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Ant crickets (Orthoptera: Myrmecophilidae) associated with the invasive yellow crazy ant *Anoplolepis gracilipes* (Hymenoptera: Formicidae): evidence for cryptic species and potential co-introduction with hosts

Po-Wei HSU, Sylvain HUGEL, James K. WETTERER, Shu-Ping TSENG, Chuan-Sen Mark OOI, Chow-Yang LEE & Chin-Cheng Scotty YANG

Abstract

The yellow crazy ant, *Anoplolepis gracilipes* (SMITH, 1857), is a widespread invasive ant in tropical and subtropical regions. In our study, we surveyed ant cricket species (Myrmecophilinae) associated with *A. gracilipes* in the Indo-Pacific region and provided a taxonomic revision using an integrative approach by combining morphological and molecular data. At least eight ant cricket species were found in *A. gracilipes* nests, which represents the greatest number of ant cricket species recorded for a single ant species. Some of these ant crickets were widespread across the Indo-Pacific and have an overlapping distribution with *A. gracilipes*. Haplotype networks showed incongruence between haplotype groupings and geographic distribution of ant cricket species, indicating co-introductions of ant cricket species with their ant hosts have occurred. A new taxonomic status of related *Myrmecophilus* species was given: 1) three new species were described (*Myrmecophilus antilucanus* **sp.n.**, *Myrmecophilus caliginosus* **sp.n.**, and *Myrmecophilus ikaros* **sp.n.**) and 2) three new synonyms and one resurrection were made (*M. quadrispina* PERKINS, 1899 = *M. formosanus* SHIRAKI, 1930 **syn.n.**, *M. hebardii* MANN, 1920 = *M. leei* KISTNER & CHONG, 2007 **syn.n.**, *M. dubius* SAUSSURE, 1877 = *M. flavocinctus* WASMANN, 1894 **stat.n.** & **syn.n.**; *M. mayaealberti* HUGEL & MATYOT, 2006 **stat.rev.**). In addition, traits that potentially promote *A. gracilipes* as a favorable host for ant crickets are discussed, along with potential ecological impacts associated with co-introduced ant crickets in their non-native range.

Key words: *Myrmecophilus*, *Myrmophilellus*, *Myrmophilina*, new species, tramp species, distribution map, male genitalia, male phallic complex.

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Introduction

Social insects including ants are known to house numerous groups of symbionts inside their resource-rich colonial environments and engage in various relationships with

these so-called ant guests. Ant guests consist of a wide range of taxa, including gastropods and various arthropods (HÖLLDOBLER & WILSON 1990, WITTE & al. 2002),

some of which (e.g., rove beetles and lycaenid butterflies) have drawn tremendous attention resulting in intensive study. Other myrmecophilous taxa, however, tend to be overlooked. Hence, studies concerning their taxonomy or fundamental biology are scarce.

Ant crickets are small, wingless, kleptoparasitic insects commonly found to associate with ants. They show a wide range of behavioral diversity towards their host ants, including stealing food from ants, grooming ants, and engaging in trophallaxis with host workers (HÖLLEDOBLER & WILSON 1990, KOMATSU & al. 2009, 2017). The 63 described species of ant crickets belong to three genera within the subfamily Myrmecophilinae (CIGLIANO & al. 2018). While most species are regionally distributed species with limited records and / or type material, a few species are widely distributed such as *Myrmecophilus americanus* SAUSSURE, 1877 and *Myrmophilellus pilipes* (CHOPARD, 1928) (WETTERER & HUGEL 2008, KOMATSU & MARUYAMA 2016a).

When identifying ant crickets, male genitalia are usually a reliable characteristic (HUGEL & MATYOT 2006, KOMATSU & MARUYAMA 2016b). However, species are sometimes described based on other characters when male specimens are not available. These distinguishing morphological characteristics include: the arrangement of hind tibial and tarsal spurs, along with coloration pattern, shape of maxillary palps, and female terminal structures. These characteristics are sometimes sex-specific or vary substantially within species (WETTERER & HUGEL 2008, INGRISCH 2010, STALLING 2013), resulting in taxonomic difficulties in discriminating morphologically similar ant crickets.

Yellow crazy ants, *Anoplolepis gracilipes* (SMITH, 1857), are an invasive species considered to be a major threat to native ecosystem and global biota (MOONEY & CLELAND 2001, CLAVERO & GARCÍA-BERTHOU 2005, BELLARD & al. 2016). This species has relatively large workers and is known for forming supercolonies that can locally reach extremely high worker densities. When at high densities, they can negatively impact both native vertebrate and invertebrate fauna and alter ecosystem functions. This impact is most severe on some oceanic islands, including the Seychelles, Christmas Island, Tokelau Islands, and Hawaii (HILL & al. 2003, O'DOWD & al. 2003, McNATTY & al. 2009, GERLACH 2011, PLENTOVICH & al. 2018). Possibly native to the Paleotropics, this ant has spread to tropical islands of the Indo-Pacific and Mexico, most likely due to human-assisted long-distance dispersal (WETTERER 2005, JANICKI & al. 2016). The ant's affinity for human activities may have also created a route for associated symbionts, including ant crickets, to spread across different biogeographic regions despite the confined mobile ability and limited ecological niche of these symbionts. This raises taxonomic issues for accurate identification of cryptic symbiont species as geographic information becomes unreliable.

In the present study, we surveyed ant crickets associated with the yellow crazy ant, *Anoplolepis gracilipes* in

the Indo-Pacific region. We studied cricket specimens by using an integrative approach combining morphological and molecular data with an objective to provide a taxonomic revision, as well as to examine possible co-dispersion of globally distributed myrmecophilous crickets with their host ants. Molecular analyses of ant crickets supported the species boundaries drawn by morphological examination, suggesting that DNA barcodes are reliable genetic markers to distinguish species in ant crickets. We then discuss the factors contributing to yellow crazy ants being a favorable host for ant crickets, and the potential ecological impacts of co-introduced ant crickets. The data in the current study not only offer new insights to the ant-cricket association in bio-invasion context, but also serve as baseline information to facilitate future research on ant crickets.

Material and methods

Sample collection: Colonies of yellow crazy ants and other neighboring ant species (if available) were sampled in disturbed and semi-disturbed areas of the Indo-Pacific region (see Tab. S1 for detailed collection records, as digital supplementary material to this article, at the journal's web pages). Stones, fallen branches, and artificial debris were searched, and ant crickets were collected using a handheld vacuum or mouth aspirator. Ant hosts were identified by comparing with the digital data from ANTWEB (2019). A few closely related ant cricket species that are not associated with yellow crazy ants were also included in this study in order to establish a comprehensive dataset. Ant crickets were classified into three functional categories based on their preference and behavioral adaptation towards their host ant species (KOMATSU & al. 2009, 2013, 2017): 1) Integrated host-specialists which prefer a specific host species and receive no hostile reactions from host workers; 2) Non-integrated host specialists which prefer a specific host species, but receive hostile reactions from host workers; and 3) Host-generalists which are able to utilize a wide range of host species and receive hostile reactions. Samples for morphological examination and DNA extraction were preserved in 70% alcohol. The distribution of ant cricket species was mapped using QGIS 3.4 based on either the collection records or those presented in previous publications. An approximate GPS coordinate was given for sample records containing only a rough description of geographic information (see Tab. S2 for the records used in the distribution maps).

Genetic analysis: A single foreleg or middle leg was removed from each cricket using forceps under a stereomicroscope and immediately preserved in 70% alcohol. For DNA extraction, Genra Puregene Tissue Kit (Qiagen, Venlo, Netherlands) was employed following the manufacturer's protocol with slight modification (i.e., extended centrifugation time to 30 min). Polymerase chain reaction (PCR) was performed to amplify cytochrome b (*cytb*) and elongation factor-1 alpha (*EF1a*) gene by using EmeraldAmp Max PCR master mix (Takara-bio, Shiga Prefecture, Japan), following the degenerated primers in

Tab. 1: Primers used in this study.

Primers	Sequence (5'–3')	Reference
Cytochrome b, <i>cytb</i> , annealing temperature = 45°C		
CB-J-10933 (CBI)	TATGTAACCATGAGGACAAATATC	SIMON & al. (1994)
CB-N-11367 (CBII)	ATTACACCTCCTAATTTATTAGGAAT	SIMON & al. (1994)
CytB 8	CATCCAACATCTCTGCTTGATGAAA	ROBILLARD & DESUTTER-GRANDCOLAS (2006)
CytB 800	CCYARTTTATTAGGAATTGATCG	ROBILLARD & DESUTTER-GRANDCOLAS (2006)
AntCri-F	TTATTYCTWGCTATACACTA	This study
AntCri-R	AAGTAYCATTGWGTTGRAT	This study
MphF	CYTGATGAAAYTTYGGWTC	This study
MphR	AARTAYCATTGWGTTGRAT	This study
Cytb-MphF2	CATTACACCGCWGATATCAA	This study
Cytb-MphR2-1	TAGGCGTTACTAAGGGGTTT	This study
Cytb-MphR2-2	CTGGGATGAAATTATCTGGA	This study
CYTB-int250F	TGAGGDCAAATATCHTTYTGAGG	This study
CYTB-int500F	CCATTYCAACCWTWCTTTAC	This study
CYTB-int250R	CCTCARAADGATATTTGHCCTCA	This study
CYTB-int500R	GTAAAGWAWGGRTGRAATGG	This study
CYTB-int-530R-Mna	ATRAAWCCTAYTRRGTCITT	This study
CYTB-int-530R-heb	ATAATRATRAATCCWRTWA	This study
CBI-R2	CCHCCYCADAYTCATTGDACYA	This study
CBI-R	GATATTTGHCCTCADGGKARDACRTA	This study
elongation factor-1 alpha, <i>EF1a</i> , annealing temperature = 55°C		
EF alpha 1F	ATCGAGAGGTTTCGAGAARGARGC	Muñoz (2010)
EF alpha 1R	CCAYCCCTTRAACCANGGCAT	Muñoz (2010)
EF1a-MphF1	ATGCTTGGGTGTTGGACAAG	This study
EF1a-MphR1	GCAGCAGGGTTGTAACCWAT	This study

Table 1, with initially 3 min at 94°C, 35 cycles of 30 sec at 94°C, 30 sec at 45°C (*cytb*) / 55°C (*EF1a*) for annealing, 45 sec at 72°C, and finally 5 min at 72°C. The target region of *cytb* overlapped with the currently known 434 bp *cytb* segments of the Japanese ant crickets reported in KOMATSU & al. (2008). PCR products were confirmed using gel electrophoresis and visualized on 2% agarose gel with SYBR Safe gel stain (Invitrogen Molecular Probes, Eugene, USA), followed by gel purification using FastGene Gel / PCR Extraction Kit (NIPPON Genetics, Tokyo, Japan). Purified PCR products were sequenced through the DNA Sequencing Core (Uji campus, Kyoto University, Kyoto, Japan) using 3130xl Genetic Analyzer (Thermo Fisher Scientific, MA, USA). The holotype of *Myrmecophilus ikaros* appears to contain inadequate quality of DNA to permit success of PCR, and hence was excluded from subsequent molecular analysis.

Cytb sequences of 230 ant cricket individuals (128 - 635 bp, mean sequence length: 620 bp) were obtained, and a subset of which (33 individuals) were selected for *EF1a* sequencing (420 - 566 bp, mean sequence length:

522 bp) based on the results of *cytb* analyses and their collection sites. A mole cricket (*Gryllotalpa orientalis*) was sequenced for both genes and used as outgroup in the analysis. In order to exclude pseudogenes as a potential source of bias, acquired sequences were compared with those of other insects and orthopterans using BLASTn and BLASTx for their similarities and the potential coding sequences. All generated sequences were deposited in GenBank with the accession numbers listed in Table S1. Unalignable sequence regions of *EF1a* were trimmed manually by comparing against the protein sequence of *Locusta migratoria* (AAL78750.1) obtained from GenBank using BLASTx, resulting into 276-bp final alignment consisted of two possible protein-coding segments (105 bp and 171 bp, respectively).

To estimate the best partitioning schemes, the software PartitionFinder 2.1.1 (LANFPEAR & al. 2012) was employed with corrected Akaike information criterion (AICc) and heuristic search algorithm under the GTR + I + G nucleotide substitution model. The data were then divided by each codon position in both *cytb* and *EF1a* genes during

Tab. 2: Terminology used in the current study and previous studies.

This study (abbreviation italicized)	DESUTTER-GRANDCOLAS (1997) and INGRISCH (2010)	GOROCHOV (2015) and TAHAMI & al. (2017)
pseudepiphallic ancora, <i>an</i>	pseudepiphallic ancora	epiphallus
pseudepiphallic apodeme, <i>ap</i>	pseudepiphallic apodeme	epiphallic apodeme
hypophallus, <i>h</i>	hypophallus	endoparameral apodeme
aedeagus, <i>ae</i>	aedeagus	endoparameral sclerite
lateral sclerites of aedeagus, <i>ae(ls)</i>	lateral sclerites of aedeagus	endoparameral sclerite
ectoparameral apodema, <i>ecap</i>	median ventral lobe	ectoparameral apodema
ectophallic (dorsal/ventral) valve, <i>v/dv/vv</i>	ectophallic (dorsal/ventral) valves	valves
abdominal tergite VI-X, <i>t6-10</i>	abdominal tergite VI-X	abdominal tergites 6 th -10 th
Other terminology used (abbreviation italicized)		
1st-4th inner-lateral spur, <i>ils1-4</i>	outer-lateral spur, <i>ols</i>	
1st-3rd inner-apical spur, <i>ias1-3</i>	1st-3rd outer-apical spur, <i>oas1-3</i>	
hypo-anal plate, <i>hap</i>	-	

phylogenetic analysis in the software RAxML 8.2.10 (STAMATAKIS 2014). Maximum likelihood (ML) phylogenies were reconstructed using the GTRCAT model and later combined with 100 bootstrapping replicates. Neighbor joining trees with Kimura-2-parameter model (NJ-K2P) were reconstructed by MEGA7 (KUMAR & al. 2016), using 1000 bootstrapping replicates and 95 percent partial deletion. The results of phylogenetic analysis were visualized by iTOL v4 (LETUNIC & BORK 2019), in which bootstrapping values of NJ-K2P trees were re-scaled to 100. The main focus of this study lies on a species-level taxonomic revision, the relationships among higher branches (i.e., higher systematics of worldwide ant crickets) will not be discussed.

To determine the genetic variation within and between species, this study followed the methods widely used in DNA barcoding research (CHEN & al. 2010, ČANDEK & KUNTNER 2015, VASCONCELOS & al. 2016). The software MEGA 7 (KUMAR & al. 2016) was used to calculate intra- and interspecific pairwise p-distances among the ant cricket species, with Kimura-2-parameter (K2P) model and partial deletion at 80 percent. Pairwise distances obtained were exported and visualized using the software Microsoft Excel.

To explore evidence of potential human-mediated transportation, haplotype networks of the five ant cricket species that have been collected from more than one area were reconstructed using the software PopART 1.7 (LEIGH & BRYANT 2015). Sequences of *Myrmecophilus americanus*, *M. albicinctus*, *M. hebari* that were too short were removed by PopART as suggested, while sequences of *M. quadrispina* and *M. antiluanus* were all be included with ambiguous and missing sites masked during network reconstruction.

Morphological examination: Morphological examination and dissection were carried out using a stereomicroscope (model SZM-223, AS ONE, Osaka, Japan).

Male genitalia were treated with KOH solution to soften muscle tissues before being photographed. Images were taken using an SZM-223 microscope with a Canon EOS Kiss X9 DSLR camera (Tokyo, Japan) or a Leica M205C stereomicroscope (Wetzlar, Germany) with a Panasonic DMC-GH1 DSLR camera (Osaka, Japan), and were overlaid by the software Helicon Focus 6.7. Brightness and contrast of the overlaid images were adjusted using Adobe Photoshop CS6. Layout was arranged using Adobe Illustrator CS6, and a scale bar was added by comparing an image of a hemacytometer (Cambridge Instruments, New York, USA) taken at same magnification. Male genitalia were illustrated using Adobe Illustrator CS6 to provide additional visualization, while those of *Myrmecophilus mayaealberti* were not available due to the fact that the type has been already archived. Terminology of male genitalia used follows that of DESUTTER-GRANDCOLAS (1997) and INGRISCH (2010). Since GOROCHOV (2015) and TAHAMI & al. (2017) also have provided detailed discussion and illustration of related orthopteran male genitalia, a comparison between the two terminologies was provided in table 2 to clarify potential terminology confusion. Two genera of ant crickets were included in this study: *Myrmecophilus* was abbreviated as “M.” while the monotypic genus *Myrmophilellus* was spelled out in full. Type specimens were deposited in the National Museum of Natural Science, Taichung, Taiwan (NMNS) and the Insect Collection at the Department of Entomology, National Taiwan University, Taipei, Taiwan (NTU). Specimen IDs were put in each figure, and a list of examined samples can be found in Table S3. All samples can be made accessible upon request to the first author or the Laboratory of Urban Pestology, Kyoto University, Kyoto, Japan.

Results

Genetic analyses and species discrimination: Our *cytb* phylogenetic analyses of 230 ant cricket individuals

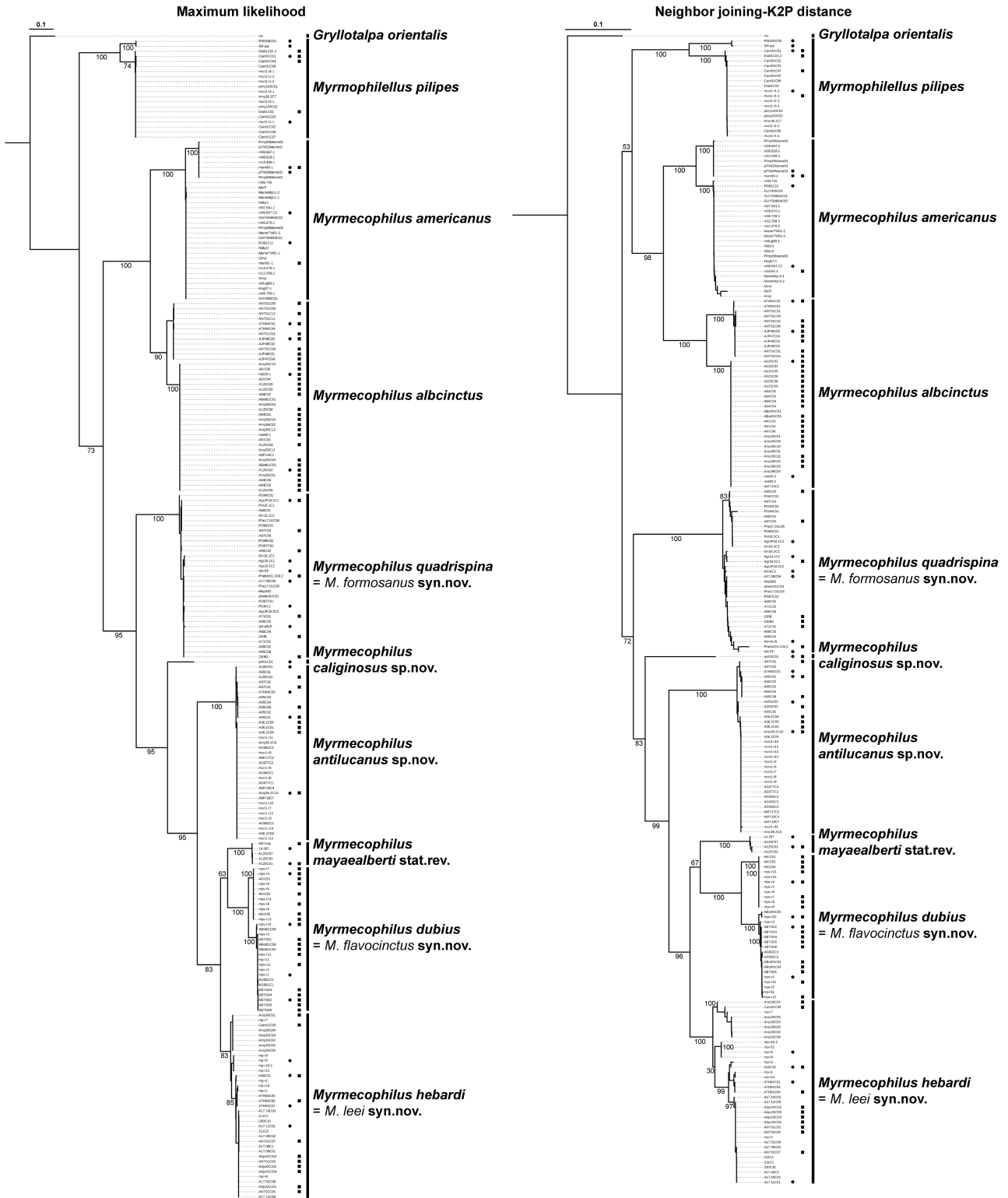


Fig. 1: Phylogenetic trees reconstructed with Maximum Likelihood (ML) and Neighbor Joining method with the Kimura-2-parameter (NJ-K2P) of 230 ant-loving crickets and a *Gryllotalpa orientalis* (outgroup) based on *cytb* sequences. Numbers at nodes indicate bootstrap value. Note that the sequence #SH-maya was removed from the NJ-K2P phylogenetic analysis due to incomplete sequence. Circles indicate individuals selected for *EF1a* sequencing (see Fig. 2), whereas squares indicate individuals that have been morphologically examined (see Tab. S3).

indicated the presence of nine clades. Every clade was strongly supported (Fig. 1) and sometimes has independent subclades within (e.g., *Myrmecophilus albicinctus* and *M. americanus*). Moreover, each clade virtually represented a

cricket species previously identified by our morphological examination, regardless of which subclade they were in. A similar clustering pattern was also observed in phylogenetic analyses based on *EF1a* (33 ant cricket individuals,

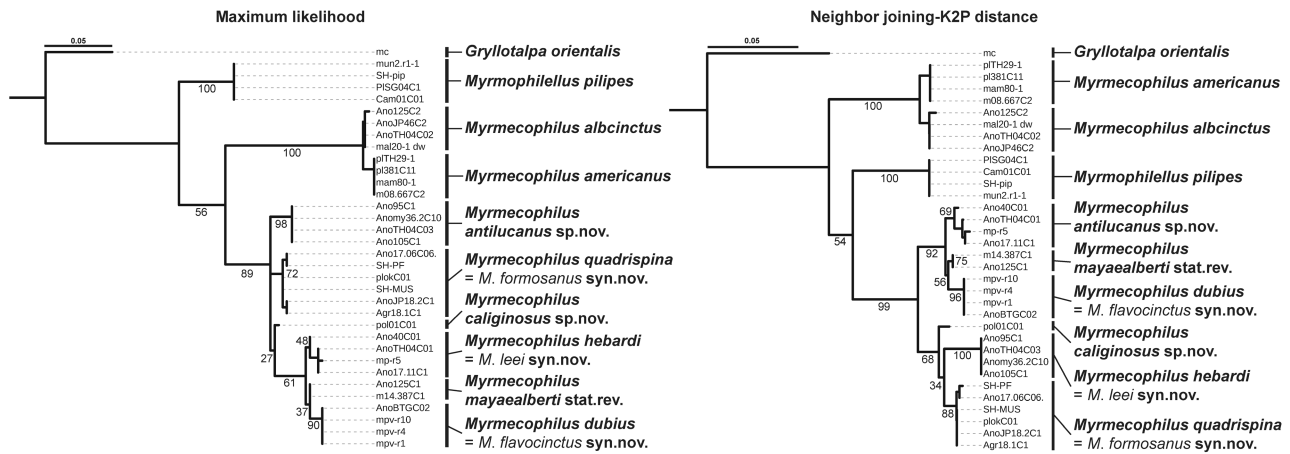


Fig. 2: Phylogenetic trees reconstructed with Maximum Likelihood and Neighbor Joining method with the Kimura-2-parameter (NJ-K2P) of 33 ant-loving crickets and a *Gryllotalpa orientalis* (outgroup) based on *EF1a* sequences. Numbers at nodes indicate bootstrap value.

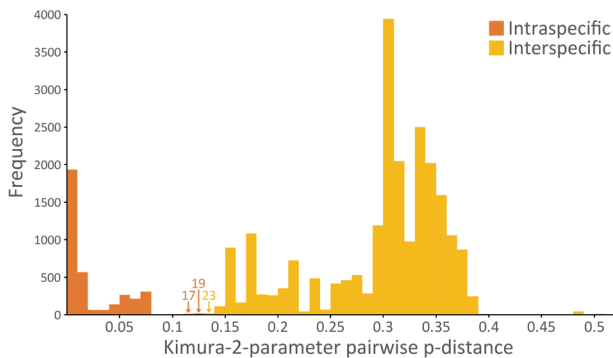


Fig. 3: Intraspecific and interspecific variations based on *cytb* sequences of ant crickets, calculated by Kimura-2-parameter corrected pairwise p-distance.

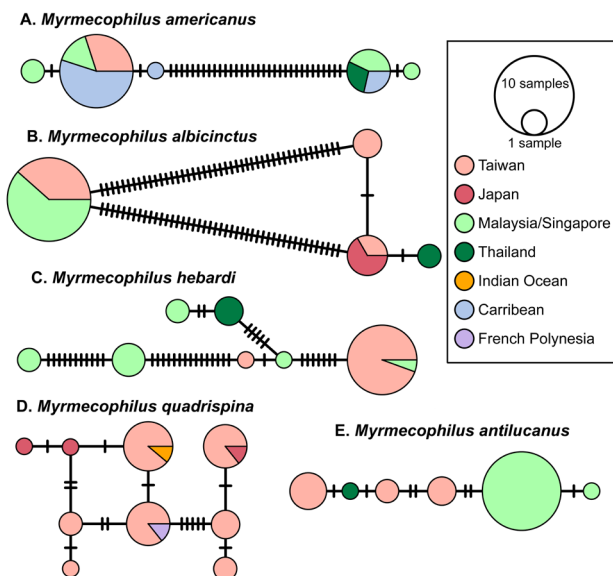


Fig. 4: Haplotype networks for five ant cricket species with collection records from at least two geographic locations.

Fig. 2), with the exception that the relationships between *M. hebardii*, *M. dubius*, and *M. mayaealberti* are relatively unstable and less supported. While the subclades observed in the phylogenetic analyses of *cytb* were not shown in the phylogenetic analyses of *EF1a*, our molecular data based on *cytb* and *EF1a* together provide full support to our morphological identifications.

Our results of phylogenetic analyses based on both *cytb* and *EF1a* also indicated the presence of three major monophyletic clades, including monotypic *Myrmophilellus pilipes* and two subgenera within *Myrmecophilus*, *M. (Myrmecophilus)* and *M. (Myrmophilina)*. The integrated host-specialist species *M. americanus* and *M. albicinctus* were grouped together forming *M. (Myrmophilina)* clade, while the other *Myrmecophilus* species belonging to *M. (Myrmecophilus)* formed another clade.

In addition to the phylogenetic analyses, intra- and interspecific K2P pairwise p-distances were also calculated using *cytb* data as another molecular evidence to verify our morphological species identifications (Fig. 3). Of nine species we studied, the intraspecific p-distance ranged from 0 to 0.13, with over 99% of which lying between 0 and 0.08. Interspecific p-distance, on the other hand, ranged from 0.13 to 0.51. Ranges of intra- and interspecific p-distance were not overlapping. Maximum intraspecific p-distances were observed in pairwise comparisons between two *Myrmophilellus pilipes* subclades (0.11 - 0.13, 36 counts, two nymphs formed a small clade; #*PLSG04C1* and #*SH-pip*; see Fig. 1), whereas minimum interspecific p-distances were observed in those between two species *M. hebardii* and *M. dubius* (0.13 - 0.14; 23 counts; Fig. 1). A gap between most of intra- and interspecific p-distances was observed, suggesting that species delimitation using morphological data was supported by our molecular data and that *cytb* can serve as a useful tool in identifying ant crickets associated with *Anoplolepis gracilipes*.

Haplotype networks and geographic distribution: Haplotype networks of the five selected ant cricket species were reconstructed and shown in Figure 4. *Myr-*

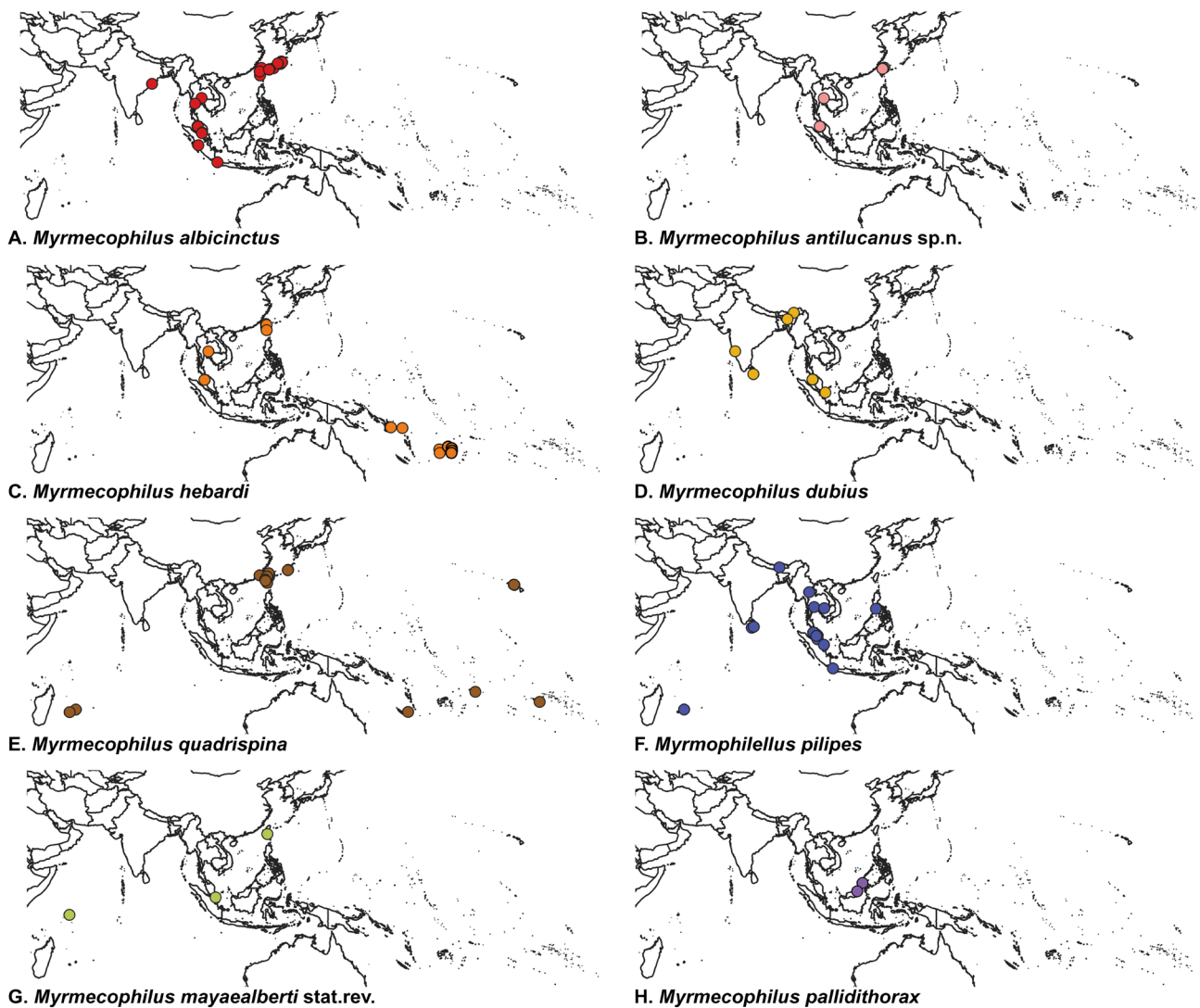


Fig. 5: Distribution maps for eight ant cricket species associated with *Anoplolepis gracilipes*.

mecophilus americanus, a host-specialist of another infamous invasive ant *Paratrechina longicornis*, was also included for discussion. In *M. americanus* and *M. albicinctus*, two distinct haplotype groups were identified (see also in Fig. 1), and both haplotype groups of either species could be recovered within the same regions, and even within the same colony. The incongruence between haplotype grouping and geographic distribution indicates the two host-specialists may have undergone non-natural dispersal. A similar pattern of incongruence was also found in *M. quadrispina*. Despite a small sample size for *M. quadrispina*, haplotypes from Japan appeared at the two ends of the network. The fact of shared similar haplotypes among the three distant sites (Taiwan, Mauritius, and French Polynesia) was consistent to non-natural dispersals by *M. quadrispina* (see also Fig. 5E). *Myrmecophilus hebari* and *M. antilucanus*, on the other hand, were collected only from Taiwan, Thailand, and Malaysia, and our current data appear to provide little support for incongruence between haplotype and geographic distribution. However, we did find that a haplotype from Thailand in *M.*

antilucanus was connected to those from Taiwan (Fig. 4), instead of nearby Malaysia, which suggests that non-natural dispersal may have occurred in this species as well.

Taxonomy: Ant cricket species associated with *Anoplolepis gracilipes*

Myrmophilellus pilipes (CHOPARD, 1928)

Type: Sri Lanka
(Figs. 5 - 6, 7A - D)

Supplementary description of male. Head, body, cerci universally brown; antennae and legs brown, about same color as body. Distal part of legs paler than proximal, making tibia and tarsus brownish yellow. Maxillary palps 1st and 2nd segment short, 3rd segment long and slightly curved on both sides, more or less crescent-shaped, 4th segment teardrop-shaped, same length as 3rd; 5th segment long and cone-shaped, around 2.5 times as large as 4th.

Hind tibia on inner-lateral side with four feathery spurs near apex, 1st spur short, half the length of the 2nd spur; 2nd slightly longer than 3rd spur; 4th spur long, no more than twice the length of 3rd spur. Hind tibia on outer-lateral side

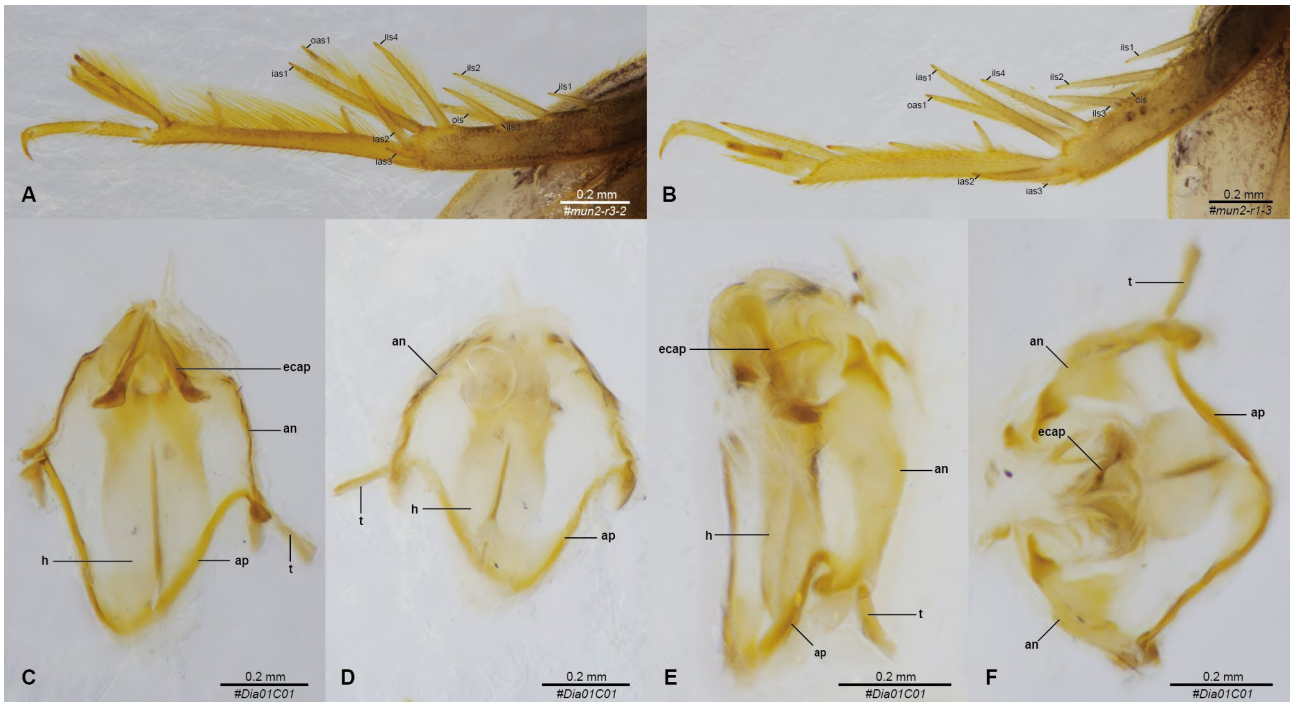


Fig. 6: *Myrmophilellus pilipes*. (A) tibia and tarsus of hind leg, male; (B) tibia and tarsus of hind leg, female; the morphology of male genitalia in (C) dorsal, (D) ventral, (E) lateral, and (F) frontal view.

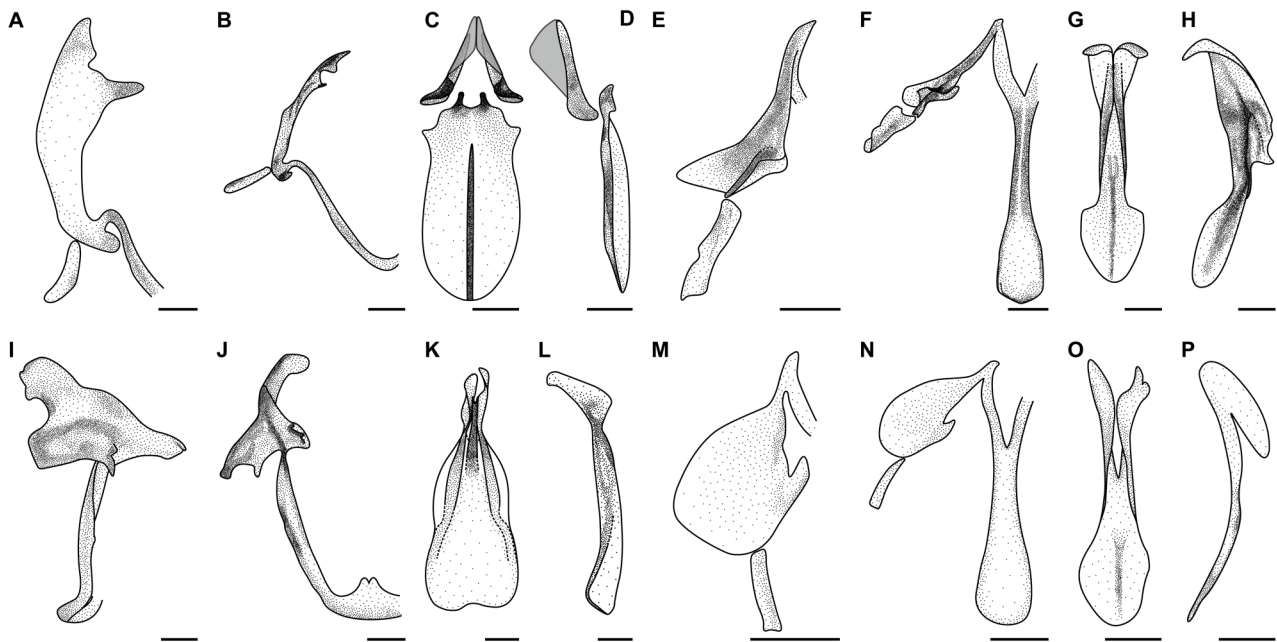


Fig. 7: Male genitalia of four ant cricket species: (A - D) *Myrmophilellus pilipes*, (E - H) *Myrmecophilus albicinctus*, (I - L) *M. hebardii*, and (M-P) *M. americanus*. (A, E, I, M) pseudepiphallallic ancora in lateral view; (B, F, J, N) pseudepiphallallic ancora and half of pseudepiphallallic apodeme in dorsal view; (C, G, K, O) hypophallus in dorsal view; (D, H, L, P) hypophallus in lateral view. Scale bar: 0.1 mm

with 1 spur, located oppositely between 2nd and 3rd spur of inner side, length equal to 2nd spur of inner side. Both inner and outer sides with three additional apical spurs next to lateral ones; 1st apical spur the longest, about 1.5 times as long as 2nd apical spur, 3rd spur minute. Hind metatarsus feathery along two dorsolateral sides, with three dorsal

spurs and two apical spurs; apical spurs with equal length, about twice the length of dorsal spurs; dorsal spurs with equal length.

For genitals, see INGRISCH (2010) and Figures 6, 7A - D. Supplementary description of female. Most characters as in male. Abdominal tergite X with two

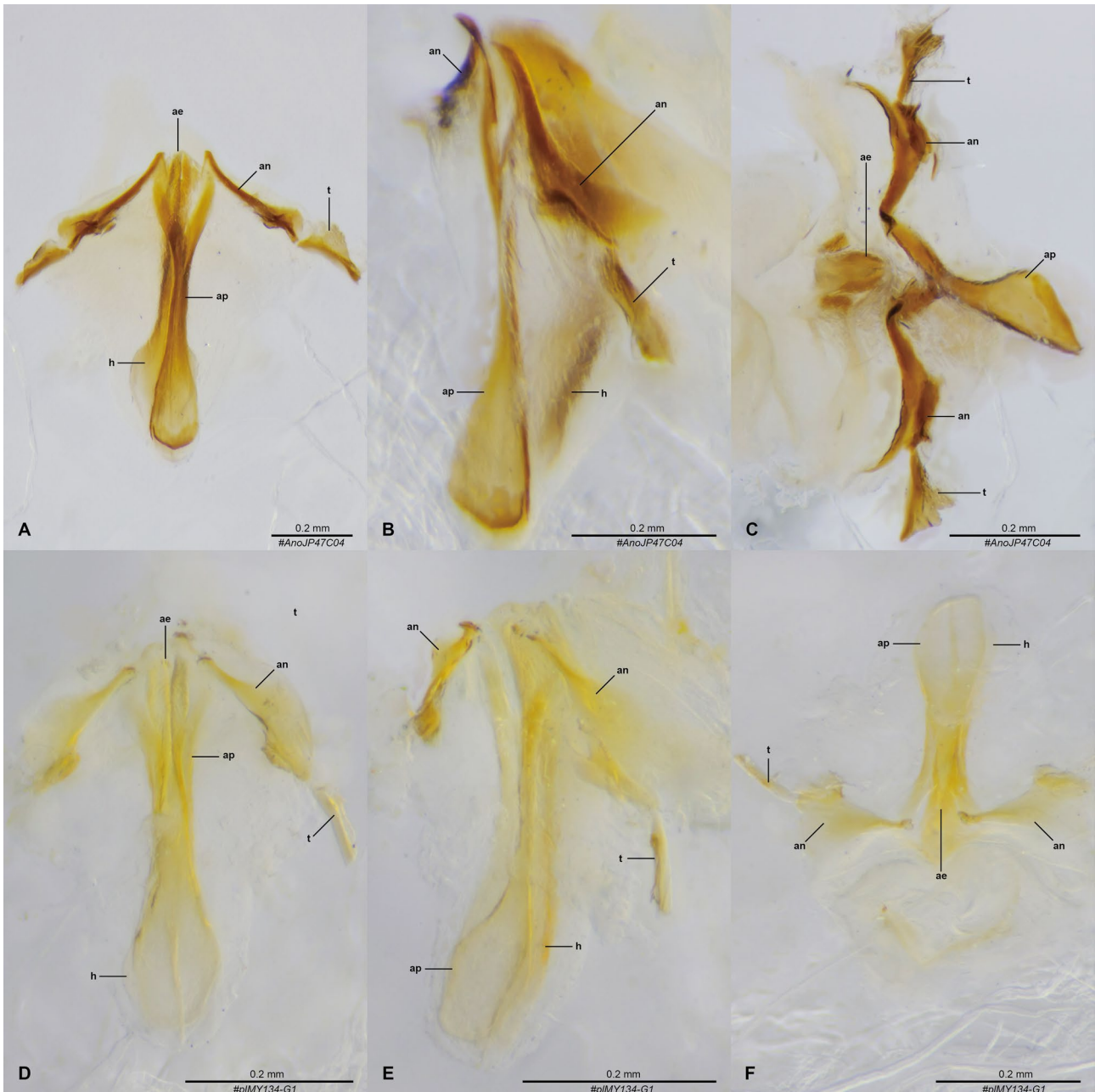


Fig. 8: The morphology of male genitalia of *Myrmecophilus albicinctus* in (A) dorsal, (B) lateral, (C) frontal view; the morphology of male genitalia of *Myrmecophilus americanus* in (D) dorsal, (E) lateral, and (F) frontal view.

distinct supra-anal lobes separated by notch, and each lobe with three apical setae. Subgenital plate wide, partly covering lateral sides of ovipositor; with two shallow notches, making it trilobate apically.

Remarks. The feathers on the hind leg are more distinct in male than in female (Fig. 6A - B), as described in KOMATSU & MARUYAMA (2016a).

Host. *Myrmophilellus pilipes* lives with various hosts, including *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Camponotus* sp. (Malaysia), *Diacamma* spp. (Cambodia, Indonesia, Malaysia, Sri Lanka), *Pheidole megacephala*, *Pheidole* sp. (Malaysia), *Solenopsis geminata*, *Dolichoderus thoracicus*, *Carebara diversus*, *Proatta butteli*, *Philidris cordata*.

Distribution records. Bhutan, Cambodia, India*, Indonesia, Peninsular Malaysia, Philippines, Mauritius, Singapore, Sri Lanka, and Thailand (Fig. 5F). Note that *INGRISCH (2010) did not provide specific locality for the record in India, therefore we omitted it from the distribution map.

References. CHOPARD (1928), INGRISCH (2010), KOMATSU & MARUYAMA (2016a).

***Myrmecophilus (Myrmophilina) albicinctus*
CHOPARD, 1924**

Type: Barkuda, India
(Figs. 5, 7E - H, 8A - C)

Description. See KOMATSU & MARUYAMA (2016b).



Fig. 9: *Myrmecophilus hebardii*. (A) bright form, female, in dorsal view; (B) dark form, female, in dorsal view; (C) terminal structures of male, in dorsal view; (D) terminal structures of female, in dorsal view. Note that color intermediates are possible between the bright and dark form we provide here.

Host. *Myrmecophilus albicinctus* is an integrated host-specific species associated with *Anoplolepis gracilipes* (KOMATSU & al. 2009), and once recorded with *Pheidole* sp. in Japan as a sole case involving non-*A. gracilipes* ant species (MARUYAMA 2006).

Distribution records. India, Java (Indonesia), Nansei Islands (Japan), Peninsular Malaysia, Thailand, and Taiwan (Fig. 5A).

References. CHOPARD (1924), MARUYAMA (2006), KOMATSU & MARUYAMA (2016b).

Discussion. The taxonomy between *Myrmecophilus albicinctus* and *M. americanus*, as well as the worldwide species that can be possible synonyms of either one, was frequently discussed. *Myrmecophilus albicinctus* was considered an independent species by HUGEL & BLARD (2005) and KOMATSU & MARUYAMA (2016b) but was once synonymized under *M. americanus* by INGRISCH (2010). All lines of evidence including body size, male genitalia, and molecular data are indeed in support of the presence of two independent species. Adult *M. albicinctus* has pronotal length at 0.81 ± 0.05 mm ($n = 8$), which is significantly longer than 0.60 ± 0.05 mm ($n = 10$) in *M. americanus* (t-test, $P < 0.05$). This size difference may result from different body size of their respective hosts, *Anoplolepis gracilipes* and *Paratrechina longicornis*, respectively. Shape of pseudepiphallic ancora and phylogenetic clusterings be-

tween two species also showed distinct differences (Figs. 1 - 2, 7 - 8). In addition, due to their extreme host-specificity (WETTERER & HUGEL 2008, KOMATSU & al. 2009, KOMATSU & MARUYAMA 2016b), host information also serves as a promising “character” for identification of the two crickets if available. Our findings here add to growing evidence that integrating morphological, molecular and ecological information can facilitate delimitating species boundaries.

***Myrmecophilus (Myrmecophilus) hebardii*
MANN, 1920**

Type: Somo Somo, Taviuni, Fiji

Myrmecophilus leei KISTNER & CHONG, 2007 in KISTNER & al. (2007) **syn.n.**

Type: Penang, Malaysia

(Figs. 5, 7I - L, 9 - 10)

Supplementary description of male. See also KISTNER & al. (2007).

Posterior margin of abdomen tergite IX smooth and without protrusion, tergite X with two bell-shaped supra-anal extensions, divided by a middle notch which is around $1/2$ to $2/3$ the height of extension (Fig. 9C). Subgenital plate with a bell-like notch apically, making it bilobed with two somehow triangular terminals. Genitalia with two pseudepiphallic ancorae roughly triangular in lateral view (Figs. 7I, 10E), one lateral side roughly

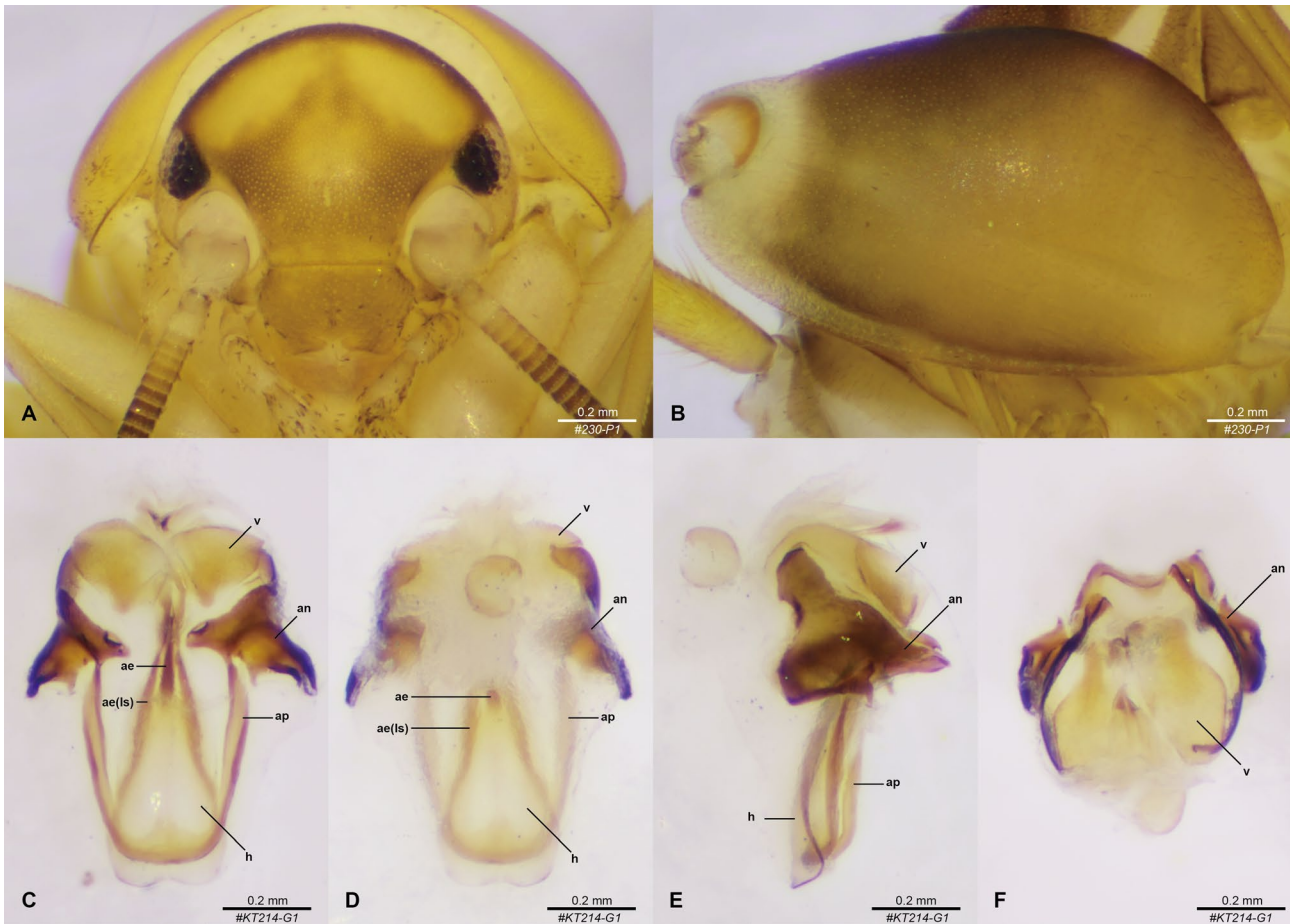


Fig. 10: *Myrmecophilus hebardii*. (A) Head, anterior view; (B) Hind femur, lateral view; the morphology of male genitalia in (C) dorsal, (D) ventral, (E) lateral, and (F) frontal view.

straight, the other undulated with two concaves, and bottom side with one concave; two pseudepiphallallic ancorae connected by a rather long U-shaped pseudepiphallallic apodeme, bottom side with a bell-shaped extension, rather transparent, with a notch at top; lateral sides roughly twice the length of bottom side. Hypophallus long triangular in dorsal view, aedeagus with two lateral sclerotizations, bottom side m-shaped without sclerotization, around half the length of lateral side (Figs. 7I - L, 10).

Supplementary description of female. Most characters as in male. Abdominal tergite X with two bell-shaped supra-anal extensions, divided by a middle notch, roughly the same shape as male (Fig. 9D). Subgenital plate bell-shaped, as wide as height.

Remarks. Yellowish pattern varies among individuals, even within the same ant colony. Heads of *Myrmecophilus hebardii* are sometimes entirely brownish, without distinct yellowish spot (KISTNER & al. 2007); or, with a pair of oval yellow spots on vertex (MANN 1920); or, with an additional round yellow spot on the central frons (Fig. 10A). The yellow spots can vary in size among individuals and are sometimes connected, forming a large yellowish area in central part of head.

Coloration of nota and abdominal tergites also varies among individuals. On pronotum, a pair of brown-

ish spots could vary in size with all possible intermediates. The spots could be small, leading to yellowish on most of the pronotum; or, the spots could extend to around half of pronotum, sometimes even making the yellowish vertical middle line indistinct. Abdominal tergites are either bicolored, with brown in the anterior half and yellow in the posterior half, or, entirely brown (Fig. 9A - B).

In lateral view, the outer side of hind femur is not uniformly colored, with yellowish in the middle part and dark brown at margins (Fig. 10B). The proportion of the yellow part differs among individuals.

Host. *Myrmecophilus hebardii* was found with *Anoplolepis gracilipes*, except once it was recorded with *Camponotus* sp. in Penang, Malaysia.

Distribution records. Fiji Islands, Peninsular Malaysia, Solomon Islands, Taiwan, and Thailand (Fig. 5C).

References. MANN (1920), KISTNER & al. (2007).

Discussion. Intraspecific color variations were found in *Myrmecophilus hebardii*, *M. mayaealberti*, and *M. dubius* that are closely related morphologically and genetically (Figs. 1 - 2). Furthermore, all three species have been transported to different places with invasive *Anoplolepis gracilipes* and expand beyond the general

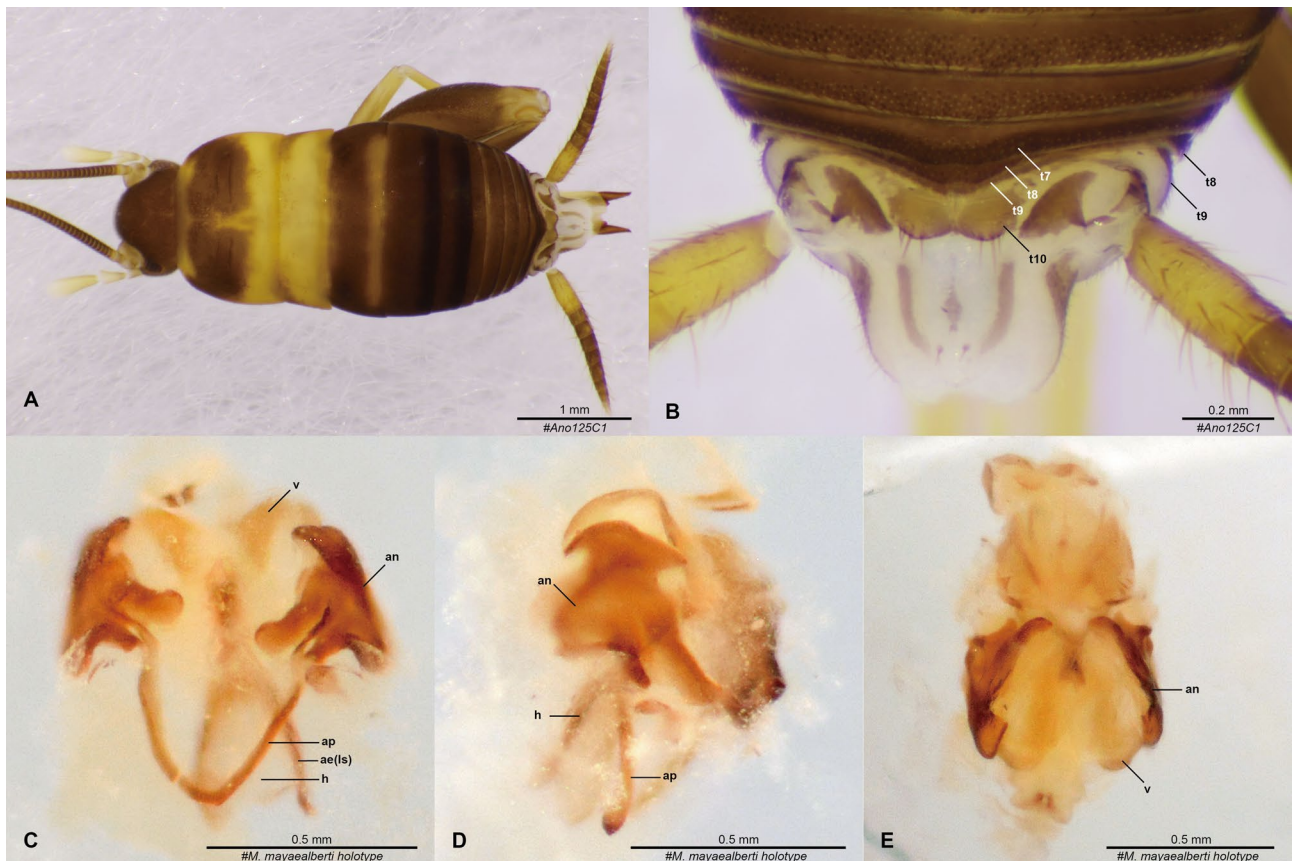


Fig. 11: *Myrmecophilus mayaealberti*. (A) female, in dorsal view; (B) terminal structures of female, in dorsal view; the morphology of male genitalia in (C) dorsal, (D) lateral, and (E) frontal view.

biogeographic boundaries, resulting into difficulties in identifying species (Fig. 5). *Myrmecophilus hebardii* appears to be among the most widely distributed (Southeast Asia and Pacific islands) and abundant species, as well as the species with the greatest variations in coloration pattern (Fig. 9A - B).

Myrmecophilus hebardii was originally described from Fiji and other pacific islands with *Plagiolepis longipes* (now *Anoplolepis gracilipes*), with the description of “Head brown, with a pair of yellow spots on the vertex” (MANN 1920). The yellow spots have never been observed in other species among our samples, of which the heads are in general homogeneously brownish or yellowish without distinct spot of second coloration. Therefore, it can be used as a diagnostic character for identifying *M. hebardii* from other morphologically similar species. By identifying yellowish *Myrmecophilus* species using this unique character, as well as the terminal structures of both male and female (abdominal tergites and male genitalia), we found that the samples collected from the type locality of *M. leei* are morphologically similar to the description of *M. hebardii*. Results of our molecular analysis also revealed that *M. leei* from Malaysia are clustered with *M. hebardii* from Taiwan and Thailand (Figs. 1 - 2). Combined with all lines of evidence, we suggest that *M. leei* should be a junior synonym of *M. hebardii* instead of *M. pallidithorax* (INGRISCH 2010).

Myrmecophilus (Myrmecophilus) pallidithorax CHOPARD, 1930

Type: Sarawak, Borneo, Malaysia
(Fig. 5)

Description. See INGRISCH (2010).

Host. *Myrmecophilus pallidithorax* was only recorded associated with *Anoplolepis gracilipes* in Sarawak (INGRISCH 2010).

Distribution records. Sarawak (Malaysia)
(Fig. 5H).

References. CHOPARD (1930), INGRISCH (2010).

Discussion. While *Myrmecophilus pallidithorax* is similar to the widely spread *M. hebardii* in coloration pattern, only one record was found to date in addition to the holotype (also in Sarawak, INGRISCH 2010). INGRISCH (2010) has provided a detailed description on the color variation and genital structure of both sexes of *M. pallidithorax*, and it can be distinguished from *M. hebardii* by the progressive extensions in the middle of posterior margins of abdominal tergite VII to IX, which is absent in *M. hebardii* (Fig. 9C - D, see also INGRISCH 2010). Another diagnostic character is the ventral lobe of pseudepiphallallic ancora, which is also absent on male genitalia of *M. hebardii* (Figs. 7I - L, 10C - F).

Myrmecophilus pallidithorax is also similar to *M. mayaealberti* and *M. ikaros*, in that all three species possess similar shapes of the extended abdominal tergites

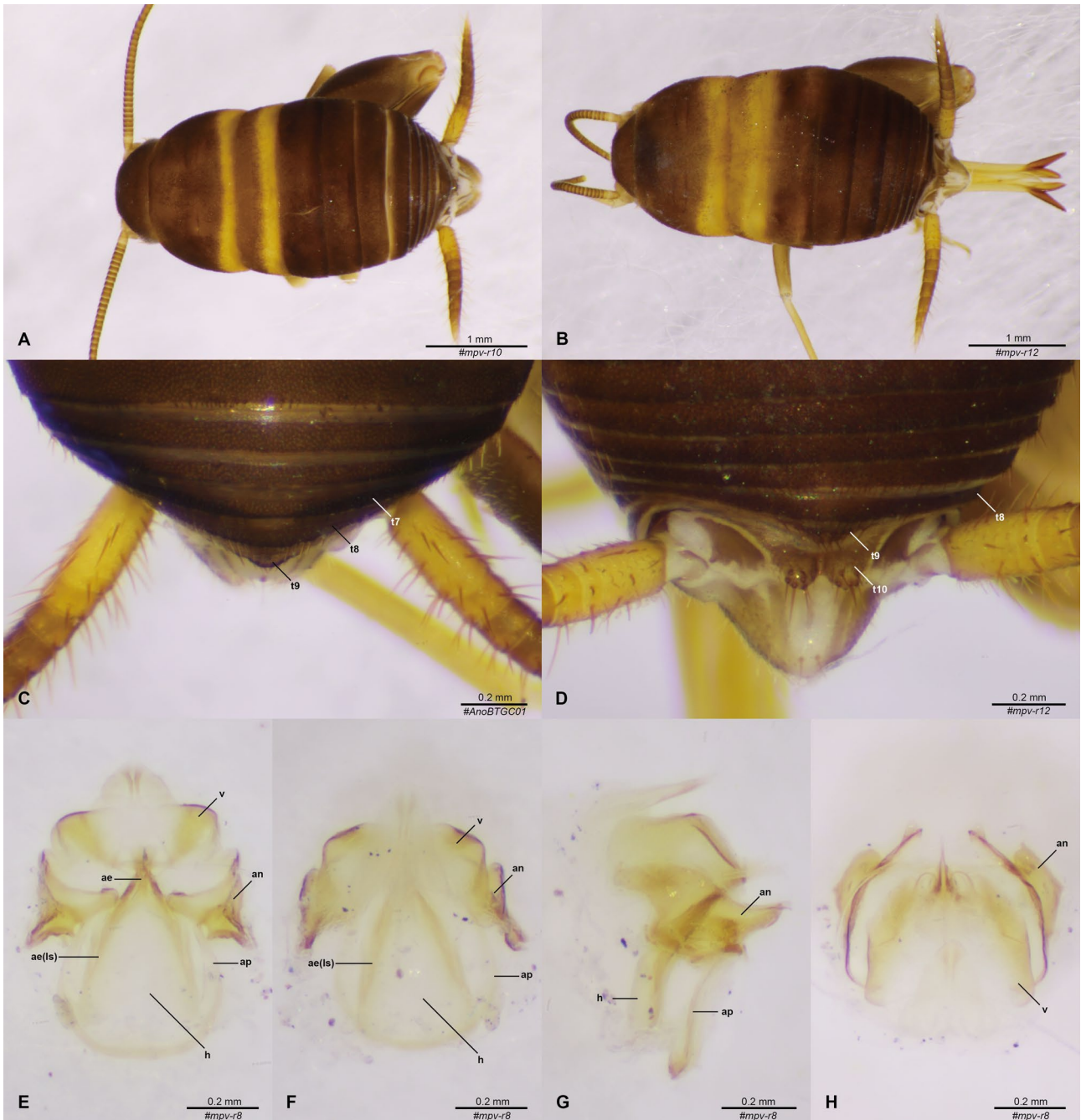


Fig. 12: *Myrmecophilus dubius*. (A) dark form, male, in dorsal view; (B) bright form, female, in dorsal view; (C) terminal structures of male, in dorsal view; (D) terminal structures of female, in dorsal view; the morphology of male genitalia in (E) dorsal, (F) ventral, (G), lateral, and (H) frontal view.

(tergite VII - IX in *M. mayaealberti* but VI - IX in *M. ikaros*, see also below) and pseudepiphallic ancora. Despite a general similarity, minor differences exist within these characters. In all three species, ventral lobe is present in pseudepiphallic ancora, however, the aedeagus and hypophallus of *M. pallidithorax* in INGRISCH (2010): Fig. 15 showed a specific sclerotized pattern, in that it possesses thicker lateral sclerites of aedeagus and a sclerotized arc at the posterior end of hypophallus. These characters were not found in both *M. mayaealberti* and *M. ikaros*. We therefore decided to revive *M. mayaealberti* from *M.*

pallidithorax after re-examination of their male phallic structures, even though the molecular data of *M. pallidithorax* is currently lacking. Further material from the type locality of *M. pallidithorax* with accessible molecular data would be needed to resolve its taxonomic status (see also in *M. mayaealberti* part).

Regarding the identity of the name *Myrmecophilus pallidithorax*, the original description by CHOPARD (1930) appears to be insufficient to test whether it is an independent species or another junior synonym under the widespread species *M. hebardi*. Considering the habitat

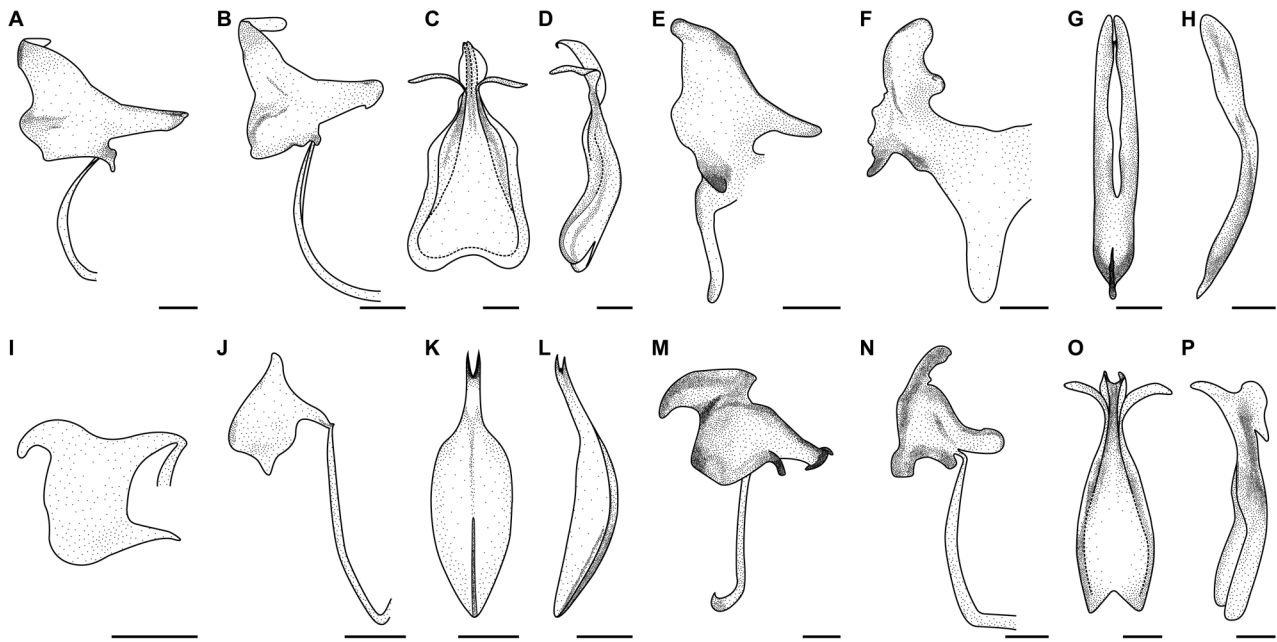


Fig. 13: Male genitalia of four ant cricket species: (A - D) *Myrmecophilus dubius*, (E - H) *M. quadrispina*, (I - L) *M. antilucanus* sp.n., and (M - P) *M. ikaros* sp.n. (A, E, I, M) pseudepiphallallic ancora in lateral view; (B, F, J, N) pseudepiphallallic ancora and half of pseudepiphallallic apodeme in dorsal view; (C, G, K, O) hypophallus in dorsal view; (D, H, L, P) hypophallus in lateral view.

similarity between the type of *M. pallidithorax* (Long Akah or Long Akar, Sarawak) and the material from INGRISCH (2010) (Poring Hot Springs, Mt. Kinabalu, Sabah), it is likely that the holotype of *M. pallidithorax* belongs to the same group as the material from INGRISCH (2010), instead of to *M. hebaridi*.

***Myrmecophilus (Myrmecophilus) mayaealberti* HUGEL & MATYOT, 2006 stat.rev.**

Type: Seychelles
(Figs. 5, 11)

Description. See HUGEL & MATYOT (2006).

Host. Currently *Myrmecophilus mayaealberti* was only recorded with two invasive ant species, *Anoplolepis gracilipes* and *Paratrechina longicornis*.

Distribution records. Seychelles, Singapore, Taiwan (Fig. 5G).

References. HUGEL & MATYOT (2006).

Discussion. Although we were only able to amplify partial *cytb* sequence from *Myrmecophilus mayaealberti* paratype, the sequence is identical to the corresponding region of the complete sequences of our samples collected from Taiwan and Singapore which show similar morphology, while different from other species we collected throughout the Indo-Pacific regions (Fig. 1). *Myrmecophilus mayaealberti* has similar sclerotized pattern of aedeagus and hypophallus to that of *M. hebaridi*, *M. dubius*, and *M. ikaros*, and therefore was considered different from *M. pallidithorax*, which has thicker sclerotized lateral sides of aedeagus and posterior part of hypophallus as shown in INGRISCH (2010) (see *M. pallidithorax* part above). Here,

we revive *M. mayaealberti* from the junior synonymy of *M. pallidithorax* to represent the small clade that includes *M. mayaealberti* paratype unless in the future molecular data of *M. pallidithorax* indicate a similar genetic clustering otherwise.

***Myrmecophilus (Myrmecophilus) dubius* SAUSURE, 1877**

Type: Bintang Island, Indonesia

Myrmecophilus acervorum var. *flavocinctus* WASMANN, 1894 stat.n. & syn.n.

Type: Kanara, India

(Figs. 5, 12, 13A - D, 14 - 15)

Supplementary description of male. Head uniformly brown. Antennae brown, slightly brighter than head. Maxillary palps 1st and 2nd segments short, 3rd segment cylinder-shaped with strongly curved upper side, 4th and 5th segments cone-shaped, with 5th segment around twice as large as 4th.

In dorsal view, pronotum brown, same color as head, with posterior margin yellow and forming a transverse line that is slightly curved. Mesonotum in anterior half brown, posterior half yellowish, resulting into another transverse yellow line. Metanotum and abdominal tergites brown. Cerci bicolored, with middle part brownish and both apices yellow.

Legs brown, about same color as head and brighter terminally. Hind tibia on inner-lateral side with 4 spurs near apex, 1st and 3rd spurs of about equal length, half the length of the 2nd spur; 2nd and 4th spurs long and of about equal length. Hind tibia on outer-lateral side with 1 spur,

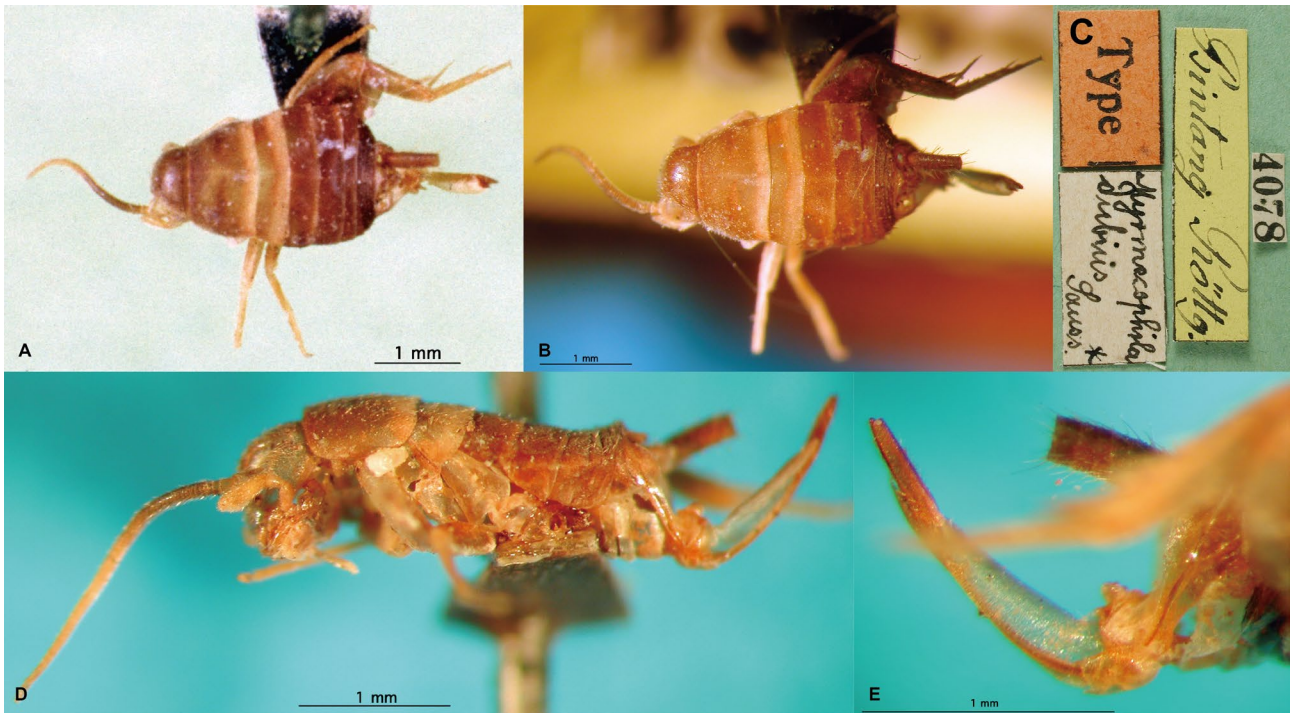


Fig. 14: *Myrmecophilus dubius* SAUSSURE, 1877 holotype. (A, B) in dorsal view; (C) specimen labels; (D) in lateral view; (E) ovipositor, in lateral view. Images source: Deutsche Orthopteren Sammlungen, DORSA; images credit: Sigfrid Ingrisch.

located oppositely between 2nd and 3rd spur of inner side, length equal to 2nd spur of inner side. Both inner and outer sides with three additional apical spurs next to lateral ones, 1st apical spur the longest, about 3 times as long as 2nd apical spur, 3rd spur minute. Hind metatarsus with three dorsal spurs and two apical spurs; apical spurs of equal length.

Posterior margin of abdomen tergite VII, VIII, and IX smooth and without protrusion, with extensions of tergite X insignificant in dorsal view (Fig. 12C). Subgenital plate with a trapezoid-like notch apically. Genitalia with two roughly triangular pseudepiphallic ancorae, with one lateral side roughly straight, the other side long-S shaped with one shallow concave, and the bottom side curved inwards forming a concave (Fig. 13A); two pseudepiphallic ancorae connected by a rather wide and round U-shaped pseudepiphallic apodeme, with three sides of roughly equal length, resembling a semi-circle; aedeagus with two lateral sclerotizations, apices strongly curved outward at around 90 degree (Figs. 12E - H, 13A - D).

Supplementary description of female. Most characters as in male. Abdominal tergite X with two bell-shaped supra-anal extensions. Subgenital plate bell-shaped, as wide as height.

Remarks. The two transverse yellow lines are found wider in some specimens (Fig. 12A - B), in which the whole mesonotum can be yellowish or only a small part of brownish is left anteriorly. The brownish color on nota is sometimes brighter and a little bit yellowish, making those brownish parts less saturated.

Host. *Myrmecophilus dubius* is only recorded associated with *Anoplolepis gracilipes*.

Distribution records. India, Bintang Island and Sumatra* (Indonesia), Peninsular Malaysia, and Sri Lanka (Fig. 5D). *Note that VASANTH (1993) did not provide a specific locality for the record in Sumatra, therefore this record is omitted from the distribution map.

Reference. SAUSSURE (1877), WASMANN (1894), CHOPARD (1925), VASANTH (1993).

Discussion. Like *Myrmecophilus hebardii*, *M. dubius* possesses a wide range of coloration pattern. The images of type *M. dubius* provided by Ingrisch in the project Deutsche Orthopteren Sammlungen (DORSA, Fig. 14) showed a typical banding pattern with a transverse yellow band in posterior margin of both pronotum and mesonotum. This coloration pattern resembles the European parthenogenetic species *M. acervorum*. In our collections, the yellow line on mesonotum is either a narrow band at posterior margin (Fig. 12A), as similar to *M. acervorum*, or on the whole mesonotum (Fig. 12B). The brownish part of pronotum also varies in that sometimes it possesses a more yellowish- or reddish-like color instead of dark brown. Problems in identifying species may sometimes arise due to variations in coloration pattern among the morphological species. However, our data including genetic analysis (Figs. 1 - 2), morphological comparisons, and the presence of male indicate that *M. dubius* is no doubt an independent species from its relatives *M. hebardii*, *M. pallidithorax*, and *M. mayaealberti*, as well as the parthenogenetic species *M. acervorum*.

By delimiting the variation of yellow banding pattern within *Myrmecophilus dubius* in the assistance of genetic analysis, we propose that *M. acervorum* var. *flavocinctus* WASMANN, 1894, a valid taxon which has been omitted



Fig. 15: *Myrmecophilus acervorum* var. *flavocinctus* Wasmann, 1894 holotype. (A) in dorsal view; (B, C) in lateral view; (D) in posterior view; (E) specimen labels.

by all hitherto authors, should be a junior synonym of *M. dubius*. In Wasmann's original description, he stated that in *M. acervorum* var. *flavocinctus* "the yellow transverse bands are twice as wide as in *M. acervorum* and only separated by a very weak brown line" (Wasmann 1894, Figs. 12B, 15). Among our collections, we found that around half of our *M. dubius* material possess the same banding pattern as described in Wasmann (1894), and that their host-specificity and ecology are consistent to those reported in Saussure (1877). In the original description of *M. dubius* by Saussure, it has been mentioned that "the species may have been transported to various countries with garden plants", and this suggests that *M. dubius* may be associated with invasive ant species that have been frequently transported as hitchhikers in plant material (Rabitsch 2011). This note is identical to the records of *M. acervorum* var. *flavocinctus*, of which the type series was collected with *P. longipes* (*Anoplolepis gracilipes*). In our collection, *M. dubius* has also been found exclusively with *A. gracilipes*. Combining all available data in this study

(morphological and ecological similarity, as well as similar distribution range), we propose that the Indian species *M. acervorum* var. *flavocinctus* Wasmann is an independent species to European *M. acervorum* and meanwhile a junior synonym of *M. dubius*.

***Myrmecophilus (Myrmecophilus) quadrispina* Perkins, 1899**

Type: Hawaii, USA

Myrmecophilus formosanus Shiraki, 1930 **syn.n.**

Type: Takao, Taiwan

(Figs. 5, 13E - H, 16)

Description. See Desutter-Grandcolas (1997).

Host. *Myrmecophilus quadrispina* lives with various hosts, including *Anoplolepis gracilipes*, *Paratrechina longicornis*, *Solenopsis invicta*, *Solenopsis geminata*, *Pheidole megacephala*, *Carebara diversus*, *Polyrhachis dives*, *Nylanderia amia*, *Camponotus kaguya*, *Pheidole noda*, *Pheidole parva*, *Pheidole* sp. (Japan), *Diacamma* sp. (Japan), *Brachyponera chinensis*.



Fig. 16: *Myrmecophilus quadrispina*. (A) female, in dorsal view; (B) terminal structures of female, in dorsal view; (C) head, in lateral view; (D) terminal structures of female, latero-ventral view; the morphology of male genitalia, in (E) dorsal, (F) ventral, (G) lateral, and (H) frontal view (hap: hypo-anal plate).

Distribution records. Hawaii (USA), Lifou, New Caledonia (France), Nansei Islands (Japan), Ogasawara islands (Japan), Mauritius, Samoa, and Taiwan (Fig. 5E).

References. HEBARD (1922), SHIRAKI (1930), DESUTTER-GRANDCOLAS (1997), KOMATSU & al. (2008), KOMATSU & al. (2009).

Discussion. DESUTTER-GRANDCOLAS (1997) had already provided a detailed morphological description, distribution and biology of *Myrmecophilus quadrispina*. Together with the record later provided by HUGEL (2006) and CHINTAUAN-MARQUIER & al. (2016), it was reported

to have discontinuous distribution records that span from Hawaii, Samoan Islands, Lifou, to Mauritius, La Reunion, and possibly Hong Kong. Our morphological and genetic comparisons between *M. quadrispina* and the East Asian species *M. formosanus* lead us to propose *M. formosanus* as a junior synonym of *M. quadrispina*. *Myrmecophilus quadrispina* has a relatively unique shape of male genitalia which can be easily identified from other crickets and serves as an informative taxonomic character. In our examination, *M. formosanus* collected from Taiwan and Okinawa, where they are commonly



Fig. 17: *Myrmecophilus antilucanus* sp.n. (A) paratype male, in dorsal view; (B) paratype female, in dorsal view; (C) terminal structures of paratype male, in dorsal view; (D) terminal structures of holotype female, in dorsal view.

found in the field (KOMATSU & al. 2009), possess identical male genitalia to that of *M. quadrispina* described in DESUTTER-GRANDCOLAS (1997). Furthermore, the molecular data of *M. quadrispina* from Mauritius and French Polynesia, with the latter lying in the range documented in DESUTTER-GRANDCOLAS (1997), are all identical to that of *M. formosanus* from Taiwan and Okinawa Islands.

Myrmecophilus quadrispina was described as an exotic species in Hawaii, originally devoid of ants, with “habitats: in gardens in the city. An imported species, living in the nests of foreign species of ants” (PERKINS 1899). Later, ZIMMERMAN (1948) documented two invasive ant species, *Pheidole megacephala* and *Solenopsis geminata*, as its hosts. Including *Anoplolepis gracilipes* reported here and in previous study (KOMATSU & al. 2009), all three invasive ant species reported to harbor *M. quadrispina* are widely distributed across tropical and sub-tropical regions, and can also be found in Taiwan and Okinawa Islands where *M. formosanus* are thought to be native. Behavior studies have indicated that this species is an extreme host-generalist (KOMATSU & al. 2009, 2017). It is therefore likely that this species can exploit both indigenous and invasive ant species, and such affinity allows this cricket to be transported with the host ant to various countries. Synonymizing the two species may also verify the record of *M. quadrispina* from Hong Kong by KIRBY

(1906), for which there is no voucher reported (YIN & LIU 1995, HE 2018). However, where the native range of this tramp species really is, becomes a new question now and needs more material to verify.

***Myrmecophilus (Myrmecophilus) antilucanus* sp.n.**

(Figs. 5, 13I - L, 17 - 18)

Type material. Holotype: ♀, MALAYSIA, Penang, Universiti Sains Malaysia, hand collected with *Anoplolepis gracilipes*, 09.V.2015, leg. Ching-Chen Lee, alcohol preserved. (collection number #Anomy36.2C10) (NMNS); Paratype: 1 ♀, 1 ♂ and 1 nymph, same data as the holotype, alcohol preserved (NMNS); 5 ♀, same location as the holotype, hand-collected with *A. gracilipes*, 10-11.X.2019, leg. Hung-Wei Hsu, mounted (NTU).

Measurements. Body length: 3.04; pronotal length: 0.83; pronotal width: 1.33; hind-femur length: 1.62; hind-tibia length: 1.16; cercus length: 1.26; ovipositor length: 1.39; maxillary palp segment lengths: 0.09, 0.08, 0.21, 0.16, 0.33.

Male. Head yellowish, lower parts slightly darker towards frons. Antennae bright yellow. Maxillary palps 1st and 2nd segments short, 3rd segment cylinder-shaped with strongly curved upper side, 4th segment teardrop-shaped, 5th segment long and cone-shaped, around 2 to 2.5 times as long as 4th.

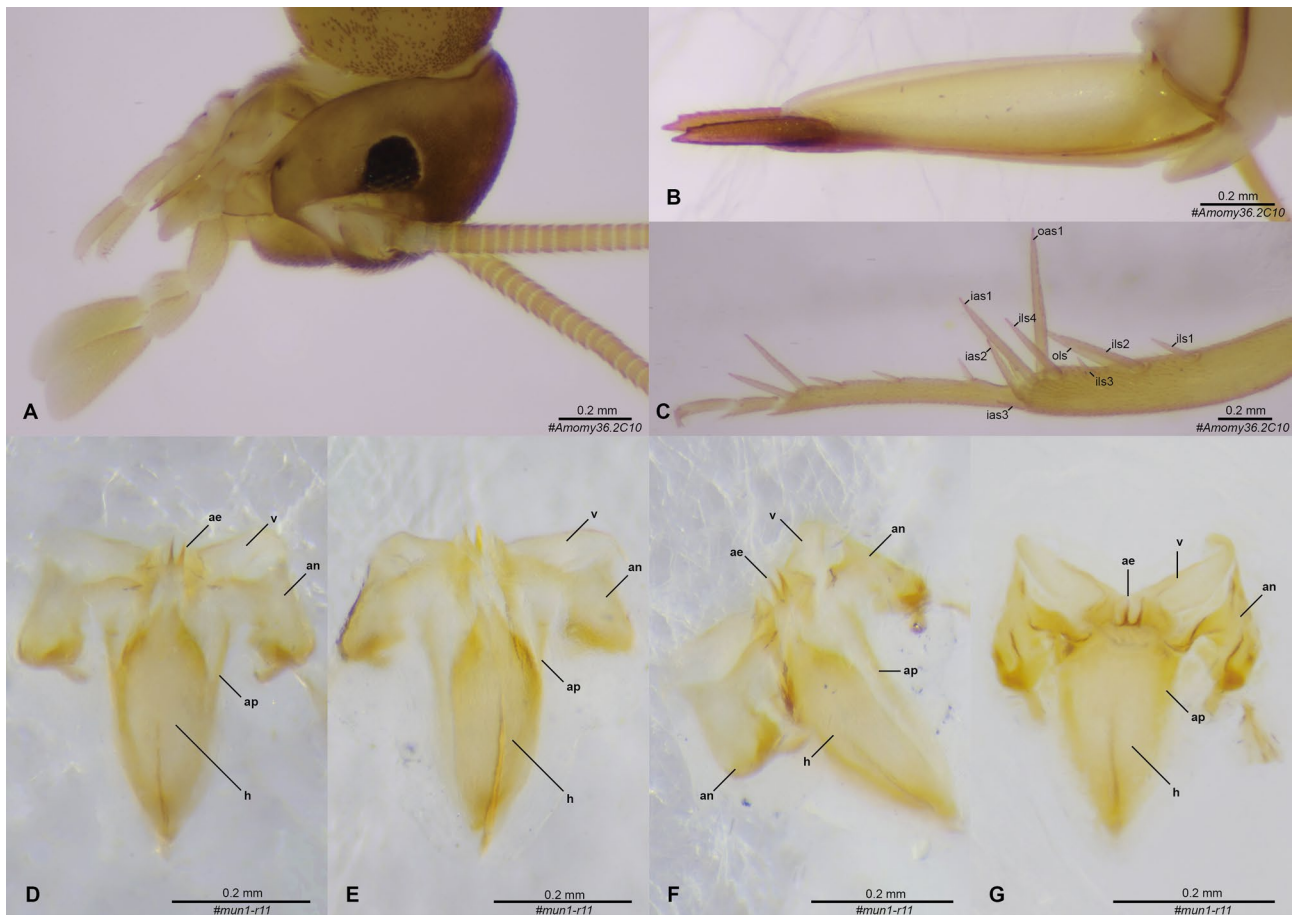


Fig. 18: *Myrmecophilus antilucanus* sp.n. (A) head of holotype female, in lateral view. (B) ovipositor of holotype female, in lateral view; (C) hind leg of holotype female, in inner-lateral view; the morphology of male genitalia in (D) dorsal, (E) ventral, (F) lateral, and (G) frontal view.

In dorsal view, pronotum yellowish-brown, same color as head, covered with dark fine scales, with two dark marks on each side of mid-pronotum. Mesonotum bicolored, with anterior half yellowish brown and posterior half yellow. Metanotum and abdominal tergites brown.

Hind tibia on inner-lateral side with four spurs near apex, 1st spur about half the length of the 2nd spur; 2nd and 4th spurs long, of about equal length; 3rd spur minute, less than half the length of 1st spur. Hind tibia on outer-lateral side with one spur, located oppositely between 2nd and 3rd spurs of inner side; length equal to 2nd spur of inner side. Both inner and outer sides with three additional apical spurs next to lateral ones, 1st apical spur the longest, about twice as long as 2nd apical spur; 3rd spur minute. Hind metatarsus with three dorsal spurs and two apical spurs; apical spurs of equal length, about two to three times as long as dorsal spurs. Cerci and legs yellowish.

Posterior margin of abdomen tergite VII, VIII, and IX smooth, slight curved, and without protrusion, tergite X with two very short trapezoid-shaped extensions separated by a middle concave. Subgenital plate with a bell-like notch apically, making it bilobed with two somehow triangular terminals. Genitalia small, two pseudepiphallallic ancorae somewhat rectangular in lateral view, with horn-

like extensions at outer-upper, outer-lower, inner-upper three corners (Fig. 13I - L). Two pseudepiphallallic ancorae connected by a V-shaped pseudepiphallallic apodeme at outer-upper corner. Hypophallus spindle-shaped in dorsal view, transparently brown, around the size of pseudepiphallallic apodeme, with outer apex prolong, lateral sides of aedeagus slightly sclerotized.

Description of female. Most characters as in male. Posterior margin of abdomen tergite VIII, and IX smooth, slight curved, and without protrusion, tergite X with two long extensions roughly bell-shaped, fused by a furrow in middle. Subgenital plate semicircular.

Remarks. Metanotum and abdominal tergites sometimes bicolored, with brownish-black anteriorly and gradually yellowish-brown posteriorly (Fig. 17B).

Etymology. The Latin word “antilucanus” means “before daybreak”, which represents the yellow coloration pattern of the species.

Host and distribution. *Myrmecophilus antilucanus* was collected with *Anoplolepis gracilipes* in Malaysia, Taiwan, and Thailand (Fig. 5B). Currently no other hosts have been recorded.

Diagnosis. Compared to genetically close-related species such as *Myrmecophilus hebardi*, *M. antilucanus*

possesses a relatively small genitalia with unique shape of pseudepiphallallic apodeme and hypophallus (Figs. 13I - L, 18D - G), as well as uniformly yellowish head and pronotum without distinct dark spot. Compared to *M. haeckeli* in Sri Lanka, the pair of dark lines on pronotum of *M. antilucanus* are not located at anterior corners; the shapes of the 3rd and 4th segments of maxillary palps in *M. antilucanus* are much more curved; abdominal tergite IX of both male and female of *M. antilucanus* does not protrude sharply in middle.

Key to the eight ant cricket species currently known to associate with *Anoplolepis gracilipes*

- 1a. In hind leg, tibial spurs and dorsal margins of metatarsus armed with densely feather-like hairs (hairs sparser in female) *Myrmophilellus pilipes* (CHOPARD, 1928)
- 1b. In hind leg, tibial spurs and dorsal margins of metatarsus unarmed and without hair 2
- 2a. In addition to 3 apical spurs, inner-lateral side of hind tibia possessing 3 spurs of increasing length, 1st shortest and 3rd longest *Myrmecophilus (Myrmophilina) albicinctus* CHOPARD, 1924
- 2b. In addition to 3 apical spurs, inner-lateral side of hind tibia possessing 4 spurs of various length, 1st and 3rd shorter than 2nd, 4th longest 3 - *Myrmecophilus (Myrmecophilus)*
- 3a. Head and body uniformly brown *Myrmecophilus quadrispina* PERKINS, 1899
- 3b. Head and body bicolored, with yellowish and brownish color 4
- 4a. Posterior margin of tergite VII to IX with protrusion at middle (indistinct in female) 5
- 4b. Posterior margin of tergite VII to IX curved smoothly without any protrusion 6
- 5a. In male genitalia, posterior margin of hypophallus with a sclerotized arc *Myrmecophilus pallidithorax* CHOPARD, 1930
- 5b. In male genitalia, posterior margin of hypophallus without sclerotization *Myrmecophilus mayaealberti* HUGEL & MATYOT, 2006 **stat.rev.**
- 6a. Head and pronotum uniformly yellowish, without any distinct spot or area of brownish color. Male genitalia no longer than 0.6 mm, with hypophallus roughly spindle-shaped *Myrmecophilus antilucanus* **sp.n.**
- 6b. Head and pronotum with brownish spots or areas. Male genitalia longer than 0.6 mm, with hypophallus roughly triangular and un-sclerotized at posterior margin 7
- 7a. Head and body brown, only with two transverse yellow lines at posterior margin of pronotum and mesonotum. In male genitalia, pseudepiphallallic ancora roughly h-shaped, hypophallus wide-triangular, with lateral side of same length as posterior margin *Myrmecophilus dubius* SAUSSURE, 1877

7b. Head usually with yellowish spots, pronotum yellowish marginally, with a pair of brown spots divided by a yellowish vertical middle line. Mesonotum, metanotum and all tergites usually bicolored with yellow and brown. In male genitalia, pseudepiphallallic ancora roughly triangular, hypophallus long-triangular, with lateral side about twice the length of posterior margin *Myrmecophilus hebardii* MANN, 1920

Other species found in this study

***Myrmecophilus (Myrmecophilus) ikaros* sp.n.**

(Figs. 13M - P, 19)

Type material. Holotype: ♂, MALAYSIA, Cameron Highland, hand collected with *Crematogaster* sp., 19.II.2017, leg. Edmund Shiuan-Dinq Hang, alcohol preserved. (collection number #palM) (NMNS).

Measurements (mm). Body length: 3.67; pronotal length: 0.89; pronotal width 1.46; hind-femur length: 1.73; hind-tibia length: 1.15; cercus length 1.28; maxillary palp segment lengths: 0.09, 0.09, 0.24, 0.15, 0.39.

Description of male. Head light brown. Antennae brown, same color as head. Maxillary palp 1st and 2nd segments short, 3rd segment cylinder-shaped with strongly curved upper side and straight bottom side, 4th segment roughly triangular with bottom side wide, 5th segment long and cone-shaped, around 2 to 2.5 times as long as 4th.

In dorsal view, pronotum light brown, same color as head, with scattered dark fine scales; posterior part yellow to whitish, forming a transverse line, posterior margin slightly curved inward, but protruded in middle with a sharp peak. Mesonotum mostly yellow, of same color as posterior part of pronotum, with a vague transverse line of brownish color and few scales in middle. Metanotum and abdominal tergite I light brown, slightly darker than head, with anterior margin yellow to whitish. Abdominal tergite II dark brown, with anterior half brighter.

Hind femur brown. Hind tibia on inner-lateral side with four spurs near apex, 1st and 3rd spur short, with 3rd spur slightly shorter than 1st spur; 2nd and 4th spurs long and of equal length, about 1.5 times as long as 1st spur. Hind tibia on outer-lateral side with one spur, located oppositely between 2nd and 3rd spurs of inner side; length about equal to 2nd spur of inner side. Both inner and outer sides with three additional apical spurs next to lateral ones, 1st outer-apical spur the longest, about 1.5 times as long as 2nd outer-apical spur; 3rd spur thin, about 1 / 3 times as long as 2nd outer-apical spur. Hind metatarsus with three dorsal spurs and two apical spurs; apical spurs with equal length, about 2 - 3 times as long as dorsal spurs, and dorsal spurs also with equal length. Cerci bicolored, with middle part light brown, about same color as head, and yellow apically. Legs light yellowish.

Abdomen tergite VI, VII, VIII, and IX distinctly protruded outward in middle of posterior margin. Protrusion of abdomen tergite VI trapezoid-shaped and straight apically; protrusion of abdomen tergite VII larger than that

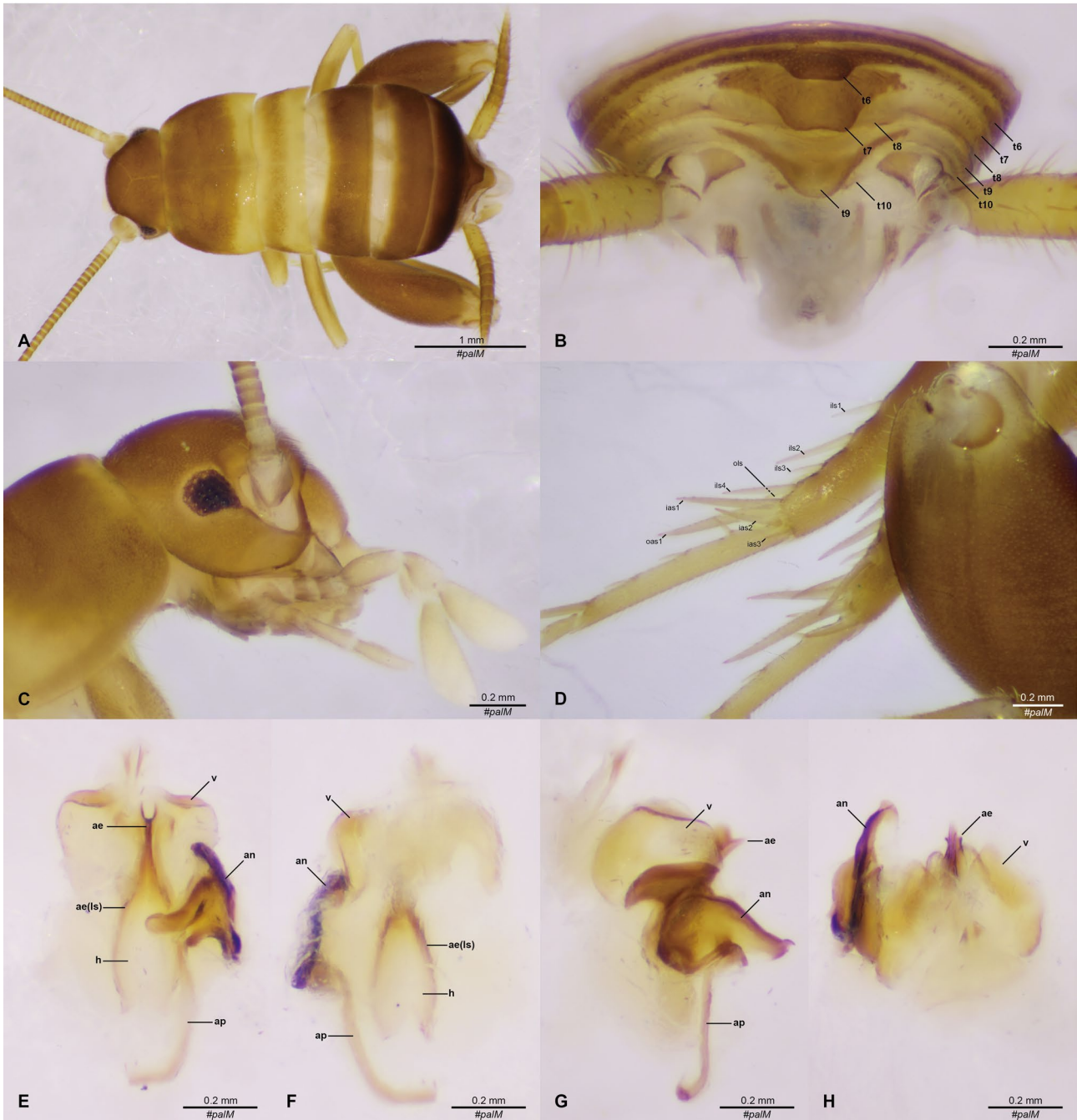


Fig. 19: *Myrmecophilus ikaros* sp.n. holotype male. (A) in dorsal view; (B) terminal structures in dorsal view; (C) head in lateral view; (D) hind tibia in lateral view; the morphology of genitalia in (E) dorsal, (F) ventral, (G) lateral, and (H) frontal view. Note that one pseudepiphallic ancora and partial pseudepiphallic apodeme were damaged during dissection.

of tergite VI, also trapezoid-shaped but slightly concave apically; protrusion of abdomen tergite VIII wider but not higher than that of VII, roughly semi-circular; protrusion of abdomen tergite IX bell-shaped, around same size as that of tergite VIII, covering bilobal subgenital plate of abdominal tergite X in dorsal view. Subgenital plates small, with a bell-like notch apically. Genitalia with two pseudepiphallic ancorae connected by a roughly long U-shaped pseudepiphallic apodeme. Pseudepiphallic ancorae roughly skew and teardrop-shaped in lateral view, with horn-like long extension at upper side; bottom part

somehow pentagonal, with a thick sickle-shaped ventral lobe connected at bottom-lateral corner (Fig. 13M). Hypophallus long, length more than three times the width, nearly spindle-shaped, with inner apex concave forming a V-shaped unsclerotized margin; aedeagus with two lateral sclerotizations, apices slightly curved.

E t y m o l o g y. The name “Ikaros” refers to a character from ancient Greek mythology.

Host and distribution. Type of *Myrmecophilus ikaros* was collected in Cameron Highland, central Malaysia, with *Crematogaster* sp. in a hollow bamboo structure.

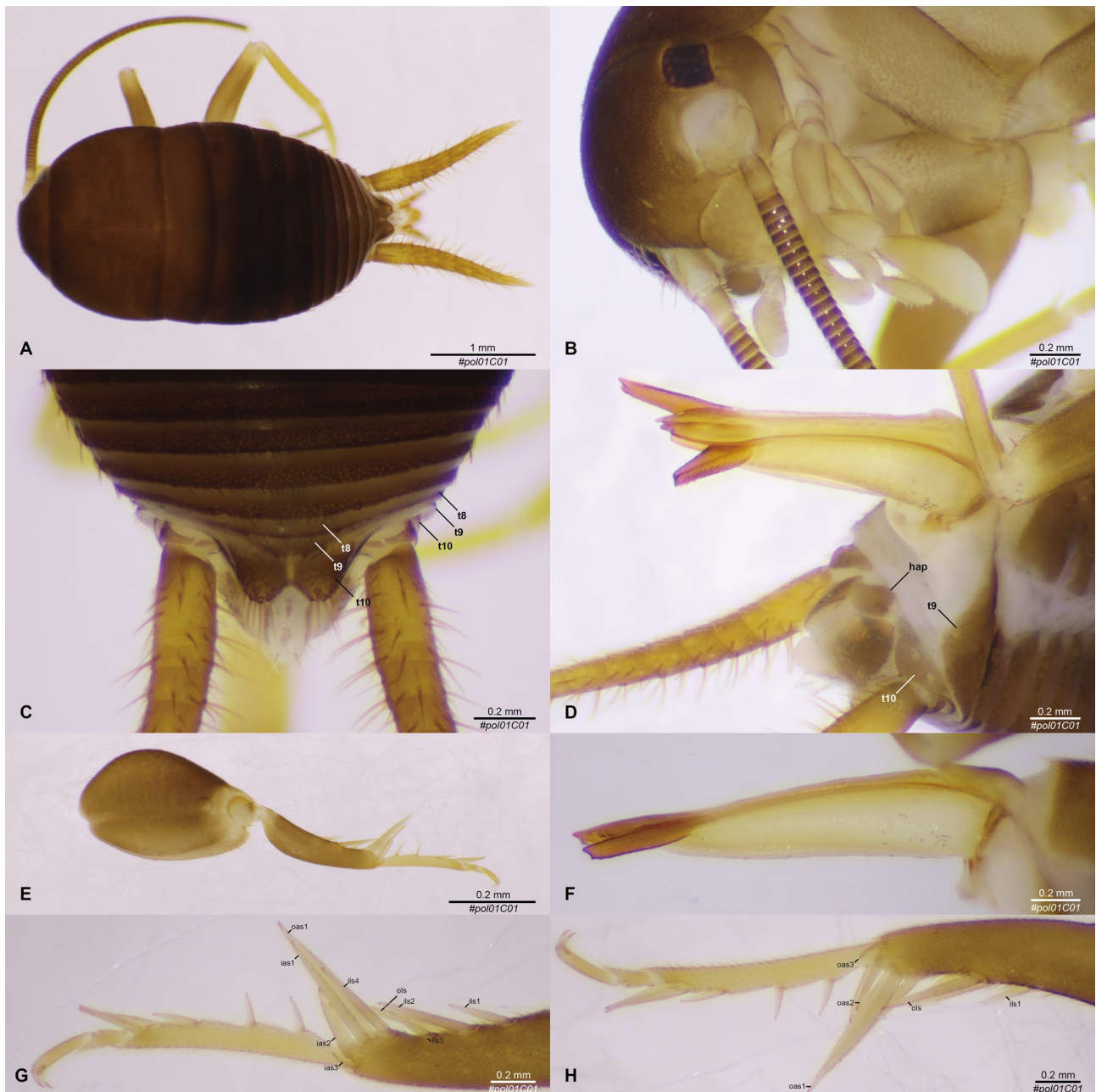


Fig. 20: *Myrmecophilus caliginosus* sp.n. holotype female. (A) in dorsal view; (B) head in latero-ventral view; (C) terminal structures in dorsal view; (D) terminal structures in latero-ventral view; (E) hind leg in lateral view; (F) ovipositor in lateral view; (G) hind tibia and tarsus in inner-lateral view; (H) hind tibia and tarsus in outer-lateral view.

Diagnosis. *Myrmecophilus ikaros* is similar to *M. pallidithorax* and *M. mayaealberti* in male genitalia where a distinct ventral lobe of pseudepiphallic ancora is present in lateral view, however, *M. ikaros* can be distinguished by the combination of its coloration pattern, the protrusion at the posterior margin of pronotum, the shape and sclerotized pattern of aedeagus and hypophallus.

Discussion. Although *Myrmecophilus ikaros* has similar male genitalia and tergal extensions to that of *M. mayaealberti* and *M. pallidithorax*, and we failed to obtain DNA from the holotype for genetic comparison, we can still distinguish it from the two species accord-

ing to overall morphological differences. In the shape of genitalia, despite the damage on the male genitalia of *M. ikaros*, we were still able to visualize that half of the pseudepiphallic apodeme overall resembles a long U-shape with a straight bottom side (Figs. 13M - P, 19E - F); on the other hand, pseudepiphallic apodeme of *M. mayaealberti* is relatively sharp and of V-shape in dorsal view (Fig. 11C). In addition, hypophallus of *M. ikaros* appears to have a relatively narrow bottom side, with two lateral sclerites of aedeagus curving inwards and therefore the whole aedeagus is somehow of oval or spindle-like shape (Fig. 19E - F). The hypophallus of *M. mayaealberti*, how-

ever, has relatively straight lateral sclerites of aedeagus and is triangularly shaped (Fig. 11C). *Myrmecophilus ikaros* also has unique characters on pronotum. Only the posterior margin shows yellowish color and possesses a sharp median protrusion, with the latter one not having been seen in any other known cricket species yet. On the other hand, the pronotum of *M. mayaealberti* resembles that of *M. hebaridi* in dark form (Figs. 9B, 11A), in which two distinct brownish spots are surrounded by yellowish peripheral margins. Unlike the other two yellowish species, *M. ikaros* is also the species that was not been found associated with *Anoplolepis gracilipes*. The holotype was collected with native *Crematogaster* species in a hollow bamboo. This suggests that this species may be ecologically differentiated from *M. mayaealberti* and *M. pallidithorax*, which were both found to associate with *A. gracilipes* so far. Combined with morphological and ecological evidence stated above, we subsequently described *M. ikaros* as a new species based on a single adult male.

***Myrmecophilus (Myrmecophilus) caliginosus* sp.n.**

(Fig. 20)

Type material. Holotype: ♀, TAIWAN, New Taipei, Linkou, hand-collected with *Polyrhachis dives*, 27.IX.2015, leg. Po-Wei Hsu, alcohol preserved. (collection number #*pol01C1*) (NMNS); Paratype: 1 ♀ & 2 nymphs, same data as the holotype, alcohol preserved. (NMNS).

Measurements. Body length: 3.57; pronotal length: 1.12; pronotal width: 1.85; hind-femur length: 0.41; hind-tibia length: 0.32; cercus length: 1.59; ovipositor length: 1.67; maxillary palp segment lengths: 0.10, 0.12, 0.31, 0.25, 0.49.

Description of female. Head and body uniformly brown. Antennae brown, same color as head, with basal segments brighter. Maxillary palp 1st and 2nd segments short, 3rd segment cylinder-shaped with curved upper side, 4th and 5th segments cone-shaped, with 5th segment around 2 times as long as 4th.

Legs brownish yellow, brighter apically. Hind tibia on inner-lateral side with four spurs near apex, 1st spur short, about half the length of the 2nd spur; 2nd and 4th spurs long, with 4th spur slightly longer; 3rd spur around the same length as 1st spur. Hind tibia on outer-lateral side with one spur, located oppositely between 2nd and 3rd spur of inner side; length equal to 2nd spur of inner side. Both inner and outer side with three additional apical spurs: next to lateral ones, 1st apical spur the longest, about three to four times as long as 2nd apical spur; 3rd spur minute. Hind metatarsus with three dorsal spurs and two apical spurs; apical spurs of equal length, about two times as long as dorsal spurs; dorsal spurs of equal length. Cerci yellowish.

Abdominal tergite VII, VIII, and IX slightly curved outward posteriorly and without protrusion, tergite X with two brown long bell-shaped extensions with numerous long setae apically, connected by a furrow in middle which has about half the length of the extension. Subgenital

plate wider than high, roughly semicircular, with apical margin straight.

Etymology. The Latin word “caliginosus” means “misty” or “gloomy”, which represents the coloration of the species and the typical climate of the type locality Linkou.

Host and distribution. Types of *Myrmecophilus caliginosus* were collected with a colony of an endemic ant species *Polyrhachis dives*, in a semi-disturbed area infested with *Anoplolepis gracilipes*, *Paratrechina longicornis*, and *Solenopsis invicta* in Linkou, Northern Taiwan.

Diagnosis. Although the appearance of *Myrmecophilus caliginosus* is generally similar to the widely distributed species *M. quadrispina* and information on male genitalia of this species is not available, *M. caliginosus* can be identified with confidence using the terminal structures of females (Figs. 16D, 20D). The lateral extensions of abdominal tergite IX of *M. caliginosus* are more distinct, forming an obtuse-angled triangle, instead of forming a slender shape as in *M. quadrispina*. In addition, the shape of hypo-anal plate (the sclerite beneath the anal opening) is also different between the two species, with that of *M. quadrispina* being roughly semicircular, while in *M. caliginosus* it is rhombic.

Discussion

Delimitating ant cricket species boundaries using molecular markers:

Although male genitalia serve as a predominant character in identifying ant cricket species, this character can become impractical if only juveniles or females are collected.

We showed that DNA barcodes can aid in species identifications in such difficult cases. Our phylogenetic analyses based on *cytb* and *EF1a* received strong clade support and the clusters were in line with our morphological identifications. The phylogenetic analyses based on *EF1a* provide sufficient power to verify the relationships between different subclades in the analyses based on *cytb*. Therefore, the two markers together allow us to identify different ant cricket species with robustness regardless of their sex, development stage, and sampling location. In our K2P pairwise p-distance analysis based on *cytb*, we also observed the presence of a so called “barcoding gap” (CHEN & al. 2010, ČANDEK & KUNTNER 2015, VASCONCELOS & al. 2016). Even with some minor counts in-between, this marker still provides additional evidence in discriminating ant crickets associated with yellow crazy ants over large geographical scales.

Human-mediated dispersal of ant crickets with

hosts: Haplotype networks for the four widespread ant cricket species associated with *Anoplolepis gracilipes* and one with *Paratrechina longicornis* showed an incongruent geographic pattern of haplotype grouping. The finding of shared haplotypes in geographically distant and discontinuous locations, for example, Mauritius, Taiwan, and French Polynesia, suggests that these ant crickets may have been transported with their associated ant host species which are also common hitchhikers with human-mediated activities. Additional lines of evidence supporting

such ant-associated dispersal include: 1) a similar pattern of geographic-genetic incongruence has been reported in both invasive ant species (*A. gracilipes*: DRESCHER 2011, *P. longicornis*: TSENG & al. 2019); 2) five ant cricket species in our study were found to be host-specialists exclusively associated with *A. gracilipes* and *P. longicornis* according to our data and others as documented also by KOMATSU & al. 2017 and C.-S.M. Ooi (unpubl.). Obligate associations between these ant crickets and *A. gracilipes* and *P. longicornis* may preclude crickets from dispersing without their host(s); 3) other tramp ant species (e.g., *Solenopsis geminata* and *Pheidole megacephala*) possessing a similar distribution with *A. gracilipes* in Indian / Pacific region (JANICKI & al. 2019) might be capable of serving as an alternative carrier that facilitates ant cricket dispersal, especially for those host-generalist species (e.g., *Myrmecophilus quadrispina*).

Diversity and spread of ant crickets associated with the yellow crazy ant: Invasive ant species often attain a high abundance in their introduced ranges (SUAREZ & al. 1999, O'DOWD & al. 2003, CHIFFLET & al. 2018), and are sometimes recorded with guest ant crickets and other arthropods. For example, the longhorn crazy ant, *Paratrechina longicornis* is arguably the most widely distributed species with records across the Old and New World (WETTERER 2008). The host-specific ant cricket, *Myrmecophilus americanus* has been frequently recorded within nests of this invasive ant (WETTERER & HUGEL 2008, 2014, KOMATSU & MARUYAMA 2016b, ORTEGA-MORALES & al. 2017). The presence of *M. americanus* in almost all biogeographic regions together with its host ant can be attributed, at least partially, to the fact that this cricket lives intimately with *P. longicornis* as its exclusive host. Similarly, *Solenopsis* ant species, including two highly invasive, widespread species *S. invicta* and *S. geminata*, were found to harbor ant crickets. In North America, native *M. nebrascensis* and *M. pergandei* were reported in the nest of *Solenopsis* species (NEECE & BARTELI 1981, 1982, TABER 2000, HILL 2009); in the Pacific regions, *Myrmophilellus pilipes* and *M. quadrispina* were also documented with *S. geminata* (DESUTTER-GRANDCOLAS 1997, KOMATSU & MARUYAMA 2016a).

The occurrence of eight ant cricket species in yellow crazy ant nests represents the highest diversity of cricket species in all ant species, and it is likely that more ant crickets in association with this host will be found (e.g., *Myrmecophilus seychellensis* in Seychelles). High ant cricket species diversity in relation to yellow crazy ants suggests that this ant may serve as a favorable ant cricket carrier, and raises the question: What factors influenced this phenomenon? While no empirical research attempts exist to date, the life history and ecological dominance of this ant may help answer this question. Yellow crazy ants usually prosper as an ecologically dominant species in introduced areas (HILL & al. 2003; O'DOWD & al. 2003, ABBOTT 2005), which may facilitate associated ant crickets thriving along with their host. In our survey, hundreds of ant crickets were often found within a single collection site

in Southern Taiwan where the infestation of yellow crazy ant is widespread. A similar pattern can also be observed in a dominant endemic ant species, *Formica rufa* L., in Canadian conifer forests where hundreds of *M. oregonensis* were found near the ant mounds (BEALL 1929). We therefore argue that the degree of ecological dominance of a host ant may be an important determinant to the abundance of single (or multiple) ant cricket species.

Life history characteristics such as nest structure, may also allow colonies of yellow crazy ants to house both high diversity and abundance of *Myrmecophilus*. Unlike certain ant species that build well-defined galleries and chambers deep in the soil, yellow crazy ants commonly nest in the pre-existing physical space such as the cavities of tree trunks, stone crevices, leaf litter or piles of artificial objects (RAO & al. 1991). As non-integrated ant crickets tend to strategically avoid intimate contacts with host ants (KOMATSU & al. 2013), a nesting chamber with irregular surfaces and spaces may be more favorable as they are able to hide and avoid hostile behavior from their hosts.

Yellow crazy ant invasion and ant cricket community assembly: While yellow crazy ants have already been reported to exert severe impacts on community structure of native invertebrates (LACH & HOOPER-BÛI 2009), they may also act as a selective force on the community structure of local ant crickets. The displacement of native ant species has often been observed as a major ecological consequence of yellow crazy ant invasion (LACH & HOOPER-BÛI 2009). Consequently, reduced native ant diversity (and / or abundance) may drive extinction of host-specialist species in two mutually non-exclusive processes: 1) Host specialist ant crickets are expected to face a high risk of local extinction due to the extinction of their hosts. Earlier studies showed that host-specialist ant cricket species possessed a poor survival rate after forced to switch the host. Japanese host-specialist ant crickets *Myrmecophilus kubotai* were killed within few days after artificially translocated in nests of Argentine ant due to evoked hostile reactions from ant workers (TAKAHASHI & al. 2018). A similar finding was reported in KOMATSU & al. (2009), in which host-specialist *M. albicinctus* was unable to switch hosts to a native ant species; 2) Host-generalist species, on the other hand, may benefit from the ability to exploit multiple ant species including ecologically dominant ones (e.g., yellow crazy ants), thus potentially possessing a competitive advantage over host-specialist species as they can freely migrate between colonies of different ant species.

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