Pollinating and non-pollinating fig wasps (Hymenoptera: Chalcidoidea) from *Ficus elastica*, the living root bridge tree of Meghalaya in northeast India

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The Indian rubber fig tree *Ficus elastica* Roxb. ex Hornem. Moraceae is the constituent of the iconic living root bridges (LRBs) in Meghalaya, India, and is characterized by a highly specific mutualism between the fig and its pollinating agaonid fig wasp, in which the wasps breed within fig inflorescences. *F. elastica* is restricted to south and southeast Asia in its distribution. We identified the pollinating fig wasp as *Platyscapa clavigera* (Mayr 1885) which was first described from *F. elastica* in Bogor in 1885 and from Singapore in 2017. This is the first record of the pollinator (family Agaonidae) from *F. elastica* in Meghalaya, northeast India, in the westernmost portion of the fig's range. We also discovered and identified in *F. elastica*, a non-pollinating fig wasp of the genus *Micranisa* which appears close to *Micranisa ralianga* Mathew and Balakrishnan 1981 (Pteromalidae). This fig wasp has not been earlier reported anywhere from the closed urn-shaped inflorescences (i.e. syconia) of *F. elastica* and was only described from the syconia of *Ficus altissima* Blume in 1981 from Meghalaya. Notes on the morphology of both fig wasps are provided and illustrated. The phenology and developmental cycle of *F. elastica* syconia are documented. Evidence of passive pollination was confirmed in *F. elastica* which sheds light on the evolution of character traits in figs and their wasps.

Keywords: *Ficus elastica*, fig wasps, *Micranisa ralianga*, Meghalaya, *Platyscapa clavigera*.

Ficus elastica Roxb. ex Hornem. (Family Moraceae; Tribe Ficeae; Section Galoglychia; Subsection Conosycea) is the Indian rubber tree. This species was reported from the Eastern Himalaya, Khasi Hills, Assam, India; Myanmar and the Malayan region[1]. In the north-eastern part of India, the species grows abundantly in the Khasi and Jaintia Hills of Meghalaya (Figure 1)[2,3]. *Ficus elastica* is well known for its remarkable utilization by the indigenous Khasi and Jaintia tribes of Meghalaya in which the aerial roots over a time period of 15–30 years are intertwined to grow 'living' bridges over hill and mountain streams (Figure 2)[4–6]. A few of these bridges are likely more than hundreds of years old and are sites for tourism. These living root bridges are locally called '*jing kieng jri*' and are widely distributed in the state of Meghalaya[7].

The genus *Ficus*, to which all figs belong, is defined by a unique brood-site insect pollination system. There are about 876 *Ficus* species globally[8] distributed in tropical and subtropical areas. The inflorescence is an enclosed urn-shaped syconium lined internally by male and uni-ovulate female flowers. Each fig is usually associated with a particular wasp species (Chalcidoidea, Agaonidae) for pollination[9,10]. During the pollen-receptive phase, the syconia of each fig species produce specific volatile compounds which attract these species-specific pollinating wasps[11]. The female pollinators laden with pollen enter the syconium via a single entrance called an ostiole that is guarded by bracts, pollinate many flowers resulting in seeds and also lay eggs in some pollinated flowers producing galls. After several weeks, the wasps developing within the galls reach maturity, wingless males emerge from their galls, mate with the females and release them from their galls. The pollen-laden female wasps disperse through the exit passage in the syconium wall made by male wasps in search of another pollen-receptive fig syconium to continue their life cycle. Apart from the pollinating fig wasps, several non-pollinating fig wasps (NPFWs) invade the syconium before or after pollination and lay eggs through the fig walls into the fig ovules or existing galls[12,13]. Some NPFWs can also enter through the ostiole for egg laying[14,15]. NPFWs occur in Agaonidae within subfamily Sycophaginae and in Pteromalidae within the subfamilies Otitesellinae, Epichrysomallinae, Sycoecinae and Sycoryctinae[16].

Pollination in figs can be either active or passive. In active pollination, the female pollinators actively collect pollen in their thoracic pollen pockets and also possess

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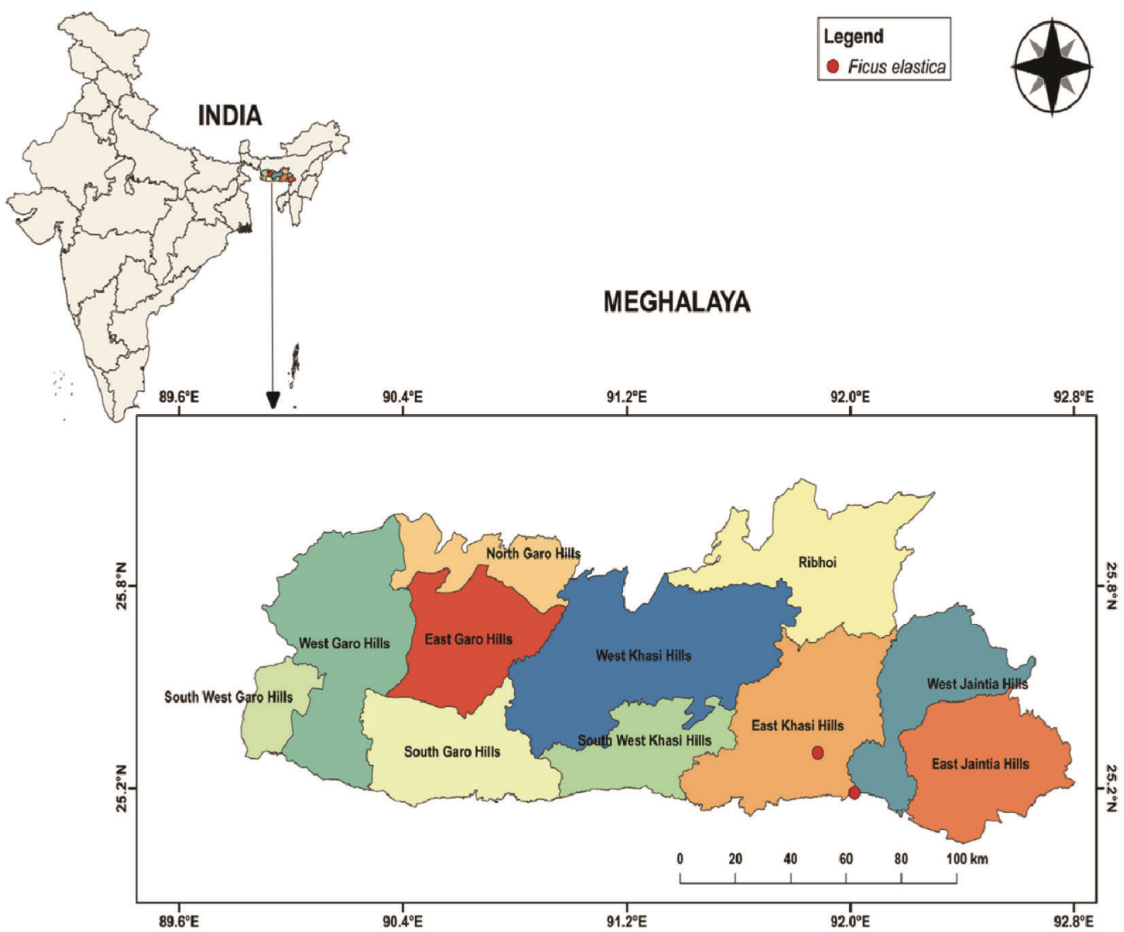

Figure 1. Map showing the study site in Meghalaya of northeast India; red dots indicate the collection locations (GPS coordinates in text).

coxal combs on their fore coxae which they use to remove pollen from the pockets and deposit it on flower stigmas[17,18]. In passive pollination, the fig syconia release large amounts of pollen during anther dehiscence at the wasp dispersal phase and the pollinators are covered with pollen when they leave the natal fig syconium, which they passively deposit on flower stigmas[18–20]. Based on previous studies[18,21,22], it is not clear whether the pollinators of *F. elastica* have coxal combs on their fore coxae or pollen pockets that would be indicative of active pollination in this system.

Till date, there is no record of fig wasps from *F. elastica* present in the north-eastern region of India. Pollinators have only been recorded from Bogor in Java, Indonesia, and in Singapore[21,23], and therefore, it is important to determine if the same pollinator species occurs in the north-eastern region of India. This is because, although the fig–fig wasp interaction is usually highly species-specific, some fig species are serviced by different pollinator species across their range[24–26], especially in the case of a widely distributed fig species. We report a pollinator (family Agaonidae) and also a NPFW (family Pteromalidae) from syconia of *F. elastica* in Meghalaya, northeast India. We present detailed morphological characters, light microscope and scanning electron microscope (SEM) images of the associated fig wasps in the current study, which were missing from earlier studies[21–23,27], and taxonomic papers[3,23,28]. We also confirm the pollination mode in *F. elastica* by examining wasp and syconial features.

Materials and methods

Under natural conditions, *F. elastica* is a hemi-epiphytic fig species; seedlings germinate on host trees and grow to ultimately strangle the host tree, eventually setting down aerial and terrestrial root systems[7]. Populations of *F. elastica* are distributed mainly in the East Khasi Hills and West Jaintia Hills districts of Meghalaya in the north-eastern part of India. Due to the difficult mountainous terrain, and since most of the fig trees did not produce syconia during our observation period, our study is limited to a few trees from East Khasi Hills district for the collection of wasps, and also for phenological studies. The map showing the study sites in Meghalaya was prepared using QGIS software (Figure 1)[29].

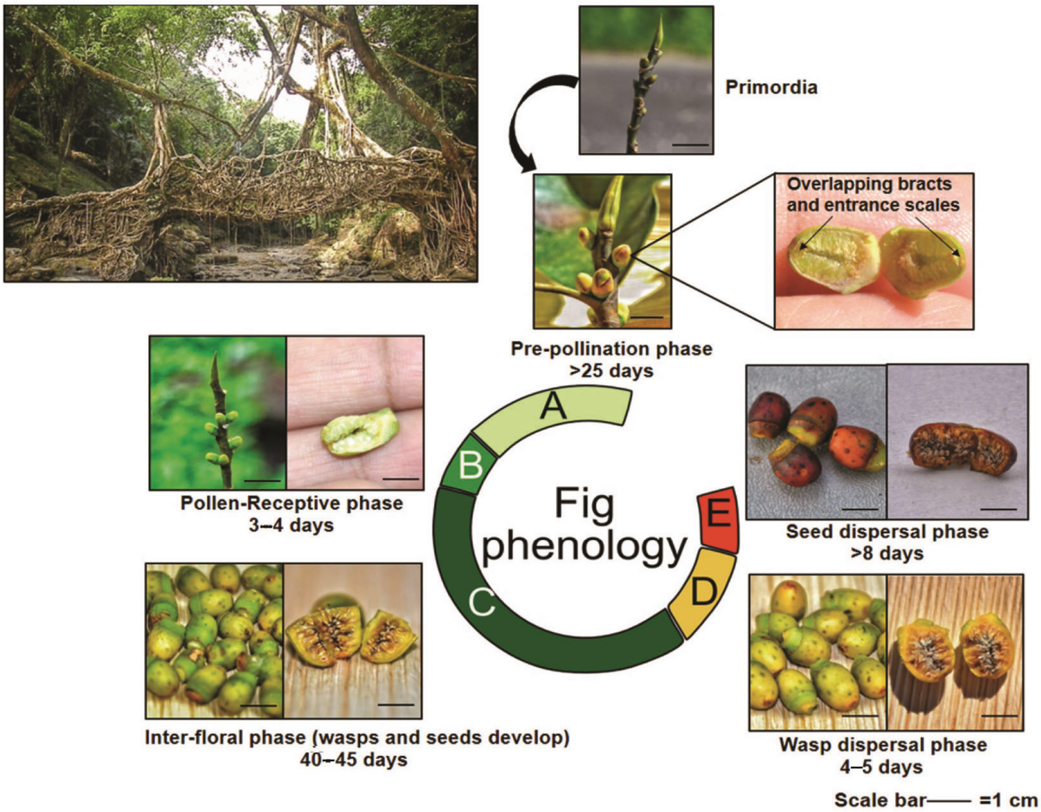

Figure 2. The cycle of syconium development in *Ficus elastica* and an example of an old living root bridge *in situ*. Size of syconium from A–E phase ranged from 0.9 to 1.5 cm in size. Phase A, The ostiole (opening) of the green syconium is tightly closed by overlapping bracts and entrance scales. Phase B, Female flowers are matured and female pollinators enter the syconium through the ostiole for pollination. Phase C, The wasp offspring and the fig seeds develop within the galled and pollinated flowers and the syconia turn yellowish in colour. Phase D, The male flowers mature with dehiscence of anthers and the wasps complete their life cycle development and reach maturity. Phase E, The mature ripened syconia turn brownish red, a transition that is accompanied by sweet, fruity odours.

Phenological observation

Owing to the difficulty of access to these fig trees, and their very sporadic flowering (only twice a year), only one easily accessible tree was selected and $N = 100$ syconia were monitored from the budding or primordial phase for observation of the syconium developmental cycle. The five developmental stages in a monoecious fig syconium cycle as reported from previous work[30] and followed in the present study are: (i) pre-pollination phase (Phase A), (ii) pollen-receptive or female flower phase (Phase B), (iii) inter-floral phase or wasp development phase (Phase C), (iv) wasp dispersal or male flower phase (Phase D), and (v) seed dispersal phase (Phase E; Figure 2).

Collection and morphological observations of fig wasps

Fig wasps (both male and female) were collected from matured unopened syconia ($N = 20$) which were in the dispersal phase and stored in ethanol (80–90%). Morphological observations were compared with previous descriptions from literature for identification[21–23,27]. All the specimens were deposited at the Centre for Ecological Sciences, Indian Institute of Science, Bengaluru, India. Images were taken at the Department of Entomology, University of Agricultural Sciences, GKVK, Bangalore using a stereo microscope LEICA M205 C fitted with a Leica DFC450C digital camera. Images at varying focal depths were stacked using Leica Auto Montage Software Version V4.3. For scanning electron microscopy, specimens were mounted on brass stubs and sputter coated with gold prior to observation, and images were captured in a JEOL IT 300 SEM at the advanced facility for microscopy and analysis, Indian Institute of Science, Bangalore, and also in the JEOL JSM-6360 SEM at the Sophisticated Analytical Instrument facility, North-Eastern Hill University, Shillong, Meghalaya.

Pollination mode in *F. elastica*

For direct evidence of active or passive pollination, we followed Kjellberg *et al.*[18]. We examined additional traits which were correlated with pollination mode: (i) For fig

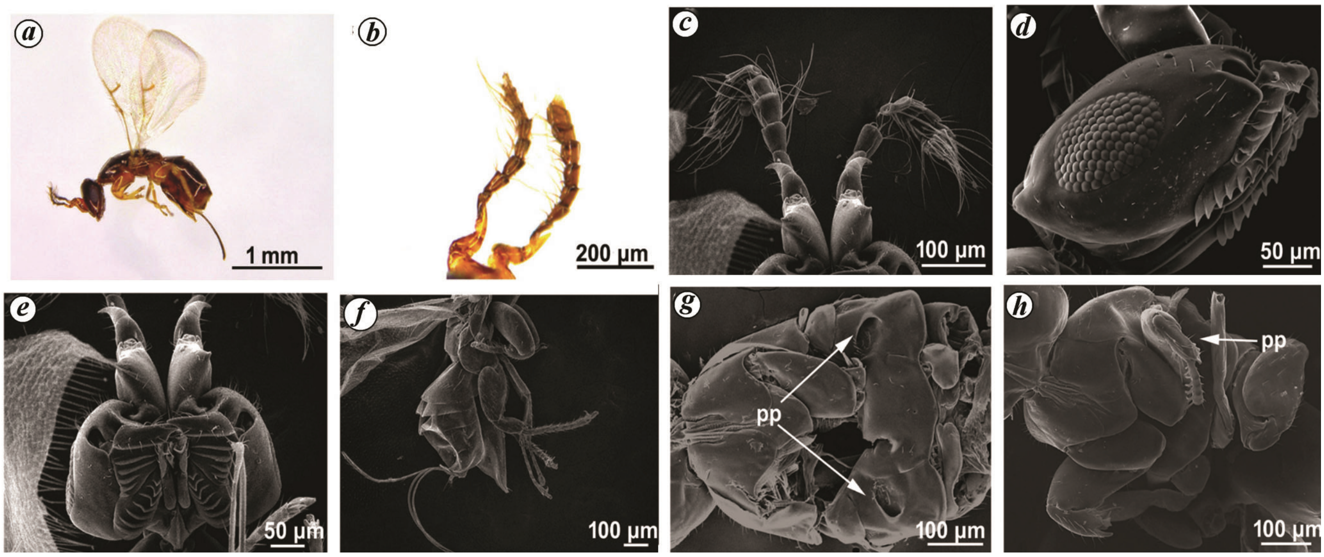

Figure 3. *Platyscapa clavigera* female: (***a***) Lateral image; (***b***) Antennae; SEM images of (***c***), Antennae; (***d*** and ***e***), Mandibular appendage; ***f***, Abdomen; ***g*** and ***h***, Ventral view of mesosoma showing pollen pockets and lack of coxal combs in the fore coxae (pp – pollen pocket, the head is pointing left).

syconium traits, we counted the number of anthers and female flowers in each syconium of *F. elastica* ($N = 10$ syconia), at the D-phase stage (before wasp emergence). Actively pollinated fig species produce fewer pollen with low anther-to-ovule ratios in comparison to passively pollinated fig species which have a higher ratio[31]. (ii) We also examined whether the fore coxae of pollinating wasps bear a comb (line of setae), and if thoracic pollen pockets were absent or present in a developed or reduced form. (iii) We examined pollen load on dispersing wasps and/or presence of pollen in pollen pockets.

Results

Development of syconia in F. elastica

F. elastica produced syconia twice a year, i.e. from April to first week of July, and September to second week of December 2017, during the period of our study. The duration of the development cycle of the syconium was 80–90 days (Figure 2). In the pre-A phase, syconium bud primordia develop along the tips of branches towards the long horn-shaped stipule which is a characteristic feature of the species. After 25–30 days from primordial stage, the outer bracteolar scales, that are prominent at the entrance of the ostiole, are shed; this shedding takes 3–4 days for the entire tree. Following this shedding, the pollen-receptive B phase commences after 7–8 days.

Morphology of fig wasps

Platyscapa clavigera (Mayr 1885)

The collected wasp was identified as the pollinator *Platyscapa clavigera* (Mayr 1885) (originally named *Blastophaga clavigera*), by following the descriptions of Mayr[21] and Harrison *et al.*[23]. The important morphological features of male and female wasps are as follows:

Material examined: 4♀ and 3♂ from India: Meghalaya, Shillong, Umsyiem (25°11.269′N; 92°00.868′E) 29. xi. 2017, Coll: Nongbri L.B., Meghalaya, Shillong, Rangthylliang (25°18.339′N; 91°52.948′E) 21. xi. 2018, Coll: Nongbri L.B.

Female: Body shiny brown; smooth and glabrous, with paler legs, antennae 11-segmented; scape of the antennae flattened, funicular segments cup shaped, ovipositor longer than gaster; hypopygium with a blunt spine. Post marginal vein of the forewing almost equal in length with the stigmal vein. Pollen pockets present on the side of the thorax. Coxal combs in the fore coxae are absent (Figure 3).

Male: Body shiny golden yellow with darker head, eyes black, head shorter than its width, face transverse in front, mandible bidentate, antennal groves deep, final antennal segments fused to form a club, meso and metanotum more or less fused (Figure 4).

Micranisa sp.

The collected wasp was identified as a NPFW belonging to the genus *Micranisa* and bears close resemblance to *Micranisa ralianga* Mathew and Balakrishnan 1981 by following the keys of Wang *et al*[32]. This wasp was found occupying the same syconium as the pollinator but was rare in occurrence. We collected only 3 specimens from 3 out of 150 syconia collected from both the sites. The morphological description of the female wasp is as follows. No males were found.

Table 1. Flowers, wasp galls and bladders in syconia of *Ficus elastica*

Syconium identity	Number of male flowers	Total number of female flowers (no. of galls + no. of seeds + no. of undeveloped flowers/bladders)	Anther-to-ovule ratio[1]	Seed-to-gall ratio[2]	Mean anther-to-ovule ratio (±SD)	Mean seed-to-gall ratio (±SD)
1	110	117 (40 + 72 + 5)	0.94	1.80	0.97 ± 0.087	1.35 ± 0.483
2	114	123 (59 + 56 + 8)	0.93	0.95		
3	124	114 (52 + 58 + 4)	1.09	1.12		
4	99	105 (44 + 54 + 7)	0.94	1.23		
5	115	117 (56 + 55 + 6)	0.98	0.98		
6	123	132 (45 + 77 + 10)	0.93	1.71		
7	99	109 (33 + 67 + 9)	0.91	2.03		
8	92	107 (58 + 42 + 7)	0.86	0.72		
9	106	92 (43 + 43 + 6)	1.15	1.00		
10	97	101 (32 + 64 + 5)	0.96	2.00		

[1]Anther-to-ovule ratio = number of male flowers/number of uniovulate female flowers.
[2]Seed-to-gall ratio = number of seeds/number of galls.

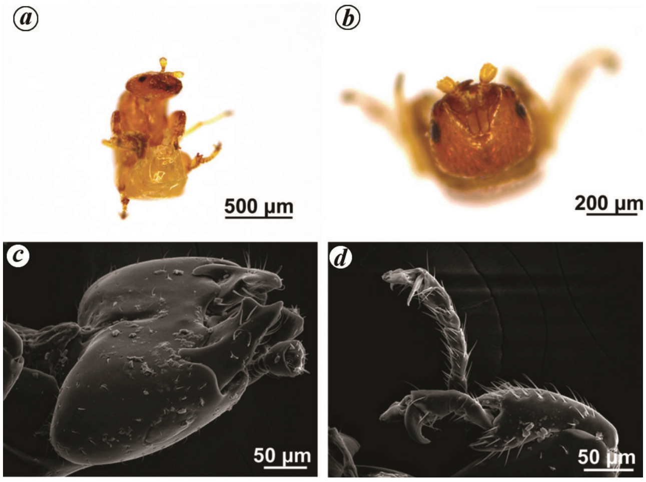

Figure 4. *Platyscapa clavigera* male: ***a***, Ventral; ***b***, Head. SEM images of (***c***) ventral view of head and (***d***) legs.

Material examined: 3♀ from India – Meghalaya, Shillong, Umsyiem (25°11.269′N; 92°00.868′E) 29. xi. 2017, Coll: Nongbri L.B., Meghalaya, Shillong, Rangthylliang (25°18.339′N; 91°52.948′E) 21. xi. 2018, Coll: Nongbri L.B.

Female: Body with reticulated dark green lustre except antennae. Fore, mid and hind coxae and distal ends of hind femora greenish, eyes reddish, antennae 13-segmented (formula – S1, P1, A3, F5, C3). Females with submarginal vein of fore wing shorter than twice the length of marginal vein but much longer than 1.3× the length of marginal vein. Metasoma with fewer reticulations than that of prosoma and mesosoma. Margins of second and third urotergites deeply incised (Figure 5).

Pollination mode

The entire bodies along with the antennae of the pollinators in *F. elastica* were covered with large amount of pollen from the natal fig syconium indicating that pollination was passive.

The number of male and female flowers were roughly the same, with female flowers being counted as those developing into seeds, galls, or bladders (Table 1). Bladders are galls in which insects did not complete development. Consequently, the male flower-to-ovule ratio (used as a surrogate for anther- or pollen-to-ovule ratio)[31] was high and ranged from 0.86 to 1.15 (mean ± sd = 0.97 ± 0.087; $N = 10$ syconia) (Table 1). Despite the presence of pollen pockets, no deposition of pollen inside the pockets was observed and coxal combs in the fore coxae were absent in *P. clavigera* which also supported passive pollination (Figure 3). The seed-to-gall ratio per syconium ranged from 0.72 to 2.03 (mean ± sd = 1.35 ± 0.483; $N = 10$ syconia; Table 1).

Discussion

Despite the usual species-specificity of pollinators in figs, there are cases in which a single species of *Ficus* is pollinated throughout its geographical range by different pollinator species[24–26], especially when the fig has a wide distribution range. At least in *F. elastica*, the same pollinator *P. clavigera* appears to be servicing the fig syconia in widely separated geographical locations throughout northeast India and southeast Asia. The pollinator from *F. elastica* was first described from the Bogor Botanical Garden in Java in 1885 (refs 21, 22). Harrison *et al.*[23,33] reported and identified the pollinator of *F. elastica* from Singapore as *P. clavigera*, which was originally described in Bogor in 1885, but incorrectly named *Pleistodontes clavigera* Mayr (Hymenoptera : Chalcidoidea : Agaoninae). There were reports of a natural breeding population of *F. elastica* from Thailand, but the presence of a pollinator was not documented[28]. In the present study, *P. clavigera* was identified as the pollinator of *F. elastica* from Meghalaya in northeastern India.

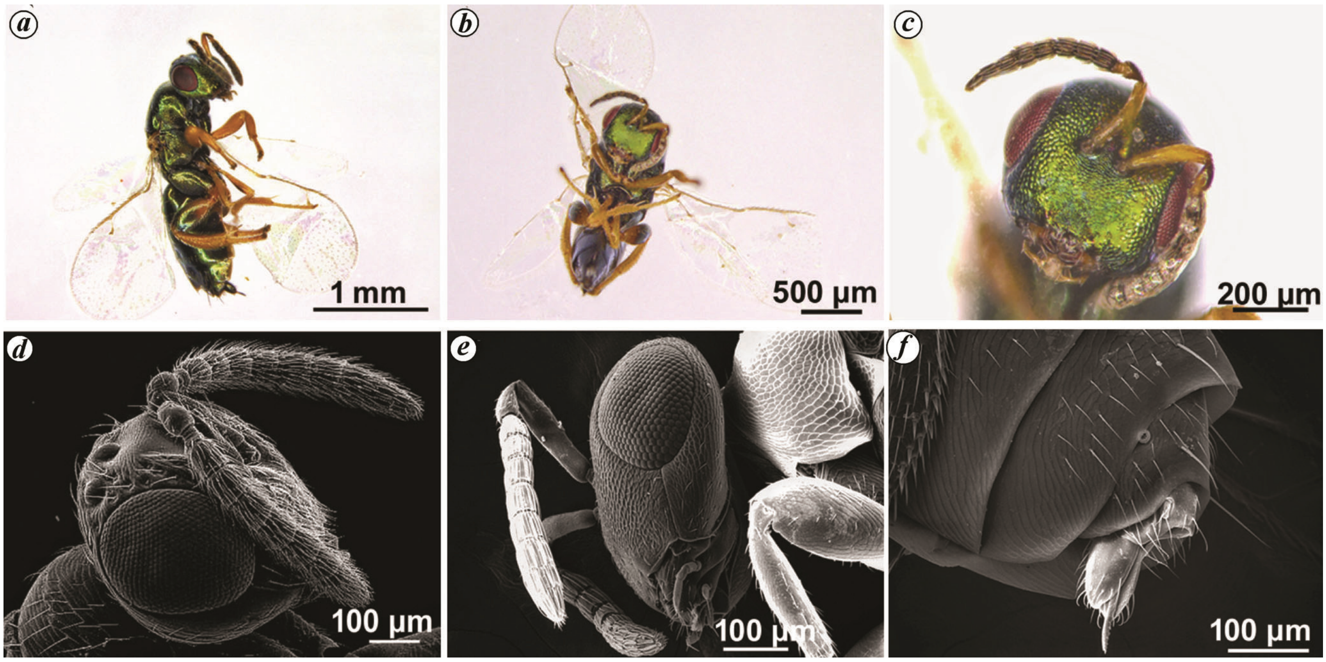

Figure 5. *Micranisa ralianga* female: ***a***, Lateral; ***b***, Ventral; ***c***, Head. SEM images of (***d***) Antennae; (***e***) Head; (***f***) Abdominal tip with exserted ovipositor.

Previous studies have indicated that some NPFW species develop morphological adaptations similar to those of pollinating wasps[34]. They enter the syconium through the ostiole at the same time as the pollinator, oviposit in the female flowers, their offspring mature inside and emerge at the same time as the pollinators during the wasp dispersal phase[35]. *M. ralianga* (Chalcidoidea, Pteromalidae, Otitesellinae) was described by Mathew and Balakrishnan in 1981 from Meghalaya in the northeastern part of India and is found in the syconia of *F. altissima* Blume[27]. The NPFW collected from *F. elastica* showed close resemblance to *M. ralianga*. Given the very short ovipositor of *Micranisa* sp., it is very likely that, like the pollinator, it enters the syconium via the ostiole, since those NPFWs that oviposit into the syconium from the exterior usually have long ovipositors that are at least greater than the thickness of the syconium wall that they need to penetrate[36,37]. Entry into the syconium through the ostiole occurs in other non-pollinating members of the sub-family Otitesellinae[14]. *F. altissima* is sympatric to *F. elastica* in Meghalaya indicating that there might be shared attractive olfactory cues from *F. altissima* syconia which result in the entry of NPFW into the 'wrong' fig species; such mistakes might also be facilitated by the synchrony of the phenophases of syconial development between the two sympatric species of figs[13,38]. That *Micranisa* was found extremely infrequently within the syconia of *F. elastica* may also be indicative of mistaken entry. Alternatively, NPFWs are believed to have lower specificity for fig species[39], and this may also explain *M. ralianga*'s presence in both *F. elastica* and *F. altissima*. Molecular data and also comparison with original specimens are needed to examine whether the NPFW collected from *F. elastica* is different from *M. ralianga*.

Since there was no information on syconium development in *F. elastica*, in this study we have documented it in brief. As in all monoecious figs, the developmental ontogeny of *F. elastica* syconia was spread over five phases. Development lasted for about 80–90 days which was longer in comparison to several other fig species[40,41], and was likely due to larger syconium size. The pollination mode in *F. elastica* is passive as evidenced from anther–ovule ratios (0.86–1.15), abundant pollen distribution on pollinator bodies, absence of coxal combs in the fore coxae, and empty pollen pockets. High anther-to-ovule ratios are characteristic of many passively pollinated fig species[18,31]. Passive pollination for *F. elastica* was suggested by Kjellberg *et al.*[18] based on the anther-to-ovule ratios of two syconia (0.2, 1.42), but there were no data on the pollinator for confirmation. Passive pollinators never possess coxal combs in their fore coxae (they sometimes bear setae on their coxae); however, they often have empty pollen pockets[18]. Some passive-pollinated species have flattened and well developed pollen pockets while in some species they are strongly reduced or absent[18]. Previous descriptions of the pollinator of *F. elastica* by Mayr[21] and Wiebes[22] did not clearly mention pollination-related traits. Investigation of the breeding and pollination system of *F. elastica* is important since this species occupies an enigmatic position in *Ficus* phylogeny, and has variously been considered within different sections that are often basal[42]. Furthermore, active pollination in *Ficus* is believed to be the ancestral trait[42]. Thus, confirming passive pollination in *F. elastica* will shed light on the evolution of character traits in fig and their wasps.

Preliminary findings in our study indicated an average seed-to-gall ratio of 1.35 which lies within the range of earlier studies[43,44]. Seeds indicate reproductive success through the female function of the tree, while the development of pollinators (pollen vectors) as demonstrated by gall numbers in our study, where NPFWs were quite few in each syconium, indicates plant reproductive success through the male function of the tree. It is possible that these ratios undergo seasonal variation and are also affected by NPFWs[45], but these aspects have been scarcely investigated.

In conclusion, this study showed that *P. clavigera* pollinates *F. elastica* in a wide geographical range westward from Indonesia, Thailand to northeast India. The basic information provided in this article will help in understanding the behavioural and evolutionary ecology of *F. elastica* and its associated fig wasps.

1. King, G., The species of *Ficus* of the Indo-Malayan and Chinese countries. *Ann. Roy. Bot. Gard.* (*Calcutta*), 1888, **1**, 1–185.
2. Haridasan, K. and Rao, R. R., *Forest Flora of Meghalaya*, Bishen Singh Mahendra Pal Singh, Dehradun, India, 1987, vol. II.
3. Chaudhary, L. B., Sudhakar, J. V., Kumar, A., Bajpai, O., Tiwari, R. and Murthy, G. V. S., Synopsis of the genus *Ficus* L. (Moraceae) in India. *Taiwania*, 2012, **57**, 193–216.
4. Mathew, R., The living root bridges of Meghalaya. *Curr. Sci.*, 2005, **89**, 10–11.
5. Shankar, S., Revitalizing plant-based knowledge in northeast India. *Solutions J.*, 2017; https://thesolutionsjournal.com/2017/03/01/revitalizing-plant-based-knowledge-northeast-india/
6. Middleton, W., Habibi, A., Shankar, S. and Ludwig, F., Characterizing regenerative aspects of living root bridges. *Sustainability*, 2020, **12**, 3267.
7. Ludwig, F., Middleton, W., Gallenmüller, F., Rogers, P. and Speck, T., Living bridges using aerial roots of *Ficus elastica*–an interdisciplinary perspective. *Sci. Rep.*, 2019, **9**, 12226.
8. POWO, Plants of the world online. Facilitated by the Royal Botanic Gardens, Kew, 2020; http://www.plantsoftheworldonline.org (accessed 16 July 2020).
9. Wiebes, J. T., Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.*, 1979, **10**, 1–12.
10. Kjellberg, F., Jousselin, E., Hossaert-McKey, M. and Rasplus, J.-Y., Biology ecology and evolution of fig-pollinating wasps (Chalcidoidea Agaonidae). In *Biology, Ecology and Evolution of Gall-inducing Arthropods* (eds Raman, A., Schaefer, W. and Withers, T. M.), CRC Press, USA, 2005, pp. 539–572.
11. Grison-Pigé, L., Bessière, J.-M. and Hossaert-McKey, M., Specific attraction of fig pollinating wasps: role of the volatile compounds released by tropical figs. *J. Chem. Ecol.*, 2002, **28**, 283–295.
12. Cook, J. M. and Rasplus, J.-Y., Mutualists with attitude: coevolving fig wasps and figs. *Trends Ecol. Evol.*, 2003, **18**, 241–248.
13. Borges, R. M., How to be a fig wasp parasite on the fig–fig wasp mutualism. *Curr. Opin. Insect Sci.*, 2015, **8**, 34–40.
14. Jousselin, E., Rasplus, J.-Y. and Kjellberg, F., Shift to mutualism in parasitic lineages of the fig/fig wasp interaction. *Oikos*, 2001, **94**, 287–294.
15. Zhang, F., Peng, Y., Compton, S. G., Zhao, Y. and Yang, D., Host pollination mode and mutualist pollinator presence: net effect of internally ovipositing parasite in the fig–wasp mutualism. *Naturwissenschaften*, 2009, **96**, 543–549.
16. Heraty, J. M. *et al.*, A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). *Cladistics*, 2013, **29**, 466–542.
17. Galil, J. and Eisikowitch, D., Further studies on pollination ecology in *Ficus sycomorus* II. Pocket filling and emptying in *Ceratosolen arabicus* Mayr. *New Phytol.*, 1974, **73**, 515–528.
18. Kjellberg, F., Jousselin, E., Bronstein, J. L., Patel, A., Yokoyama, J. and Rasplus, J.-Y., Pollination mode in fig wasps: the predictive power of correlated traits. *Proc. R. Soc. London B*, 2001, **268**, 1113–1121.
19. Galil, J. and Ne'eman, G., Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.*, 1977, **79**, 163–171.
20. Jousselin, E., Kjellberg, F. and Herre, E. A., Flower specialization in a passively pollinated monoecious fig: a question of style and stigma? *Int. J. Plant Sci.*, 2004, **165**, 587–593.
21. Mayr, G., Feigeninsecten. *Verh. Zool. Bot. Ges. Wien*, 1885, **35**, 147–250.
22. Wiebes, J. T., The Indo-Australian Agaoninae (pollinators of figs). *Verh. Kon. Ned. Akad. Wetensch.*, 1994, **92**, 1–208.
23. Harrison, R. D. *et al.*, Pollination of *Ficus elastica*: India rubber re-establishes sexual reproduction in Singapore. *Sci. Rep.*, 2017, **7**, 11616.
24. Michaloud, G., Michaloud-Pelletier, S., Wiebes, J. T. and Berg, C. C., The co-occurrence of two pollinating species of fig wasp and one species of fig. *Proc. Kon. Ned. Akad. Wet. C*, 1985, **88**, 93–119.
25. Rasplus, J.-Y., The one-to-one species-specificity of the *Ficus* – Agaoninae mutualism: how casual? In *The Biodiversity of African Plants* (eds van der Maesen, L. J. G., van der Burgt, X. M. and van Medenbach de Rooy, J. M.), Kluwer Academic Publishers, Wageningen, The Netherlands, 1996, pp. 639–649.
26. Kerdelhué, C., Hochberg, M. E. and Rasplus, J.-Y., Active pollination of *Ficus sur* by two sympatric fig wasp species in West Africa. *Biotropica*, 1997, **29**, 69–75.
27. Balakrishnan Nair, P., Joseph, M. and Abdurahiman, U. C., New fig wasps (Hymenoptera: Chalcidoidea) from *Ficus altissima*. *Proc. Kon. Ned. Akad. Wet.*, 1981, **84**, 145–154.
28. Chantarasuwan, B., Tongsrikem, S., Pinyo, P., Kanithajata, P. and Kjellberg, F., A natural population of *Ficus elastica* Roxb. ex Hornem., in Thailand. *Thailand Nat. Hist. Mus. J.*, 2016, **10**, 7–14.
29. QGIS Development Team, QGIS Geographic Information System. Open source geospatial foundation project, 2020; http://qgis.osgeo.org
30. Galil, J. and Eisikowitch, D., Flowering cycles and fruit types of *Ficus sycomorus* in Israel. *New Phytol.*, 1968, **67**, 745–758.
31. Pellmyr, O. *et al.*, Active pollination drives selection for reduced pollen–ovule ratios. *Am. J. Bot.*, 2020, **107**, 164–170.
32. Wang, Z. J., Ma, Y. C., Peng, Y. Q. and Yang, D. R., Description of a new species of *Micranisa* Walker, 1875 (Pteromalidae, Otitesellinae) from China with a key to species of the genus. *J. Kans. Entomol. Soc.*, 2016, **89**, 231–240.
33. Harrison, R. D., Yan, C. K., Tan, H. and Rasplus, J.-Y., After over a century of abstinence, *Ficus elastica* rediscovers sex in Singapore. *Proc. Peradeniya Univ. Int. Res. Sess., Sri Lanka*, 2014, **18**, 530.
34. Van Noort, S. and Compton, S. G., Convergent evolution of agaonine and sycoecine (Agaonidae, Chalcidoidea) head shape in response to the constraints of host fig morphology. *J. Biogeogr.*, 1996, **23**, 415–424.
35. Galil, J., Dulberger, R. and Rosen, D., The effects of *Sycophaga sycomori* L. on the structure and development of the syconia of *Ficus sycomorus* L. *New Phytol.*, 1970, **69**, 103–111.
36. Zhen, W. Q., Huang, D. W., Xiao, J. H., Yang, D. R., Zhu, C. D. and Xiao, H., Ovipositor length of three *Apocrypta* species: effect on oviposition behavior and correlation with syconial thickness. *Phytoparasitica*, 2005, **33**, 113–120.

37. Ghara, M., Kundanati, L. and Borges, R. M., Nature's Swiss army knives: ovipositor structure mirrors ecology in a multitrophic fig wasp community. *PLoS ONE*, 2011, **6**, e23642.
38. McLeish, M. J., Beukman, G., van Noort, S. and Wossler, T. C., Host-plant species conservatism and ecology of a parasitoid fig wasp genus (Chalcidoidea; Sycoryctinae; Arachonia). *PLoS ONE*, 2012, **7**, e44804.
39. Deng, X. *et al.*, Low host specificity and broad geographical ranges in a community of parasitic non-pollinating fig wasps (Sycoryctinae; Chalcidoidea). *J. Anim. Ecol.*, 2021, **7**, 1678–1690.
40. Galil, J., Fig biology. *Endeavour*, 1977, **1**, 52–56.
41. Yang, H., Tzeng, H. and Chou, L., Phenology and pollinating wasp dynamics of *Ficus microcarpa* L.f.: adaptation to seasonality. *Bot. Stud.*, 2013, **54**, 11.
42. Rasplus, J.-Y. *et al.*, Exploring systematic biases, rooting methods and morphological evidence to unravel the evolutionary history of the genus *Ficus* (Moraceae), *Cladistics*, 2020; doi:10.1101/2020.04.15.042259.
43. Herre, E. A., Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia*, 1989, **45**, 637–647.
44. Wang, H., Ridley, J., Dunn, D. W., Wang, R., Cook, J. M. and Yu, D. W., Biased oviposition and biased survival together help resolve a fig-wasp conflict. *Oikos*, 2013, **122**, 533–540.
45. Krishnan, A., Ghara, M., Kasinathan, S., Pramanik, G. K., Revadi, S. and Borges, R. M., Plant reproductive traits mediate tritrophic feedback effects within an obligate brood-site pollination mutualism. *Oecologia*, 2015, **179**, 797–809.

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