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Novel observations of chiropterophily in *Palaquium obovatum* and flower visitation by *Cynopterus brachyotis*

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Abstract. Observation of flower visitations and pollination behaviour of the lesser dog-faced fruit bat, *Cynopterus brachyotis* (Pteropodidae), to *Palaquium obovatum* (Sapotaceae) in the Singapore Botanic Gardens is presented. Floral anthesis was found to occur in the evening and last around 24 hours, displaying typical chiropterophilous features. Although the Sapotaceae family is thought to be entomophilous, no insects were recorded as engaging in pollination activity despite the use of sticky traps and daytime observations. Bat visitation led to successful fruit set, which suggests that these mammals may have more positive ecological contributions to native ecosystems in Singapore than previously thought.

Key words. bat-plant interaction, mutualism, phenology, pollination, Sapotaceae, Pteropodidae.

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INTRODUCTION

Information is scarce on the pollinators of the tropical tree genus *Palaquium* (Sapotaceae). Pennington (2004) asserted that most species in the family are entomophilous (insect-pollinated). However, studies in Sarawak and Peninsular Malaysia (Momose et al., 1998; Hodgkison et al., 2004) have recorded pollination and flower visitation of *Palaquium* species by various species of birds and bats, specifically *Loriculus galgulus* (blue-crowned hanging parrot), *Arachnothera robusta* (long-billed spiderhunter) and *Eonycteris spelaea* (cave nectar bat). Species in *Madhuca*, a closely related genus in Sapotaceae, have been observed to be pollinated by various species of squirrels, bats, birds as well as carpenter bees (Momose et al., 1998; Nathan et al., 2009; Stephenraj et al., 2010). In the case of *Madhuca longifolia* var. *latifolia*, two species of bats, *Pteropus giganteus* (Indian flying fox) and *Cynopterus sphinx* (greater short-nosed fruit bat), were observed to destructively consume the flower corollas (Nathan et al., 2009), a behaviour also historically observed in *Madhuca macrophylla* (Hassk.) H.J.Lam, *Palaquium gutta* (Hook.) Baill. and *Palaquium quercifolium* de Vriese (Burck) on Java (van der Pijl, 1936; Pennington, 2004). Some studies suggest that such observations of flower destruction are misleading or account insufficiently for the bats' positive ecosystem contributions as pollinators (Stephenraj et al., 2010; Aziz et al., 2017), and Nathan et al. (2009) recognised the possibility of pollen transfer during corolla chewing, finding notably higher fruit set in bat-visited flowers than self-pollinated ones.

Chiropterophilous (bat-pollinated) plants often exhibit specific visual and olfactory characteristics that attract nocturnal members in the order Chiroptera, including representatives of Phyllostomidae and Pteropodidae (Faegri & van der Pijl, 1966; Marshall, 1983). A comprehensive literature review (Aziz et al., 2021) of 311 studies on Old World pteropodid (fruit bat)-plant interactions between 1985 and 2020 compiled evidence of pollination in six families: Bignoniaceae, Fabaceae, Lythraceae, Malvaceae, Musaceae and Sapotaceae. For Sapotaceae, pollination was only recorded for the genus *Madhuca* (Nathan et al., 2009; Stephenraj et al., 2010). Aziz et al. (2021) found that an earlier study citing bat pollination in *Palaquium* (Lee et al., 2002) was erroneous, as solely recording pollen in diets and/or flower visitation is insufficient to establish pollinator effectiveness without exclusionary experiments, assessment of floral ontological traits or bat visitation effects on fruit set.

Palaquium obovatum (Griff.) Engl., a native species distributed across Malesia, was of major economic importance in the past as a source of latex (gutta-percha). Records at the Singapore Botanic Gardens note that plantations were created on the island due to the loss of wild trees felled for gutta-percha harvesting (Ridley, 1901; Corlett, 1992). Fragmented wild populations are still present in the Bukit Timah Nature Reserve, the Nee Soon Swamp Forest, as well as Pulau Ubin, Sentosa, Lazarus and St. John's islands. The conservation status of *Palaquium obovatum* is assessed as Vulnerable (VU) in Singapore (Lindsay et al., 2022), and several large trees grow ex situ in the Singapore Botanic Gardens (SBG). Unlike

other native *Palaquium* species, *Palaquium obovatum* trees in cultivation have been observed to flower and set fruit more regularly (some every 1–2 years).
No specific flowering season has been recorded for *Palaquium obovatum*, but individuals of the same species of Sapotaceae have a tendency to flower in synchronicity within a small area (Ng, 1972). As three *Palaquium obovatum* trees in the Singapore Botanic Gardens were observed to be simultaneously setting bud around October 2021, a camera trap was deployed to record inflorescence development and visitations. During flowering, sticky flytraps were also placed close to flower clusters. It was hoped that observations from the recordings and traps would establish (1) flower emergence timing and corolla persistence, (2) what insects or animals visited the flowers and (3) if interactions had a bearing on pollination and success of reproduction.

MATERIAL & METHODS

In October 2021, three individuals of *Palaquium obovatum* (8–10 m tall, within 5 m of each other) opposite Ridley Hall at the Singapore Botanic Gardens were observed to be setting flower buds. Other medium to large trees of the same species in other locations within the Gardens were not found in similar fertile states. Of the three trees setting bud, only one had branches at eye-level or accessible using a 2 m tall step ladder; the other two only had inflorescences on branches above 5 m that would have required specialised tree climbing and safety equipment, constraining accessibility and regular monitoring, and as such could not be included in this study. A camera trap (Bushnell Trophy Trail Camera; Bushnell Corporation, Kansas, USA) was deployed on the accessible tree, facing two branches with budding inflorescences, and whenever the camera was automatically triggered by movement (trigger speed estimated at less than one second, although this may depend on animal distance from camera trap, see Palencia et al., 2021), it would record a ten-second video. Footage was checked weekly from October to December 2021. In January 2022, once the tree started showing signs of flowering, ten sticky traps (6 × 6 cm each) were wire-tied onto separate branches nearest the inflorescences, and camera footage checked daily. Additional opportunistic observations were made at least three times a week during the day (between 0800 and 1800 hours when there was sufficient natural light) using binoculars from the ground. Buds developing into flowers, which were observable at eye-level, were monitored by sight and smell hourly between 0800 and 2300 hours. The camera was removed in May 2022, after all trees had completed fruiting.

RESULTS

Inflorescences of *Palaquium obovatum*, like many Sapotaceous taxa, were clustered in fascicles near leaf scars away from fresh foliage (Fig. 1A), providing unobstructed flying pollinator access and landing areas.

Flowering lasted two weeks, from 12 to 25 January 2022, with flowers observed to open mostly from the uppermost branches first, followed by lower branches. Flower buds, once opened, emitted a strong, sweet, medicinal scent tinged with fermentation, and elevated pungency between 1700 to 2100 hours. Anthesis occurred between 1600 to 2000 hours and dehiscence of anthers between 1900 to 2000 hours. The corollas with stamens attached (Fig. 1B) fell off within 24 hours, or rarely up to 48 hours after anthesis, but were often knocked off before this by wind/rain or biotic interactions (during the monitoring period, thunderstorms dislodged several flowers or fruit).

Fig. 1. A, Inflorescence of *P. obovatum* showing close clusters of flowers. B, Fallen corollas, with stamens still attached. C, Ants (indicated by red arrows) feeding on nectar in fallen corolla. (Photographs by: L. Neo [A] and A. Phang [B-C]).

None of the sticky flytraps captured any insects, although corollas fallen on the ground were heavily visited by ants, indicating significant nectar presence (Fig. 1C). The camera trap revealed a pteropodid bat (identified from white-edged wing bones as *Cynopterus brachyotis,* a species known to have roosts in the Singapore Botanic Gardens (Chan et al., 2021). The bat visited the flowers on two separate occasions, once on 18 January at 0030 hours (Branch 1) and on 19 January at 0159 hours (Branch 2). During the first visit, the bat was seen inserting its muzzle into two separate open flowers (the video can be viewed at https://youtu.be/XPnX-kDBMMs); the corollas of those flowers remained intact even ten hours after the visit (Fig. 2B), indicating that nectar was the primary food target, not the corolla. Both corollas had dropped off by 1200 hours on 18 January. For the second visit (video capture lasting two seconds) (Branch 2), video footage resolution was less clear and although there was physical contact between the bat and the inflorescence as the corollas on the flowers were no longer seen after the bat visit, the nature of the interaction was ambiguous, and it was not possible to ascertain if the corollas were eaten or knocked off.

On Branch 1, only three buds developed into full open flowers. Both of the flowers visited by the bat developed into fruit. The third flower on the branch (Fig. 2B), where the corolla had dropped off before the bat visitation, did not set fruit. Of the two developing fruits, one fell off the branch while still immature, while the remaining fruit developed into a mid-sized berry before dropping to the ground on 30 February (Figs. 2C–D).

On Branch 2, the two flowers likely visited, appeared to develop into fruit. However, only one fruit developed into a small berry (not full-sized) and fell off prematurely on 24 February (Fig. 3).

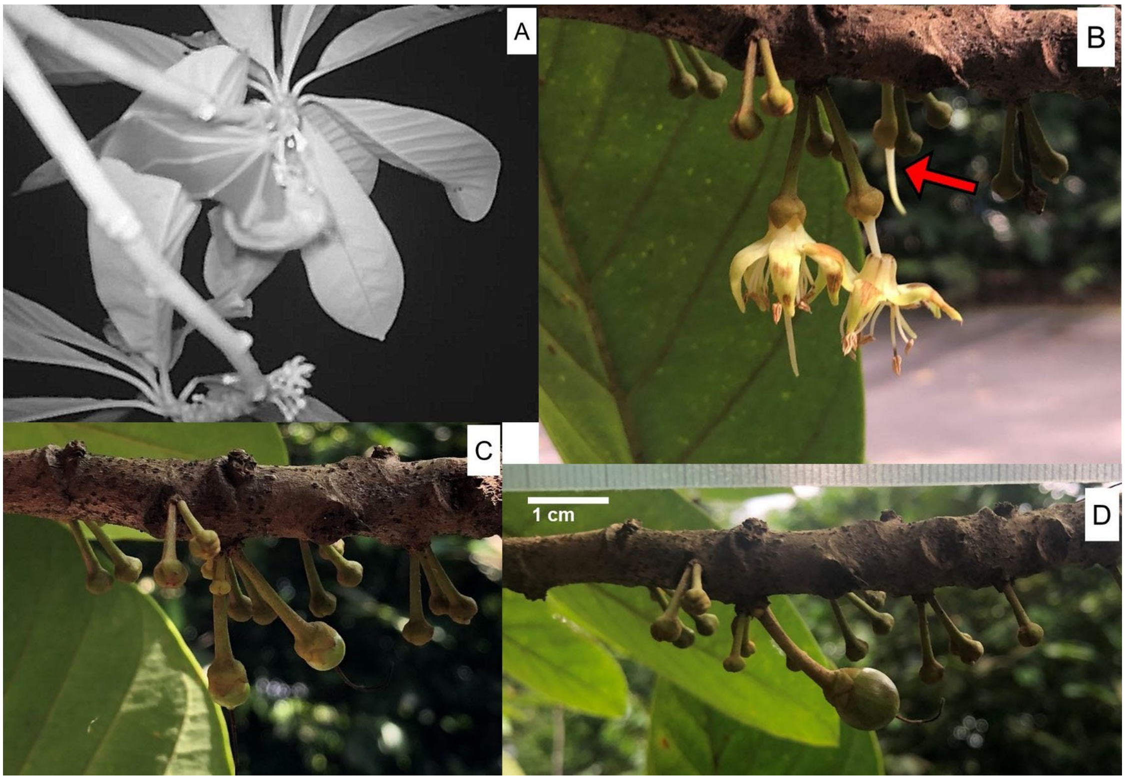

Fig. 2. Branch 1. A, Video still of *Cynopterus brachyotis* feeding by inserting its muzzle into flower corollas (18 January 2022, 0030 hours). B, Corollas of both flowers still attached the following morning (18 January 2022, 1000 hours); partial flower indicated by red arrow not visited by bat, as corolla had spontaneously fallen off earlier in the day. C, Development of immature fruit from same flowers visited by bat (14 February 2022). (D) Single fruit remaining (28 February 2022). (Photographs by: A. Phang).

DISCUSSION

This study confirms *Palaquium obovatum* as a chiropterophilous species with flower characteristics that attract *Cynopterus brachyotis.* Chiropterophilous syndromes in the literature, including nocturnal anthesis, strong night odour, large quantities of nectar, numerous anthers with pollen, cauliflorous position outside the foliage with aggregate or brush inflorescences of small flowers (Faegri & van der Pijl, 1979; Marshall, 1983), were cross-checked and confirmed by observation, with floral development similar to other bat-pollinated groups, e.g., *Durio* (Soepadmo & Eow, 1976). Peak stigma receptivity, as well as increased nectar secretion, although not observed, was proposed to be around 2000 hours by Aziz et al. (2017) in a pollination study of durian trees.

Fig. 3. Branch 2. A, Two open flowers, likely visited by *Cynopteris brachyotis* (18 January 2022, 1700 hours). B, Immature fruit development from same flowers (7 February 2022). (C) Continued fruit development of single remaining berry, same fruit from panel B indicated by red arrow (21 February 2022). (Photographs by: A. Phang).

This investigation also provides the first evidence that the lesser dog-faced fruit bat engages in non-destructive flower foraging and pollination behaviour. The only other bat species recorded in the literature with flower parts of *Palaquium obovatum* in its diet is *Eonycteris spelaea* (Hodgkison et al., 2004), a nectar specialist compared to the more frugivorous *Cynopterus brachyotis* (Stewart & Dudash, 2017).

As *Cynopterus brachyotis* is well known as a seed disperser of *Palaquium obovatum* (Phua & Corlett, 1989; Tan et al., 1998; Hodgkison et al., 2004), its additional role as a pollinator implies the occurrence of double mutualism, where beneficial interactions take place through two different functions between partner species. In this instance, a single bat species operates both as pollinator and seed disperser of the same plant.

More work is needed to ascertain if *Cynopterus brachyotis*, a species that tends to forage opportunistically near its roosts (Chan et al., 2021), plays a key role in wild pollination of *Palaquium* species across Singapore, as this investigation was confined to individuals in cultivation. A study in Thailand of several species of flower-visiting bats indicated that *Cynopterus* sp. there were not considered true pollinators, in part due to insufficient carriage of pollen load. They were outcompeted in floral foraging by abundant nectar specialists such as *Eonycteris spelaea* (Stewart & Dudash, 2017), a species known as a significant pollen disseminator (Start & Marshall, 1976) and found in Singapore. Stewart & Dudash (2017) also recorded that certain plant taxa were dependent on a single bat species, and as such, susceptible to changes in pollinator abundance.

Unlike *Palaquium obovatum*, the other species of *Palaquium* in Singapore flower rarely and irregularly. No fertile collection of *Palaquium impressinervium* Ng, locally found only in the Bukit Timah Nature Reserve, has been made in the last fifty years, and it remains to be determined whether interactions with animal pollinators (or the lack thereof) play a role in fecundity.

Other forms of pollination remain possibilities. Self-pollination has been recorded in other genera in the same family (*Manilkara* and *Madhuca*), although bagging experiments indicate that significantly less fruit set is produced than with cross-pollinated flowers (Nathan et al., 2009; Hiwale, 2015). Bees and butterflies have also been observed to pollinate Sapotaceae taxa such as *Micropholis* species in the New World (Terra-Araujo et al., 2012).

The observations presented in this paper are notable as chiropterophily, compared to bird or insect pollination, is relatively uncommon among angiosperms, likely due to the energy expense of copious nectar production (e.g., 8–20 times more calories per flower in bat-pollinated cactus species, compared to those pollinated by hawkmoths or hummingbirds (Fleming, 2002)), and often ephemeral, intense periods of "big-bang" flowering (Stewart & Dudash, 2017). Fleming et al. (2009) proposed that bat-flower evolution was likely to have occurred in plants adapting to low densities and fragmented landscapes, factors that are extremely relevant to Sapotaceae taxa like *Palaquium* found in limited abundance (LaFrankie, 1996) and also in the context of Singapore's extreme urbanisation (Yee et al., 2011); bats are thus valuable to preserving gene flow between isolated individuals, and their roles as both pollinators and seed dispersers mean they have a profound impact on healthy ecosystems.

CONCLUSION

An understanding of the pollination ecology of numerous tropical trees, particularly for species that flower infrequently, remains exceedingly limited. Although this study is the first to record flower visitation and pollination behaviour by the lesser dog-faced fruit bat, *Cynopterus brachyotis*, toward *Palaquium obovatum*, more data and subsequent interpretation are required to ascertain the prevalence and effectiveness of specific pollinators.

Studies such as this one can help mitigate generally held negative attitudes against pteropodids (Aziz et al., 2021), and highlight their important ecological role in different landscapes, including urban or disturbed areas. Further work on mutually beneficial bat-plant interactions, both in remnant forest patches or degraded environments, would help to uncover evidence that can influence conservation priorities and actions for thriving natural communities.

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LITERATURE CITED

Aziz SA, Clements GR, McConkey KR, Sritongchuay T, Pathil S, Abu Yazid MNH, Campos-Arceiz A, Forget P-M & Bumrungsri S (2017) Pollination by the locally endangered island flying fox (*Pteropus hypomelanus*) enhances fruit production of the economically important durian (*Durio zibethinus*). Ecology and Evolution, 7: 8670–8684.

Aziz SA, McConkey KR, Tanalgo K, Sritongchuay T, Low M-R, Yong JY, Mildenstein TL, Nuevo-Diego CE, Lim V-C & Racey PA (2021) The critical importance of Old World fruit bats for healthy ecosystems and economies. Frontiers in Ecology and Evolution, 9: 641411.

Chan AAQ, Aziz SA, Clare EL & Coleman JL (2021) Diet, ecological role and potential ecosystem services of the fruit bat, *Cynopterus brachyotis*, in a tropical city. Urban Ecosystems, 24: 251–263.

Corlett RT (1992) The ecological transformation of Singapore, 1819–1990. Journal of Biogeography, 19: 411–420.

Faegri K & van der Pijl L (1966) The Principles of Pollination Ecology. Pergamon Press, New York, 258 pp.

Fleming TH (2002) Pollination biology of four species of Sonoran Desert columnar cacti. In: Fleming TH & Valiente-Banuet A (eds.) Columnar Cacti and Their Mutualists: Evolution, Ecology and Conservation. University of Arizona Press, Tucson, pp. 207–224.

Fleming TH, Geiselman C & Kress WJ (2009) The evolution of bat pollination: a phylogenetic perspective. Annals of Botany, 104: 1017–1043.

Hiwale S (2015) Sapota [*Manilkara achrus* (Mill) Forsberg]. In: Hiwale S (ed.) Sustainable Horticulture in Semiarid Dry Lands. Springer, New Delhi, pp. 115–134.

Hodgkison R, Balding ST, Zubaid A & Kunz TH (2004) Temporal variation in the relative abundance of fruit bats (Megachiroptera: Pteropodidae) in relation to the availability of food in a lowland Malaysian rain forest. Biotropica, 36: 522–533.

LaFrankie JV (1996) Distribution and abundance of Malayan trees: Significance of family characteristics for conservation. Gardens' Bulletin Singapore, 48: 75–87.

Lee S, Yaakob NS, Boon K & Chua L (2002) The role of selected animals in pollination and dispersal of trees in the forest: implications for conservation and management. Journal of Tropical Forest Science, 14: 234–263.

Lindsay S, Middleton DJ, Ho BC, Chong KY, Turner IM, et al. (2022) Flora of Singapore: A checklist and bibliography. Gardens' Bulletin Singapore, 74 (Supplement 1): 3–860.

Marshall AG (1983) Bats, flowers and fruit: evolutionary relationships in the Old World. Biological Journal of the Linnean Society, 20: 115–135.

Momose K, Yumoto T, Nagamitsu T, Kato M, Nagamasu H, Sakai S, Harrison RD, Itioka T, Hamid AA & Inoue T (1998) Pollination biology in a lowland dipterocarp forest in Sarawak, Malaysia. I. Characteristics of the plant-pollinator community in a lowland dipterocarp forest. American Journal of Botany, 85: 1477–1501.

Nathan PT, Karuppudurai T, Raghuram H & Marimuthu G (2009) Bat foraging strategies and pollination of *Madhuca latifolia* (Sapotaceae) in southern India. Acta Chiropterologica, 11: 435–441.

Ng F (1972) Sapotaceae. In: Whitmore TC (ed.) Tree flora of Malaya, 1: 388–439.

Palencia P, Vicente J, Soriguer RC & Acevedo P (2022) Towards a best-practices guide for camera trapping: assessing differences among camera trap models and settings under field conditions. Journal of Zoology, 316: 197–208.

Pennington TD (2004) Sapotaceae. In: Kubitzki K (ed.) The Families and Genera of Vascular Plants. VI. Flowering Plants Dicotyledons. Springer-Verlag, Berlin, pp. 390–421.

Phua PB & Corlett RT (1989) Seed dispersal by the lesser short-nosed fruit bat (*Cynopterus brachyotis*, Pteropodidae, Megachiroptera). Malayan Nature Journal, 42: 251–256.

Ridley H (1901) Annual Report on the Botanic Gardens, Singapore, for the Year 1909–1913. Government Printing Office, Singapore.

Soepadmo E & Eow B (1976) The pollination ecology of durian (*Durio zibethinus*, Bombacaceae) in southern Thailand. Gardens' Bulletin Singapore, 29: 25–33.

Start A & Marshall A (1976) Nectarivorous bats as pollinators of trees in West Malaysia. In: Burley J & Styles BT (eds.) Tropical Trees: Variation, Breeding and Conservation. Academic, New York, pp. 141–150.

Stephenraj D, Isaac S, Kunz T & Stanley J (2010) Foraging behaviour of megachiropteran bats (Chiroptera: Pteropodidae) in Courtallam, Tamilnadu, South India. Bioinfolet, 7: 175–180.

Stewart AB & Dudash MR (2017) Flower-visiting bat species contribute unequally toward agricultural pollination ecosystem services in southern Thailand. Biotropica, 49: 239–248.

Tan K, Zubaid A & Kunz T (1998) Food habits of *Cynopterus brachyotis* (Müller) (Chiroptera: Pteropodidae) in Peninsular Malaysia. Journal of Tropical Ecology, 14: 299–307.

Terra-Araujo MH, de Faria AD, da Silva Ribeiro JEL & Swenson U (2012) Flower biology and subspecies concepts in *Micropholis guyanensis* (Sapotaceae): evidence of ephemeral flowers in the family. Australian Systematic Botany, 25: 295–303.

van der Pijl L (1936) Fledermäuse und Blumen. Flora oder Allgemeine Botanische Zeitung, 131: 1–40.

Yee ATK, Corlett RT, Liew SC & Tan HT (2011) The vegetation of Singapore — an updated map. Gardens' Bulletin Singapore, 63: 205–212.