Indian Journal of Entomology Online published Ref. No. e23750 DoI. No.: 10.55446/IJE.2023.750

A NEW SPECIES OF *CERATOSOLEN* (AGAONIDAE) ASSOCIATED WITH *FICUS HISPIDA* L. AND PROPOSED CHANGES IN STATUS OF TWO OTHER POLLINATOR FIG WASPS

Da-Mien WONG[1,2], Songle FAN[1,2], Stephen G. COMPTON[3] and Hui YU[1, 2]*

[1]Key Laboratory of Plant Resource Conservation and Sustainable Utilization,
South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China
[2]Guangdong Provincial Key Laboratory of Digital Botanical Garden,
Chinese Academy of Sciences, Guangzhou 510650, China
[3]School of Biology, University of Leeds, LS2 9JT, U.K.
*Email: yuhui@scib.ac.cn (corresponding author): ORCID ID: 0000-0003-0074-9153

ABSTRACT

An increasing number of fig trees are known to support more than one species of pollinator fig wasp (Agaonidae). This brings into question the relative importance of co-evolution, radiation and host switching in the development of this mutualistic association. The functionally dioecious *Ficus hispida* has a wide distribution in Asia. It supports at least three morphologically distinct *Ceratosolen* pollinators, one of which we describe as *C. abscondus* Wong & Yu sp. n., based on collections in China and Thailand. The other two taxa were originally described as separate species, but subsequently downgraded to sub-species. The morphological differences between the three taxa are similar in extent to those recorded between other *Ceratosolen* species and we therefore re-instate them as the distinct species, *C. solmsi* (Mayr) and *C. marchali* (Mayr). An identification key is provided to distinguish between them and relationships between *Ficus* species and their *Ceratosolen* pollinators of this and related species are discussed.

Key words: *Ceratosolen abscondus*, Chalcidoidea, coevolution, dioecious, Ficus spp., Kradibiinae, morphological differences, mutualism, pollinator specificity, subspecies

The pollinating fig wasps (Hymenoptera: Chalcidoidea: Agaonidae) serve as a model for behavioral, ecological, and evolutionary studies because of their well-known obligate mutualism with fig trees (*Ficus*, Moraceae) across the tropics and subtropics (Weiblen, 2002). The plants and insects are mutually dependent, with the larval fig wasps depending on *Ficus* inflorescences (figs) for food and fig trees depending on adult female fig wasps for pollination (Galil and Neeman, 1977). There are perhaps as many as 1000 species of fig trees, most of which support host-specific pollinator fig wasps (Berg, 1989). For many years it was believed that a 'one-to-one rule' applied, with each species of fig tree supporting a single species of host specific pollinator fig wasp. However, closely related fig wasps are often morphologically similar as adults, especially if they share a host, because their morphology reflects shared selection pressures imposed by the physical structure of their host figs (van Noort and Compton, 1996). Recent studies have revealed that the conclusion of a one-to-one pollinator-plant relationship often resulted from a low sampling intensity, with fig tree pollinators described from one or a small number of samples collected across a small geographical area (Peng et al., 2008; Compton et al., 2009; Yu et al., 2019). An assumption of strict sense co-evolution of the mutualists has therefore been replaced by an appreciation that there is often a less specific form of broad-sense coevolution, involving host switching and radiations of pollinators that better describes the relationship between fig wasps and their hosts (Cook and Segar, 2010).

The Agaonidae are presently divided into four subfamilies based on morphological and molecular evidence (Cruaud et al., 2010; www.figweb.org, accessed December 2021). The subfamily Kradibiinae Saunders contains two genera, *Ceratosolen* Mayr and *Kradibia* Saunders, that are distributed in Africa and Asia. *Ceratosolen* (Chalcidoidea: Agaonidae: Kradibiinae) is monophyletic and was originally placed as a subgenus of *Blastophaga* Gravenhorst before being upgraded to genus level (Mayr, 1906; Cruaud et al., 2010). *Ceratosolen* is a large genus with over 30 described species and many additional species that remain undescribed. The genus displays a strong conservation of host association, being associated

exclusively with *Ficus* subgenus *Sycomorus* (Weiblen and Bush, 2002; Cruaud et al., 2010). There are an increasing number of examples of more than one species of *Ceratosolen* pollinator being associated with a particular species of fig tree (for example Yu et al., 2021). Historically, when two *Ceratosolen* taxa were reared from figs of a single *Ficus* they were described as belonging to different sub-species, rather than species, or if originally described as being distinct species they subsequently had their status downgraded to that of sub-species (Table 1). Definitions vary, but Mayr and Ashlock (1991) defined a sub-species as "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species." Geographical distribution was not an explicit consideration when the *Ceratosolen* sub-species were established, but they were described from different countries. However, the full extent of their distributional ranges remains largely uncertain. The assignment of a sub-species rank to the *Ceratosolen* species therefore appears to have reflected an unspoken assumption that a single *Ficus* species could only support a single species of pollinator, even if morphological differences were present between them.

Ficus hispida L. f. is a widespread moderate-sized functionally dioecious tree found throughout much of Asia (Berg and Corner, 2005). It is favored by disturbance and other human activities and has been cultivated for its edible, ethnobotanical and folklore value (Cheng et al., 2020). The tree's previously described pollinators, currently designated as *Ceratosolen solmsi solmsi* Mayr, 1885 and *C. s. marchali* Mayr, 1906, develop inside the figs on male plants. Pollinated flowers inside figs on female trees develop into seeds. The two *Ceratosolen* taxa were originally described as distinct species, before being synonymized by Wiebes (1963). Wiebes based his decision after carefully considering the extent of morphological variation within the complex. He concluded that while individuals of most populations could clearly be placed in one or other of the two taxa, there were some populations that were intermediate in terms of the characters that had been originally used to distinguish between them. More recently, molecular analyses have revealed that the extent of differentiation between three *Ceratosolen* taxa associated with *F. hispida* in China is similar in extent to that typically exhibited by different *Ceratosolen* species, suggesting that they represent different species (Deng et al., in preparation). In order to clarify the status of the *Ceratosolen* pollinators of *F. hispida* we examined the morphological variation exhibited by their adult females. Based on clear differences in their morphology, we conclude that three distinct species are present. The original rank of two of the species is restored and a third species is described as new. Species descriptions and a key to distinguish females of the three *Ceratosolen* species are provided and we discuss the nature of their evolutionary relationship with *F. hispida*.

MATERIALS AND METHODS

The specimens of *Ceratosolen* were collected during the years 2010 to 2018 from ten sites distributed over South China and Thailand (Table 2). All the wasps that exited their natal figs were collected and stored in 75% ethanol. The figs were then dissected and the wasps therein were collected. Later, the wasps were dehydrated through an ethanol series (80%, 90%, and 100%) and critical-point dried (LEICA EM CPD300, Leica Microsystems GmbH, Germany) before being mounted on cards following Noyes (1982). A scalable dome was made to cover to the specimens before each photo was taken (Kawada and Buffington, 2016) using a digital camera connected to a stereomicroscope (LIECA M205 FA, Leica Microsystem GmbH, Germany) and processed using the LAS X 3.08.19082 software to

Table 1. Asian fig trees of the *Ficus* subgenus *Sycomorus* that have previously been recorded as being hosts to two different subspecies of *Ceratosolen* pollinator fig wasps (extracted from Wiebes, 1994)

Host *Ficus*	*Ceratosolen* current status	Original status
F. septica Burm.f.	*C. bisulcatus bisulcatus*	*Blastophaga bisulcata* Mayr, 1885
F. septica Burm.f.	*C. bisulcatus jucundus*	*C. jucundus* Grandi, 1927
F. fistulosa Reinw.	*C. constrictus contrictus*	*Blastophaga constricta* Mayr, 1885
F. fistulosa Burm.f.	*C. constrictus hewitti*	*C. hewitti* Waterston, 1921
F. ribes Reinw.	*C. crassitarsus crassitarsus*	*Blastophaga crassitarsus* Mayr, 1885
F. ribes Reinw.	*C. crassitarsus gracilis*	*C. crassitarsus gracilis* Wiebes, 1963
F. hispida L.f.	*C. solmsi solmsi*	*C. solmsi* Mayr, 1885
F. hispida L.f.	*C. solmsi marchali*	*C. marchali* Mayr, 1906

Table 2. Sampling sites of *Ceratosolen* fig wasp species associated with *Ficus hispida* fig trees with names used herein

Ceratosolen	Country	Province	City/County	Coordinates
C. abscondus sp. n.	China	Hainan	Ding'an	19°40'49.0"N, 110°22'05.0"E
	Thailand	Chiang Mai	Chiang Mai	18°48'00.0"N, 98°54'00.0"E
C. marchali status n.	China	Guangdong	Guangzhou	23°16'48.0"N, 113°34'48.0"E
	China	Guangdong	Huizhou	23°22'12.0"N, 114°22'12.0"E
	China	Guangdong	Zhaoqing	23°09'47.7"N, 112°33'17.7"E
	China	Guangxi	Nanning	22°46'48.0"N, 108°22'48.0"E
	China	Yunnan	Mengla	21°40'48.0"N, 101°25'12.0"E
C. solmsi status n.	Thailand	Chanthaburi	Khao Khitchakut	12°46'26.4"N, 102°05'45.6"E
	Thailand	Tak	Mueang Tak	16°46'55.2"N, 98°55'40.8"E
	Thailand	Trang	Thung Khai	7°28'01.2"N, 99°38'20.4"E

create a stacked image with increased focal depth. Physical characteristics were measured using ImageJ 1.8.0_172 software (National Institutes of Health, USA). Specimen measurements were taken with an accuracy of 0.001 mm, rounded to the nearest 0.01 mm. Specimens were mounted on brass stubs and sputter-coated with gold (Leica EM ACE600, Leica Microsystem GmbH, Germany) before observation and photography using SEM (Jeol JSM-6360LV, Jeol Ltd, Japan). Morphological terminology follows Gibson (1997) and the Hymenoptera anatomy ontology (HAO) Portal (Yoder et al., 2010). The holotype and a group of paratypes are deposited in the Insect Museum of National Taiwan University (25°00'40.4"N; 121°32'26.7"E). Other paratypes and examined materials are deposited in the Plant Science Center, South China Botanical Garden, Chinese Academy of Sciences, China (23°10'48"N; 113°21'8"E).

RESULTS AND DISCUSSION

A. Taxonomic treatment

***Ceratosolen* Mayr**

Type species *Blastophaga* (*Ceratosolen*) *appendiculatus* Mayr, 1885.

Diagnosis: Females. Head generally as long as wide across compound eyes, or a bit longer or shorter. Antenna with 9–11 segments, club 1–3 segmented. Mandibular appendage with four to ten ventral lamellae; maxillary bacilliform process present or absent. Pollen pockets large. Spiracular peritremata variable but usully large.

Distribution and host relationships: Old world. Pollinators of monoecious and dioecious fig trees of *Ficus* subgenus *Sycomorus*, with larvae developing in galled ovules.

1. *Ceratosolen abscondus* Wong and Yu sp. n.

Types: Holotype, ♀, China, Ding'an (Hainan province), 19°40'49.0"N, 110°22'05.0"E, 3 OCT 2010, H. Yu; Paratypes, China: 2♀, Ding'an, 19°40'49.0"N, 110°22'05.0"E, 3 OCT 2010, H. Yu.

Additional material: Thailand: 4♀, Chiang Mai (Chiang Mai province), 18°48'00.0"N, 98°54'00.0"E, 7 JUL 2013, H. Yu.

Description: Color and size. Antennal flagellum yellowish brown, scape yellowish brown; head, mesosoma and metasoma dark brown; mandibles and legs yellowish brown. Body length including head, mesosoma and metasoma 2.76 mm (Fig. 1A). Fore wing finely pubescent, length 2.54 mm, striae radiating from stigmal vein present but indistinct, uncus and stigma distinct; submarginal, marginal, stigmal, and postmarginal veins in ratio 3: 1: 1: 2 (Fig. 1D).

Head. Longer than wide across compound eyes (Fig. 2A); length 0.56 mm, width 0.50 mm. Compound eye as long as gena, with length 0.23 mm and gena length 0.21 mm; face with sparse setae. Three ocelli. Epistomal margin bilobed with a central tooth. Maxilla apically with finger-like projections with long bacilliform process; mandible bidentate, length 0.14 mm with four ventral lamellae; mandibular appendage with six ventral lamellae, with no lamellar teeth developed (Fig. 2D). Distance between toruli smaller than diameter of one torulus; antennal scape robust, a trapezium in outline (Fig. 3A); pedicel with sensilla obscura (Li et al., 2009); hook-shaped apical projection reaching to about middle of fifth antennal segment; eighth flagellomere (tenth antennal segment) longer than ninth flagellomere, with length 0.10 mm, ninth flagellomere length 0.08 mm (Fig. 3D).

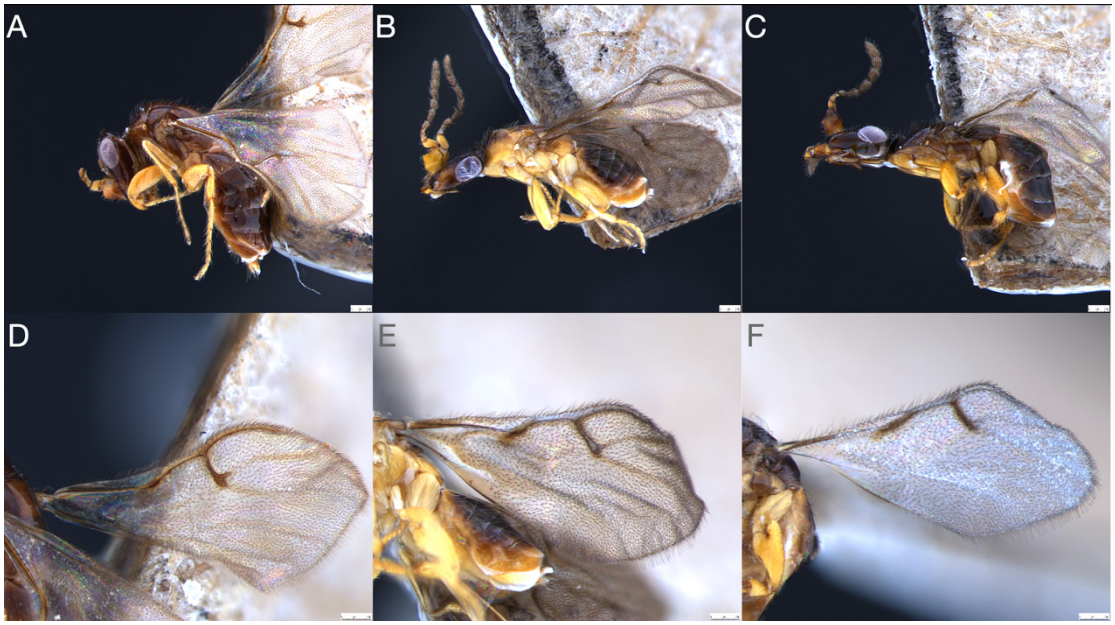

Fig. 1. Habitus, lateral of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Fore wing of D: *C. abscondus*; E: *C. marchali*; F: *C. solmsi*. Scale bars represent 250 μm

Mesosoma. Length 0.81 mm (Fig. 4A). Spiracular peritremata large, slipper-like in outline; cilia in spiracle aperture bifurcated (Fig. 4D). Mesosternum without longitudinal median groove (Fig. 5A); pollen pocket nearly closed with 11 spines anteriorly, pocket length 0.12 mm (Fig. 5D). Hind femur length 0.68 mm, tibia length 0.36 mm, with two apical spurs (Fig. 6A).

Metasoma. Length 0.70 mm in specimens extracted from alcohol and without petiole; dorsal surface brown, ventral parts lighter. Ovipositor scarcely projecting. Hypopygium with one row of hyaline setae, cercal bristles long (Fig. 6D).

Males: unknown.

Etymology: The specific name refers to the Latin word "hidden".

Biology: Presumed ovule galler, in male figs of *F. hispida*.

***Ceratosolen marchali* Mayr, 1906**

Type species *Ceratosolen marchali* Mayr, 1906.

Ceratosolen marchali Mayr, 1906: 155–156.
Ceratosolen solmsi marchali Wiebes, 1963: 68.

Material examined: China: 2♀, Guangzhou, 23°16'48.0"N, 113°34'48.0"E, 9 AUG 17, H. Yu; 2♀, Huizhou, 23°22'12.0"N, 114°22'12.0"E, 17 JUN 18, H. Yu; 2♀, Mengla, 21°40'48.0"N, 101°25'12.0"E, 25 DEC 18, H. Yu; 2♀, Nanning, 22°46'48.0"N, 108°22'48.0"E, 17 SEP 16, H. Yu; 2♀, Zhaoqing, 23°09'47.7"N, 112°33'17.7"E, 17 AUG 18, H. Yu.

Redescription: Color and size. Antennal flagellum yellowish brown, scape yellow; head, mesosoma and metasoma yellowish brown; mandibles and legs yellow. Body length 2.25 mm (Fig. 1B). Fore wing finely pubescent with length 2.67 mm, striae radiating from stigmal vein distinct, uncus less distinct; submarginal, marginal, stigmal, and postmarginal veins in ratio 3: 1: 1: 2 (Fig. 1E).

Head. Female head longer than wide across compound eyes (Fig. 2B); length 0.51 mm, width 0.48 mm. Compound eye as long as gena with length 0.22 mm, gena length 0.18 mm; face with sparse setae. Three ocelli. Epistomal margin bilobed with a central tooth. Maxilla apically with finger-like projections with long bacilliform process; mandible bidentate, length 0.10 mm with four ventral lamellae; mandibular appendage with six ventral lamellae, teeth less distinct on lamellae (Fig. 2E). Distance between toruli smaller than diameter of one torulus; antennal scape robust, trapezoid in outline (Fig. 3B); pedicel with sensilla obscura; hook-shaped apical projection reaching to about middle of fifth antennal segment; eighth flagellomere distinctly longer than ninth flagellomere, eight flagellomere with length 0.15 mm, ninth flagellomere length 0.07 mm (Fig. 3E).

Mesosoma. Length 0.76 mm (Fig. 4B). Spiracular

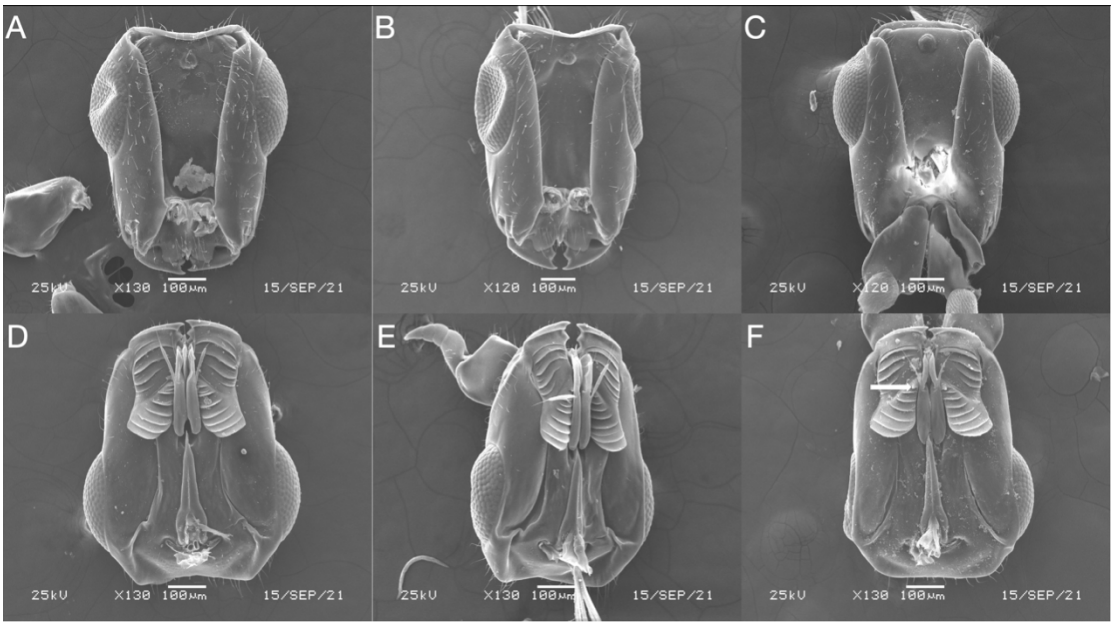

Fig. 2. Head, dorsal view of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Head, ventral view of D: *C. abscondus*; E: *C. marchali*; F: *C. solmsi*. The tooth-like structure on mandibular lamellae was pointed.

peritremata large, slipper-liked in outline; cilia in spiracles bifurcated (Fig. 4E). Mesosternum without longitudinal groove (Fig. 5B); pollen pocket nearly closed with 13 spines anteriorly, pocket length 0.12 mm (Fig. 5E). Hind femur length 0.65 mm, tibia length 0.31 mm, with two apical spurs (Fig. 6B).

Metasoma. Length 0.75 mm and without petiole; dorsal surface dark brown, ventral parts yellowish brown. Ovipositor scarcely projecting. Hypopygium with one row of hyaline setae, cercal bristles long (Fig. 6E).

Distribution: (from van Noort and Rasplus, accessed 2021): Australia (Queensland), Hong Kong, India, Mainland China (Guangdong, Guangxi, Yunnan provinces), Malaysia, Vietnam.

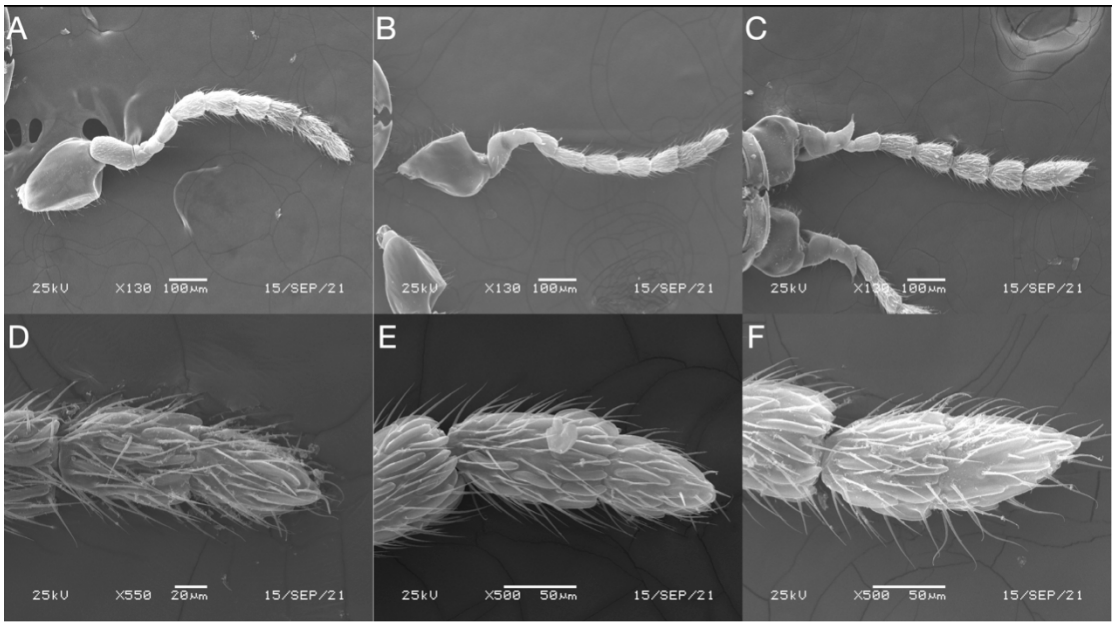

Fig. 3. Antenna of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Eight and ninth flagellomeres of

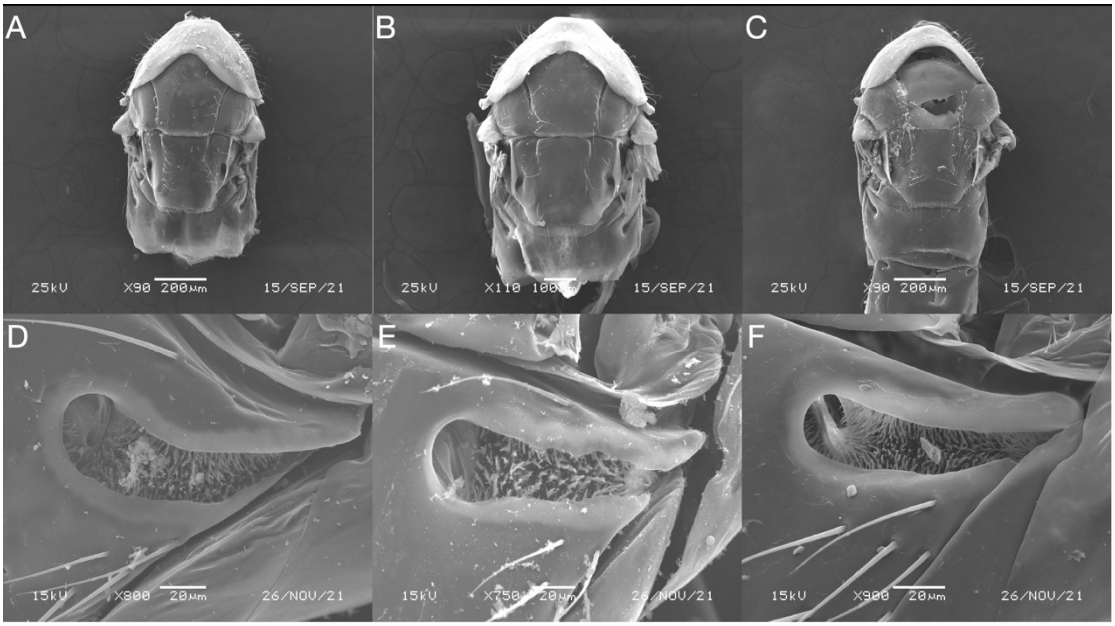

Fig. 4. Mesosoma, dorsal view of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Spiracle of D: *C. abscondus*; E: *C. marchali*; F: *C. solmsi*. The spiracular cilia in *C. s. abscondus* and *C. s. marchali* were apparently bifurcated.

B. *Ceratosolen solmsi* Mayr, 1885

Type species *Blastophaga (Ceratosolen) solmsi* Mayr, 1885.

Blastophaga (Ceratosolen) solmsi Mayr, 1885: 168-169.

Ceratosolen berlandi Grandi, 1928: 74-79.
Ceratosolen solmsi solmsi Wiebes, 1963: 65-67.

Material examined: THAILAND: 2♀, Khao Khitchakut, 13°28’12.0”N, 98°34’48.0”E, 29 SEP 17, H. Yu; 2♀, Mueang Tak, 16°46’55.2”N, 98°55’40.8”E, 7 JUL 13, H. Yu; 2♀, Thung Khai, 7°28’01.2”N, 99°38’20.4”E, 1 OCT 17, H. Yu.

Redescription: Color and size. Antennal flagellum yellowish brown, scape yellowish brown; head, mesosoma and metasoma dark brown; mandibles and

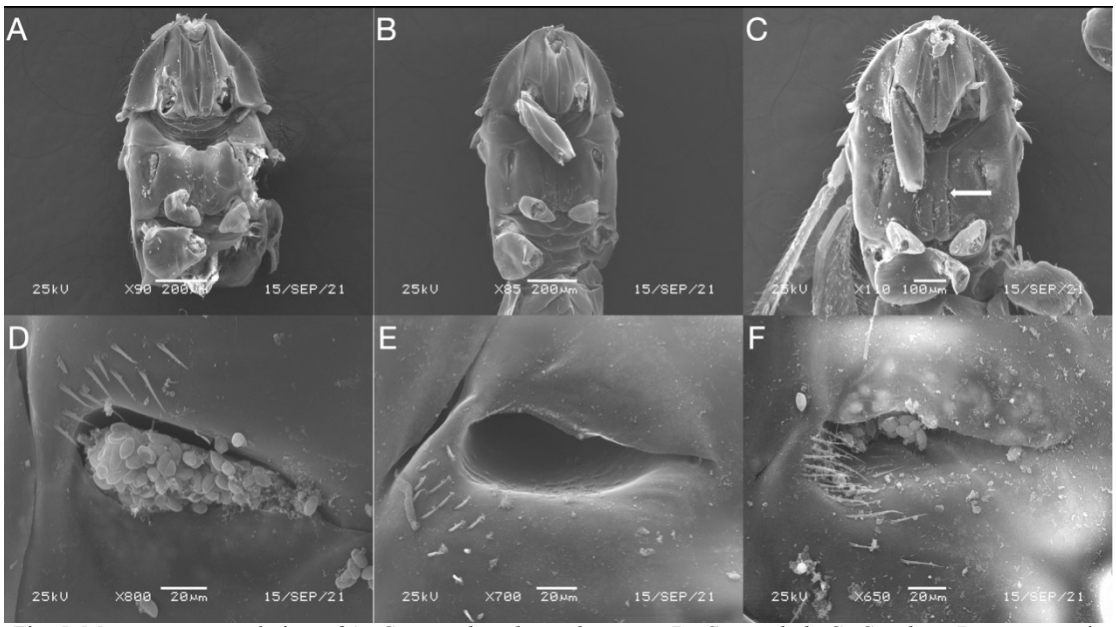

Fig. 5. Mesosoma, ventral view of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Deep groove in mesosternum of *C. s. solmsi* was pointed. Pollen pocket of D: *C. abscondus*; E: *C. marchali*; F: *C. solmsi*.

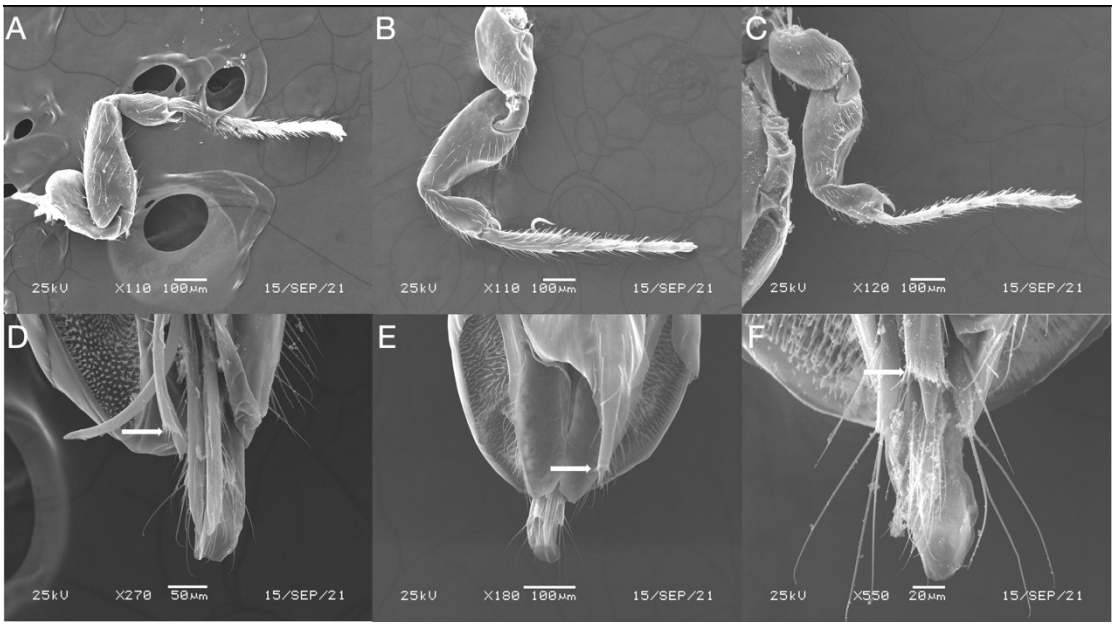

Fig. 6. Hind leg of A: *Ceratosolen abscondus* sp. n.; B: *C. marchali*; C: *C. solmsi*. Hypopygium of D: *C. abscondus*; E: *C. marchali*; F: *C. solmsi*. Hypopygial setae were pointed.

legs yellowish brown. Body length 2.73 mm (Fig. 1C). Fore wing hyaline, finely pubescent with length 2.70 mm; submarginal, marginal, stigmal, and postmarginal veins in ratio 3: 1: 1: 2 (Fig. 1F).

Head. Female head longer than wide across compound eyes (Fig. 2C); length 0.59 mm, width 0.55 mm. Compound eye as long as gena with length 0.26 mm, gena length 0.25 mm. Three ocelli. Epistomal margin bilobed with a central tooth. Maxilla apically with finger-like projections with long bacilliform process; mandible bidentate, length 0.14 mm with five ventral lamellae; mandibular appendage with seven ventral lamellae, teeth present on lamellae (Fig. 2F). Distance between toruli smaller than diameter of one torulus; antennal scape robust, trapezoid in outline (Fig. 3C); pedicel with sensilla obscura; hook-shaped apical projection reaching to about middle of fifth antennal segment; eighth flagellomere as long as ninth flagellomere, eight flagellomere with length 0.17 mm, ninth flagellomere length 0.15 mm (Fig. 3F).

Mesosoma. Length 0.95 mm (Fig. 4C). Spiracular peritremata large, slipper-liked in outline; cilia in spiracles with no or little bifurcation (Fig. 4F). Mesosternum with longitudinal groove (Fig. 5C); pollen pocket nearly closed with 17 spines anteriorly, pocket length 0.12 mm (Fig. 5F). Hind femur length 0.70 mm, tibia length 0.25 mm, with two apical spurs (Fig. 6C).

Metasoma. Length 0.70 mm and without petiole; dorsal surface dark brown, ventral parts lighter. Ovipositor scarcely projecting. Hypopygium with one row of hyaline setae, cercal bristles long (Fig. 6F).

Distribution (from van Noort and Rasplus, accessed 2021)**:** Australia, India, Indonesia, Malawi, Malaysia, Sri Lanka, Thailand (Chanthaburi, Tak, Trang provinces), Vietnam.

Diagnoses of the three *Ceratosolen* and comparison with other Indomalayan species

The female of *C. abscondus* is close to *C. marchali* but the funicle segments are sub-quadrate rather than rectangular (Table 3). The antennal segments of *C. abscondus* and *C. marchali* are more tightly adpressed than in *C. solmsi*. The facial groove width behind the antennal toruli of *C. abscondus* is similar to *C. marchali* but wider than in *C. solmsi*. The fore wings of *C. abscondus* are paler than *C. marchali* but darker than *C. solmsi* with the striae radiating from the stigmal vein less distinct than in *C. marchali*. The anterior pollen pocket spines of *C. abscondus* are 2x longer than in *C. marchali* but shorter and looser than in *C. solmsi*.

In comparison with *Ceratosolen* species associated with other host plants (Wiebes, 1994), *C. fusciceps* Mayr has a head shorter than wide (0.95). *C. marshalli* Grandi has ahead longer the wide (1.25). *C. internatus* has ten antennal segments. *C. pygmaeus* Grandi has a very short postmarginal vein, one-quarter of the stigmal. *C. adenospermae* Wiebes has a very long postmarginal vein, twice the length of the stigma. *C. bisulcatus* Mayr

Table 3. Morphological characteristics of the *Ceratosolen* fig wasp species associated with *Ficus hispida*

Ceratosolen	Mean body length (mm)	Facial groove behind toruli	Petiolated flagellomere	Eight: ninth flagellomere	Mesosoma color	Mesosoma ventral groove	Spiracular cilia bifurcation	Pocket spines
C. abscondus sp. n. (N=12)	2.76± 0.11	Wide	No	1.2: 1	Brown	No	Yes	Loose, long
C. marchali status n. (N=12)	2.74± 0.15	Wide	No	1.6: 1	Yellowish brown	No	Yes	Loose, short
C. solmsi status n. (N=10)	2.91± 0.37	Narrow	Yes	1: 1	Dark brown	Yes	No	Dense, long

The pollen pockets are associated with active pollination behaviour and are located on the underside of the thorax. MX± SD

has simple maxillae. *C. jucundus* Grandi has very short maxillary bacilliform processes. *C. emarginatus* Mayr has an eye:cheek ratio in 2: 1. *C. solitarius* Wiebes has an eye:cheek ratio in 0.8: 1.

Key to the females of *Ceratosolen* fig wasp species associated with *Ficus hispida*

1a. Facial groove behind toruli wider (Fig. 2A, 2B); tooth-like structure absent on mandibular lamellae (Fig. 2D, 2E); cilia in spiracles clearly bifurcated (Fig. 4D, 4E); dark striae radiating from stigmal vein distinct (Fig. 1D, 1E); scape yellowish brown to brown (Fig 1A, 1B) …… 2

1b. Facial groove behind toruli narrower (Fig. 2C); tooth-like structure present on mandibular lamellae (Fig. 2F); cilia in spiracles with no or minimal bifurcation (Fig. 4F); dark striae radiating from stigmal vein less distinct or wing hyaline (Fig. 1F); scape dark brown (Fig. 1C)…… *C. solmsi*

2a. Eighth flagellomere >1.5x lengh of ninth (Fig. 3E); uncus and stigma less distinct (Fig. 1E); pocket spines short (Fig. 5E)…….....… *C. marchali*

2b. Eighth flagellomere <1.5x length of ninth (Fig. 3D); uncus and stigma well-developed (Fig. 1D); pocket spines long (Fig. 5D) …*C. abscondus* sp. n.

Increasing numbers of *Ficus* species are know to routinely host two or more species of pollinator fig wasps (Cruaud et al., 2012), particularly if the host *Ficus* has a wide continental or multi-island distribution (Yu et al., 2019; Rodriguez et al., 2020). Such breakdowns of one-to-one pollinator-host relationship may result from colonization events followed by pollinator host shifts (Kerdelhue et al., 1999; Cook and Segar, 2010). Evidence for this scenario is provided when two or more relatively un-related fig wasps share a host. An example is provided by the two *Ceratosolen* species associated with *Ficus sycomorus* in Africa (Compton et al., 1991). Alternatively, two or more pollinator species sharing one host can result from more rapid speciation rates among the fig wasps than their much longer-lived hosts, generating diversification within a fig wasp lineage that is already associated with a particular host in the absence of host diversification (Souto-Vilarós et al., 2019). This pollinator diversification pattern is seen when sister-species share a host. In *F. hirta*, a fig tree with several associated pollinators, one apparent example of the colonization scenario was detected, but the majority of the pollinators represent sister-species (Yu et al., 2019).

Molecular data is required to confirm whether the three fig wasps that we identified in association with *F. hispida* can be considered as sister species, but their specific status, rather than being considered as sub-species, is supported by clear morphological differences between adult females and also unpublished molecular data (X. Deng et al., unpublished). They were described from different countries, but the extent of overlap in their distributions (if any) is unclear, because the sampling density from this and other Asian fig trees remains low. Further samples, especially from elsewhere in the wide range of *F. hispida,* may also detect further associated fig wasps in addition to the three species already detected.

The three species known to be associated with *F. hispida* possess functional pollen pockets and are therefore likely to be active pollinators. *C. abscondus* and *C. solmsi* share a dark body coloration, indicating that they are likely to disperse between trees in daylight, whereas the paler colouration of *C. marchali* suggests

that it may fly at night. Other biological differences between the three species remain unknown, especially whether the species vary in their effectiveness as pollinators.

ACKNOWLEDGEMENTS

The authors thank Finn Kjellberg from French Center for Functional and Evolutionary Ecology, Anthony Bain from National Sun Yat-sen University, and Po-An Chou from National Chung Hsing University for their valuable suggestion and discussion. We also thank Guangyi Dai and Xiaoying Hu from South China Botanical Garden for their professional technical assistance.

FINANCIAL SUPPORT

This research was funded by the National Natural Science Foundation of China (31971568; 32150410364), and The Chinese Academy of Sciences PIFI Fellowship for Visiting Scientists (2022VBA0002).

AUTHOR CONTRIBUTION STATEMENT

W.D.M. and Y.H.; Data curation, W.D.M. and Y.H.; Formal analysis, W.D.M. and F.S.L.; Method-ology, W.D.M. and Y.H.; Validation, W.D.M., F.S.L. and Y.H.; Writing–original draft, W.D.M.; Writing–review and editing, W.D.M., F.S.L. and Y.H. All authors have read and agreed to the published version of the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

Ashmead W H. 1904. Classification of the chalcid flies of the superfamily Chalcidoidea, with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Memoirs of the Carnegie Museum 1: 233-234.

Baker C J. 1913. A study of caprification in Ficus nota. Philippines Journal of Science 8: 63-68.

Berg C C. 1989. Classification and distribution of Ficus. Experientia 45: 605-611.

Berg C C, E J H. Corner. 2005. Moraceae- Ficus. Flora Malesiana Series I (Seed Plants) Volume 17/ Part 2. National Herbarium of the Netherlands, Leiden.

Chen C H, L Y Chou. 1997. The Blastophagini of Taiwan (Hymenoptera: Agaonidae: Agaoninae). Journal of Taiwan Museum 50: 113-154.

Cheng J X, B. Zhang W Zhu, C Zhang, Y Qin, M Abe, T Akihisa, W Liu, F Feng, J Zhang. 2020. Traditional uses, phytochemistry, and pharmacology of Ficus hispida L.f.: a review. Journal of Ethnopharmacology 248: 112204.

Compton S G, K Grehan, S van Noort. 2009. A fig crop pollinated by three or more species of agaonid fig wasps. African Entomology 17: 215-222.

Compton S G, K. Holton V K. Rashbrook S. van Noort, S Vincent, A B Ware. 1991. The biology of Ceratosolen galili, a non pollinating agaonid fig wasp (Hymenoptera, Agaonidae). Biotropica 23: 188-194.

Conquerel C. 1855. Description de parasite anormaux d'un figuier de l'île de Bourbon. Revue Zoologique and Magasin de Zoologie 7: 422-427.

Cook J M, S T. Segar. 2010. Speciation in fig wasps. Ecological Entomology 35: 54-66.

Cruaud A, R Jabbour-Zahab, G Genson, C Cruaud, A Couloux, F Kjellberg, S van Noort, J Y Rasplus. 2010. Laying the foundations for a new classification of Agaonidae (Hymenoptera: Chalcidoidea), a multilocus phylogenetic approach. Cladistics 26: 359-387.

Cruaud A, N Ronsted, B Chantarasuwan, L S Chou, W L Clement, A Couloux, B Cousins, G Genson, R D Harrison, P E Hanson, M Hossaert-McKey, R Jabbour-Zahab, E Jousselin, C Kerdelhue, F Kjellberg, C Lopez-Vaamonde, J Peebles, Y Q Peng, R A S. Pereira, T Schramm, R Ubaidillah, S van Noort, G D Weiblen, D R Yang, A Yodpinyanee, R Libeskind-Hadas, J M Cook, J Y Rasplus, V Savolainen. 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Systematic Biology 61: 1029-1047.

Galil J, G Neeman. 1977. Pollen transfer and pollination in the common fig (Ficus carica L.). New Phytology 79: 163-171.

Gibson G A P. 1997. Morphology and terminology. Gibson G A P et al. (eds.), Annotated keys to the genera of Nearctic Chalcidoidea (Hymenoptera). NRC Research Press, Ottawa, Canada. pp. 16-44.

Girault A A. 1915. Australian Hymenoptera Chalcidoidea- XIII. The family Agaonidae with descriptions of new (genera and) species. Memoirs of the Queensland Museum 4: 310-313.

Grandi G. 1927. Hymenopteres sycophiles recoltes aux lles Philippimnes par C F Baker, i. Agaonini. Philippines Journal of Science 33: 309-329.

Grandi G. 1928. Hymenopteres sycophiles recoltes dans l'lnde par le Frere E Gombert. Bulletin de la Société zoologique de France 53: 69-81.

Grandi G. 1952. Insectti dei fichi messicani, malesi ed australiani. Bollettino dell'Istituto di Entomoloie Universitas.Bologna 19: 47-67.

Gravenhorst J L C. 1829. Disuisito de Cynipe psene auctorum et descripto Blastophagae, novi Hymenopterum generis. Beitrage zur Entomol., besonders in Bezug auf die schlesische Fauna 1: 27-33.

Harrison R D. 2000. Repercussions of El Nino: drought causes extinction and the breakdown of mutualism in Borneo. Proceedings of the Royal Society, London B 267: 911-915.

Harrison R D. 2003. Fig wasp dispersal and the stability of a keystone plant resource in Borneo. Proceedings of the Royal Society, London B (Suppl.) 270: S76-S79.

Kerdulhue C, I. Le Clainche, J Y Rasplus. 1999. Molecular phylogeny of the Ceratosolen species pollinating Ficus of the subgenus Sycomorus sensu stricto: biogeographical history and origins of the species-specificity breakdown cases. Molecular Phylogenetics and Evolution 11: 401-414.

Joseph K J. 1953. Contributions to our knowledge of fig insects (Chalcidoidea: Parasitic Hymenoptera) from India. IV. Descriptions of three new and records of four known species of Agaonini. Agra University Journal of Research (Science). 2: 267-284.

Kawada R, M L Buffington. 2016. A scalable and modular dome illumination system for scientific microphotography on a budget. PLOS One 11: e153426.

Li Z, P Yang, Y Peng, D Yang. 2009. Ultrastructutre of antennal sensilla of female Ceratosolen solmsi marchali (Hymenoptera: Chalcidoidea: Agaonidae: Agaoninae). Canadian Entomologist 141: 463-477.

Mayr E, P D Ashlock. 1991. Principles of systematic zoology, 2nd edition. McGraw-Hill, New York. xx + 475 pp.

Mayr G. 1885. Feigeninsecten. Verhandlungen des Zoologisch-Botanischen Vereins in Wien 35: 147-250.

Mayr G. 1906. Neue feigen-insekten. Wiener Entomologische Zeitung 25: 153-187.

McLeish M, S van Noort. 2012. Codivergence and multiple host species use by fig wasp populations of the Ficus pollination mutualism. BMC Evolutionary Biology 12: 1.

Molbo D, C A Machado, J G Sevenster, L Keller, E A Herre. 2003. Cryptic species of fig-pollinating wasps: Implications for the evolution of the fig-wasp mutualism, sex allocation, and precision of adaptation. Proceedings of the National Academy of Sciences. U S A. 100: 5967-5872.

Noyes J S. 1982. Collecting and preserving chalcid wasps (Hymenoptera: Chalcidoidea). Journal of Natural History 16: 315-334.

Peng Y Q, Z B Duan, D R Yang, J Y Rasplus. 2008. Co-occurrence of two Eupristina specie on Ficus altissima in Xishuangbanna, SW China. Symbiosis 45: 9-14.

Ramirez W B. 1970. Host specificity of fig wasps (Agaonidae). Evolution 24: 680-691.

Ramirez W B. 1978. Evolution of mechanisms to carry pollen in Agaonidae (Hymenoptera: Chalcidoidea). Tijdschrift voor Entomologie 121: 279-293.

Rodriguez L J, A Cruaud, J Y Rasplus. 2020. Low sampling effort and high genetic isolation contribute to underdocumented diversity in Philippine fig wasps. Philippines Journal of Science 150: 173-180.

Saunders S S. 1883. Descriptions of 3 new genera and species of fig insects allied to Blastophaga, from Calcutta, Australia, and Madagascar, with notes on their parasites and on the affinities of the respective races. Transactions of the Royal Entomological Soceity London 1883: 1-7.

Souto-Vilaros D, A Machac, J Michalek, C T Darwell, M Sisol, T Kuyaiva, B Isua, G D Weiblen, V Novotny, S T Segar. 2019. Faster speciation of fig-wasps than their host leads to decoupled speciation dynamics: snapshots across the speciation continuum. Molecular Ecology 28: 3958-3976.

van Noort S, S G. Compton. 1996. Convergent evolution of agaonine and sycoecine (Agaonidae, Chalcidoidea) head shape in response to the constraints of host fig morphology. Journal of Biogeography 23: 415-424.

van Noort S, J Y Rasplus. 2021. Figweb: figs and fig wasps of the world. URL: www.figweb.org. accessed July 2021.

Walker F. 1846. List of the specimens of Hymenopterous insects in the collection of the British Museum. Part 1 Chalcidites. London, United Kingdom: British Museum.

Walker F. 1875. Descriptions of new genera and species of parasites, belonging to the families Proctotrupidae and Chalcididea, which attack insects destructive to the fig in India. Entomologist 8: 15-18.

Waterston J. 1921. On some Bornean fig-insects (Agaonidae-Hymenoptera Chalcidoidea). Bulletin of Entomological Research 12: 35-40.

Weiblen G D. 2002. How to be a fig wasp? Annual Review of Entomology 47: 299-330.

Weiblen G D, G L. Bush. 2002. Speciation in fig pollinators and parasites. Molecular Ecology 11: 1573-1578.

Wiebes J T. 1963. Taxonomy and host preferences of Indo-Australian fig wasps of the genus Ceratosolen (Agaonidae). Tijdschrift voor Entomologie 106: 1-112.

Wiebes J T. 1978. The genus Kradibia Saunders and an addition to Ceratosolen Mayr (Hymenoptera Chalcidoidea, Agaonidae). Zoologische Mededeelingen Leiden 53: 165-184.

Wiebes J T. 1980. Records and descriptions of Agaonidae from New Guinea and the Solomon Islands. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 83: 89-107.

Wiebes J T. 1991. Ceratosolen ramirezi, a new fig wasp from the Philippine Ficus rivularis: a prediction come true. Entomologische Berichten Amsterdam 51: 108-111.

Wiebes J T. 1994. Agaonidae (Hymenoptera Chalcidoidea) and Ficus (Moraceae): fig wasps and their figs, xiii. (Ceratosolen & additions). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series C 97: 123-136.

Yang D R, Y Q Peng, Q S Song, G M Zhang, R W Wang, T Z Zhao, Q Y Wang. 2002. Pollination biology of Ficus hispida in the tropical rainforests of Xishuangbanna, China. Acta Botanica Sinica 44: 519-526.

Yoder M J I Miko, K C Seltmann, M A Bertone, A R Deans. 2010. Gross anatomy ontology for Hymenoptera. PLOS One 5: e15991.

Yu H, E Tian L Zheng, X Deng, Y Cheng, L Chen, W Wu, W Tanming, D Zhang, S G Compton, F Kjellberg. 2019. Multiple parapatric pollinators have radiated across a continental fig tree displaying clinal genetic variation. Molecular Ecology 28: 2391-2405.

(Manuscript Received: September, 2022; Revised: March, 2023;
Accepted: March, 2023; Online Published: March, 2023)
Online First in www.entosocindia.org and indianjournal.com Ref. No. e23750