collect.

Only a few other nocturnal visitors were seen, including moths, beetles and a cockroach. No bats were observed. Inflorescences cut from the crown and placed at *c*. 1.8 m above the ground received no visits at all during the period when observations were made in the canopy.

DISCUSSION

These observations are from a single tree, apparently acting as a male, and there is no direct evidence of pollen transfer to a stigma and subsequent seed

set. Nevertheless, the opening of the flowers in late afternoon, the absence of other visitors (especially bats and moths), and the evidence of a particular behaviour pattern amongst the bees, all suggest that nocturnal *Megalopta* bees are the probable pollinators of this species.

Evidence of nocturnal bee-pollination in a non-chiropterophilous species of *Parkia* in Amazonian Brazil is interesting on three counts. Firstly, there are few reports of pollination by nocturnal bees and rather little is known about the biology of *Megalopta.* Secondly, nocturnal melittophily is associated with a distinct set of characters that differs from those of both diurnal bee-pollination, as seen in *Parkia ulei,* and from occasional nocturnal visits by bees to the capitula of bat-pollinated species, as reported, for instance, at *P. speciosa* Hassk. in Java (Docters van Leeuwen 1938). Thirdly, it suggests a possible intermediate stage in the evolution of chiropterophily from diurnal entomophily, which is the presumed ancestral condition in mimosoid legumes, including *Parkia.*

Since these data are from only one tree, it is possible that they may eventually prove to be unrepresentative. However, the difficulty of working in rain forest canopy at night to gain information on the floral visitors of particular species of tree under natural conditions and the apparent paucity of observations of flower-visiting by nocturnal bees in the canopy demonstrate their potential interest, despite the small sample size.

Nocturnal foraging in Megalopta

Megalopta is the largest of three nocturnal bee genera in the neotropical tribe Augochlorini, family Halictidae, the others being *Megaloptidia* and *Megommation* subgenus *Megommation* (Engel 2000). Members of the genus are up to *c.* 2 cm long, and have large ocelli and compound eyes, which are related to nocturnal foraging; the loss of most of their body pigmentation and the loss of their ability to reflect UV are also associated with nocturnal activity (Engel 2000, Kerfoot 1967). They nest in small excavations in tree branches and are communal or perhaps primitively eusocial (Wolda & Roubik 1986); two species, however, are cleptoparasitic on other *Megalopta* species (Engel 2000, Engel *et al.* 1997), i.e. they are 'cuckoo bees' in which the females lay eggs in the nest of another species. *Megalopta* bees are attracted in large numbers to high-canopy light-traps (Roubik 1993) and the timing of flight, shortly after dusk, shortly before dawn, or both, differs somewhat according to species (Roulston 1997; M.S. Engel, *pers. comm.).* Other neotropical night-flying and/or crepuscular to matinal bees include *Ptiloglossa* (Colletidae) and some members of the families Apidae and Anthophoridae (Janzen 1968, Wolda & Roubik 1986), and in general, little is known about their biology. In addition to these nocturnal bees, some diurnal species forage after dark on moonlit nights (Roulston 1997).

Information on flower-visiting in *Megalopta* species comes from scattered sources and so far there have been no detailed studies. Janzen (1968) suggested that *Megalopta* bees probably forage in the canopy in primary forest though his records are from near ground level. In Costa Rica, he reported *M. centralis*

taking pollen at *Solanum sp.* (Solanaceae), nectar at *Calathea insignis* (Marantaceae), and pollen from *Ipomoea trifida* (Convolvulaceae) (Janzen 1968, 1983). In Mexico, *Megalopta* sp. forages at the flowers of *Ipomoea wolcottiana,* a small tree with nocturnal anthesis (Bullock *et al.* 1987) whose flowers are also visited by sphingid moths and several species of diurnal bees. This record probably refers to *M. tabascana* as this is the only species of *Megalopta* currently recognized from Mexico (M.S. Engel, *pers. comm.).* Mori & Boeke (1987) reported *M. genalis* as a probable pollinator of *Gustavia augusta* (Lecythidaceae) in forest understorey in French Guiana, the bees collecting pollen by vibrating the anthers (buzz-pollination); the flowers are open day and night but first open in the morning (S. Mori, *pers. comm*.). However, in most of these records it is not stated whether *Megalopta* is likely to have a significant role in the pollination of the flowers. Wolda & Roubik (1986) suggest that *Tachigali versicolor* is a major resource of *Megalopta* in Panama, as they caught large numbers at canopy light-traps during flowering, but they do not report any observations of foraging nor pollen loads on captured bees.

Where *Megalopta* has been observed collecting pollen from the inflorescences of several species of monocots (Cyclanthaceae: *Asplundia cf peruviana* [Gottsberger 1991]; Palmae: *Bactris* spp. and *Desmoncus* [Listabarth 1996] and *Oenocarpus* spp. [Küchmeister 1997]) the plants are primarily cantharophilous. *Megalopta* species also take pollen from flowers thought to be primarily chiropterophilous (Bombacaeae: *Pseudobombax septanatum* and *Ochroma pyramidale* [Roulston 1997]). In these cases, the bees may be opportunistic visitors or facultative pollinators.

Information on the feeding habits of *Megaloptidia* and *Megommation* is sparse (see summary in Engel & Brooks 1998). Of note, however, is the record of *Megaloptidia nocturna* visiting the night-opening, nectarless flowers of the herb *Dichorisandra ulei* (Commelinaceae), which has poricidal anthers suggesting buzz-pollination (Engel & Brooks 1998).

Thus these observations at *Parkia velutina* appear to be amongst the first accounts of *Megalopta* as the likely primary pollinator of a night-flowering tree. Nocturnal bees also occur in the palaeotropics, the best known example probably being *Apis dorsata* (references in Roubik 1989). Since the nocturnal canopy is relatively unexplored, the phenomenon of pollination by nocturnal bees may be commoner than these limited observations suggest.

Syndrome of nocturnal melittophily in Parkia

The pollination syndrome in *Parkia velutina* is characterized by nocturnal anthesis, the absence of detectable nectar, and a strong, sweet-musty scent (Table 2). The morphology of the capitula suggests they are not well adapted for pollination by other nocturnal vectors such as bats or moths. The capitula of bat-pollinated species of *Parkia* produce an unpleasant, fruity-musty odour and abundant nectar, and they are typically pendent on elongated peduncles and held free of the foliage. Where moth-pollination occurs in the related

Table 2. Table 2. Comparison of pollination syndromes in *Parkia*.

	Chiropterophily	Pollination syndrome Nocturnal melittophily	Diurnal melittophily
Taxonomic sections	*Parkia* and *Platyparkia*	*Sphaeroparkia* (P. velutina)	*Sphaeroparkia* (P. ulei)
Geographical distribution	Pantropical	Neotropical	Neotropical
Maximum diameter of capitula	4–9 cm	*c.* 4 cm	*c.* 1.4 cm
Number of flowers per capitulum	1000–3000	430	140
Shape of capitula	Clavate, pyriform, biglobose or oblete	Spherical	Spherical
Floral specialization	Yes	No	No
Colour of capitula	Reddish, cream-yellow, or both	Bright deep red	Pale cream-yellow
Inflorescence:			
Main axis	Unbranched	Unbranched	Much branched
Position	Usually distal to leaves	Proximal to leaves	Distal to leaves
Peduncles	Usually long and pendent	Short, neither pendent nor erect	Very short, neither pendent nor erect
Scent	Musty-fruity	Heavy, sweet, sickly, musty	Sweet, pleasant
Nectar	Very abundant	None detected	None detected
Timing of anthesis	Late afternoon	Late afternoon	Morning?
Visitors	Bats as pollinators; Non-flying mammals, birds and insects largely as thieves	*Megalopta* bees Augochlorini: Halictidae)	?Meliponine bees (Meliponini: Apidae), and other insects

neotropical genus *Inga,* the small to medium-sized tubular flowers are arranged in loose clusters, the anthers are much further exserted than in *Parkia,* and nectar is produced (Koptur 1983). According to Faegri & van der Pijl (1971), moth-pollinated flowers as a group produce larger volumes of nectar than nectariferous bee-flowers, although there are exceptions.

The characters associated with nocturnal melittophily in *Parkia velutina* are compared with those of the other pollination syndromes in *Parkia* in Table 2. Assigning a species to a particular syndrome is a reflection of its major pollinator, and does not mean that pollen is not sometimes transferred by other vectors, such as insects and non-flying mammals in 'chiropterophilous' species (e.g. Grünmeier 1990, Hopkins 1984, Ouédraogo 1995). *Megalopta* bees are somewhat larger than other flower-visiting bees reported from *P. ulei* and *P. multijuga.*

As Table 2 shows, the colour of the capitula in *P. velutina* is similar to that of some chiropterophilous species, and in both cases the capitula function for a single night. In general, flowers that attract pollinators at night are white, cream, pale green, or sometimes dull purple in bat-pollinated species (see Faegri & van der Pijl 1971), and *Parkia* is unusual in having nocturnal flowers that are reddish, yellowish or occasionally a mixture of both colours. Various hypotheses to account for the often bright colours in the bat-pollinated species of *Parkia* were discussed by Hopkins (1984) but none is entirely satisfactory,

and the possible functional significance of colour in this genus requires further investigation.

In addition to colour, two notable features of the floral biology of *P. velutina,* sexual expression and the presence of anther glands, show no association with pollination mechanism across the genus. The occurrence of male fertile-flowers (ignoring the gender of nectariferous and staminodial flowers in sections *Parkia* and *Platyparkia)* on the same tree as hermaphrodite ones either in the same or separate capitula, has been reported in many species of *Parkia* (Hopkins 1983, 1984) and andromonoecy is common in mimosoid legumes (Arroyo 1981); in no species of *Parkia* have functionally female flowers been reported. Andromonoecy probably minimizes wastage of resources where numerous, small flowers are produced in dense inflorescences, but only few, large or heavy fruits reach maturity.

Since this tree was nearing the end of flowering when observations were made, we do not know whether hermaphrodite flowers had been produced earlier and failed to set fruit or whether almost none were produced. While the survey of herbarium material at Kew found that functionally male flowers were common, it would have been too destructive to determine the relative proportions of capitula composed of different types of flowers (all male, all hermaphrodite, or a mixture) in different inflorescences. In the chiropterophilous species of *Parkia,* it was rare but not unknown for flowering trees to fail to set fruit, though the proportion of fruiting capitula is always a small proportion of the total (H.C. Hopkins & M.J.G. Hopkins, unpubl. data in 1979).

Anther glands are quite widespread in mimosoid legumes (tribes Parkieae, Mimoseae and Acacieae; Luckow & Grimes 1997) and they occur in most neotropical species of *Parkia* though they are almost entirely absent in the palaeotropical ones (Luckow & Hopkins 1995). In section *Sphaeroparkia* the stalk-like, basal attachments are longer than in the other two sections (Luckow & Hopkins 1995). Although several hypotheses have been put forward, their function remains largely unexplored (Luckow & Grimes 1997). In *Acacia* species in Africa, the anther glands are probably osmophores, secreting volatile, aromatic oils as the flowers open (Tybirk & Jorgensen 1994).

Nocturnal melittophily in Parkia multijuga?
Field observations of *Parkia multijuga,* a widespread canopy species in Amazonia and the third member of sect. *Sphaeroparkia,* have failed to demonstrate the pollination mechanism. Observations at trees in Belém (1979) and Manaus (1994, 1995, 1999) indicate that the flowers open in the late afternoon, with the stigmas extruded from the opening flowers before the corollas and anthers are exserted, and the flowers apparently remain fully open for several hours after dark. Bees were seen visiting flowers in the late afternoon in Belém, but in Manaus, despite several nights of observation, only a very few visitors were recorded, including beetles and nocturnal bees, but visits are so infrequent that

regular pollination is not indicated. Although the flower colour is different (bright yellow), and the odour stronger, *P. multijuga* appears similar in its floral biology to *P. velutina.*

Nectar was not detected in the field for *P. multijuga* and the anatomical evidence for nectar secretion is equivocal. According to Ancibor (1969), there is a scarcely thickened ring of nectariferous tissue around the base of the gynoecium. However, she demonstrated the same phenomenon in bisexual flowers in *P. discolor* Benth. (as *P. auriculata)* (section *Parkia),* and we know of no study that reports nectar secretion by the fertile flowers in any species in this section, where nectar appears to be secreted exclusively by specialized nectariferous flowers. Such flowers are found in both sections *Parkia* and *Platyparkia,* but not in sect. *Sphaeroparkia.* They are much thickened at the base, and at anthesis, abundant nectar is exuded from the mouth of the flower; in a few species it accumulates in a depression or 'nectar-ring' (Baker & Harris 1957). This suggests that if nectar is produced by the flowers of *P. multijuga,* it is likely to be in very small quantities.

It is particularly intriguing that the capitula of *Parkia multijuga* have a pungent scent similar to that of some neotropical chiropterophilous *Parkia* species. This led to the suggestion that they might be degenerate bat-flowers in the process of reverting to entomophily (Hopkins 1984), but it may be that this type of scent is also attractive to some nocturnal bees and is a 'preadaptation' for chiropterophily. So far, only the odour of the West African bat-pollinated *P. biglobosa* (Jacq.) G.Don has been analysed (Pettersson 1998). Its chemical composition differed strikingly from that of some neotropical chiropterophilous scents, such as those of *Parmentiera alata* (Bignoniaceae) and *Pilosocereus tweedyanus* (Cactaceae) (Knudsen & Tollesten 1995), as it lacks sulphur-containing compounds. Further information on the chemical composition of scents in *Parkia* is potentially useful in understanding the evolutionary pathways between different pollination mechanisms.

Significance of nocturnal melittophily for the evolution of chiropterophily in Parkia

Chiropterophily in *Parkia* poses an interesting evolutionary problem (Baker & Harris 1957) because pollination involves different groups of bats in different areas, pteropodid bats (Megachiroptera) in the palaeotropics and phyllostomids (Microchiroptera) in the neotropics. Several authors have speculated on where the genus might have originated, how and when it achieved a widespread distribution, and how many times chiropterophily has evolved within it (Baker & Harris 1957; Hopkins 1986, 1998; Luckow & Hopkins 1995; Vogel 1968–69). Some of these authors have also discussed what the ancestral pollination mechanism in *Parkia* might have been. For instance, Baker & Hurd (1968) suggested that the red colour of the capitula in some bat-pollinated species might be evidence of an ornithophilous ancestor, since vivid red is often associated with bird-pollination but is unusual in chiropterophilous plants, except in *Parkia.*

A cladistic analysis of *Parkia* based on morphological characters (Luckow & Hopkins 1995) showed that sect. *Sphaeroparkia* is basal within the genus though paraphyletic. The two chiropterophilous sections are derived, and a single origin of bat-pollination is implied (Figure 2). If this hypothesis is accepted, chiropterophily is likely to have been derived from entomophily, and not the other way round, as speculated by Hopkins (1984). The discovery of nocturnal melittophily in *Parkia velutina* does not solve the evolutionary paradox of the geographical and temporal origin of bat-pollination in *Parkia* first discussed by Baker & Harris (1957), but it does suggest a possible intermediate step in the switch between diurnal entomophily and chiropterophily.

In the consensus cladogram of Luckow & Hopkins (1995), the position of *Parkia velutina* is not resolved; it is either the sister taxon to *P. ulei* or sister to the rest of the genus (Figure 2). We will interpret the evolution of pollination mechanisms using the second topology for two reasons. The first is the pollination mechanism in the outgroup. While the sister taxon to *Parkia* is still undetermined, the likely candidates are diurnally pollinated as far as is known (M. Luckow, *pers. comm.).* For instance, members of the genus *Dichrostachys* in Madagascar appear to be pollinated by small, fast-flying, diurnal bees (M. Luckow, *pers. comm.).* Secondly, *P. multijuga* presents a similar floral syndrome to that in *P. velutina,* and probably has the same pollinators; it is therefore most parsimonious to hypothesize a single origin for nocturnal melittophily. If *P. velutina* and *P. multijuga* showed very different floral syndromes, nocturnal melittophily in *P. velutina* could be viewed as a uniquely derived condition and of no consequence in the path from diurnal entomophily to chiropterophily.

While too much reliance should not be placed on extant species as representing hypothetical ancestors, *P. ulei* and *P. velutina* can be used, with caution,
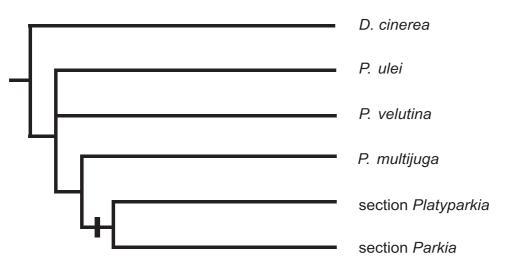

Figure 2. Simplified consensus cladogram of *Parkia,* showing the phylogenetic relationships between the outgroup (including *Dichrostachys cinerea),* the three species of *Parkia* section *Sphaeroparkia (P. ulei, P. velutina* and *P. multijuga),* and sections *Parkia* and *Platyparkia,* modified from Luckow & Hopkins (1995). The solid bar indicates the origin of bat-pollination.

to suggest the types of change that might have been involved in the evolution of bat-pollination in this genus. The first stage of the switch, from diurnal to nocturnal bee-pollination, would have involved a change in the timing of anthesis and perhaps changes in the chemical composition of the scent. Other differences between *P. ulei* and *P. velutina,* such as increases in the size of the capitula and the number of flowers per capitulum and a reduction in the degree of branching of the compound inflorescence, cannot easily be related to pollination by nocturnal bees although it can be argued that they are ultimately related to chiropterophily.

Character changes involved in the second step of the switch, seen by a comparison of *Parkia velutina* and the species in sections *Parkia* and *Platyparkia,* are: (a) the production of nectar, (b) the specialization of floral types within capitula, and (c) a further increase in the number of flowers per capitulum. With a few exceptions, there has also been a further increase in the size of capitula, changes in their shape including the development of a staminodial fringe in some, an increase in the length of the peduncles, and elongation of the main inflorescence axis. Some of these characters can be seen, to some extent at least, as adaptations to chiropterophily, making capitula easily accessible to bats, providing abundant nectar and pollen as food rewards while reducing their theft by other potential visitors, providing landing sites for bats, and perhaps involved in the dissemination of scent (see Hopkins 1998, table 3).

This hypothesis for the evolutionary pathway to chiropterophily in *Parkia* still leaves many questions unanswered. For instance, one rather perplexing change in character expression in this scenario would be the production of abundant nectar in the chiropterophilous species from entomophilous ancestors that either lacked floral nectar or produced only very small amounts; abundant nectar production, as seen in sphingid- and bird-pollinated flowers, has been suggested as a feature likely to facilitate the evolution of bat-pollination.

In a broader context, the possible role of nocturnal melittophily in the evolution of chiropterophily is not clear. Many of the neotropical bat-pollinated flowers described by Vogel (1968–69) are pollinated by specialized flower-visiting glossophagine bats, which are smaller and more manoeuvrable than *Phyllostomus discolor,* the most frequently recorded pollinator of neotropical *Parkia,* so the syndromes they present are rather different. The sister groups of most of these chiropterophilous plants are polinated by hawkmoths or birds, and relatively few are known to be pollinated by bees (Vogel 1968–69). Since chiropterophily has evolved in different groups of plants at different times and from different ancestral mechanisms, the significance of crepuscular and night-flying bees in this process cannot be assessed until we know more about their biology and that of the plants at which they forage.

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