

Integrated taxonomy unveils three new species of *Foenobethylus* (Hymenoptera, Bethylidae) from China

Yang Li^{1*}, Zheng Wang^{2*}, Hua-Yan Chen³, Shi-Xiao Luo³

1 Sichuan Provincial Key Laboratory for Development and Utilization of Characteristic Horticultural Biological Resources, College of Chemistry and Life Sciences, Chengdu Normal University, Chengdu 611130, China

2 Key Laboratory of Genetic Improvement and Quality Regulation for Tropical Spice and Beverage Crops of Hainan Province, Research Institute of Spice and Beverage, Chinese Academy of Tropical Agricultural Sciences, Wanning 571533, China

3 Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China

Corresponding author: Hua-Yan Chen (huayanc@scbg.ac.cn)

Academic editor: Michael Ohl | Received 4 December 2021 | Accepted 16 January 2022 | Published 28 February 2022

<http://zoobank.org/74E70C08-3253-4CA6-BFCF-BDAAEF80D5BD>

Citation: Li Y, Wang Z, Chen H-Y, Luo S-X (2022) Integrated taxonomy unveils three new species of *Foenobethylus* (Hymenoptera, Bethylidae) from China. *Journal of Hymenoptera Research* 89: 89–108. <https://doi.org/10.3897/jhr.89.78856>

Abstract

Species of the genus *Foenobethylus* Kieffer, 1913 are parasitoids wasps rarely collected and are only found in the Oriental region. In this study, based on both morphological and molecular evidence, we describe three new species from China: *F. robusta* Li & Chen, **sp. nov.**, *F. xinglongsensis* Wang & Chen, **sp. nov.**, and *F. yunkaishanensis* Chen & Luo, **sp. nov.** An updated key to species of the genus is provided. Additionally, the phylogenetic relationships between *Foenobethylus* and other three morphologically similar genera are discussed based on the analyses of *COI* and *28S* genes.

Keywords

Flat wasps, key, new species, parasitoid wasp, phylogeny, Pristocerinae

* These two authors contributed equally to this work.

Introduction

Foenobethylus Kieffer is a rare genus of Pristocerinae in the flat wasp family Bethyridae, with only 11 described species Oriental (Várkonyi and Polaszek 2007; Liu et al. 2011; Saverognini and Azevedo 2013; Chen and Azevedo 2020). Of the 11 described species, 10 species were described based on only males. Until recently, the first female of the genus was discovered by Chen and Azevedo (2020). The new finding suggested that *Foenobethylus* might be a synonym under *Parascleroderma*. Although the morphological differences between *Foenobethylus* and *Parascleroderma* were intensely discussed (Azevedo and Lanés 2007; Várkonyi and Polaszek 2007; Chen and Azevedo 2020), Chen and Azevedo (2020) concluded that the precise taxonomic delimitation of both genera only could be solved under phylogenetic analyses. Interestingly, before the discovery of the female of *Foenobethylus*, considering the extreme sexual dimorphism in Pristocerinae, Várkonyi and Polaszek (2007) also suspected that the females of *Foenobethylus* might be already known to science under a different generic name and the exact phylogenetic status of *Foenobethylus* could be resolved by preferably molecular evidence.

Recently, we have accumulated some fresh specimens of several *Foenobethylus* species collected by Malaise traps in South China. In this study, we aim to identify this new material to species using an integrated taxonomic approach that combines both morphology and molecular data and to conduct a preliminary phylogenetic analysis between *Foenobethylus* and morphologically similar genera based on DNA sequences.

Materials and methods

Collection and identification

This work is based on specimens of *Foenobethylus* collected by Malaise traps (MT) set up across southern China. Specimens were identified using the keys of Chen and Azevedo (2020). All studied specimens are deposited in the Insect Collection of South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (**SCBG, curator:** Huayan Chen). The morphological terms generally follow Lanés et al. (2020) and Brito et al. (2021), and the sculptural and texture of integument nomenclature follows Harris (1979).

Abbreviations and morphological terms used in text are:

WH width of the head;

LH length of the head;

WF width of the frons;

HE height of the eye;

OOL ocello-ocular line;

WOT width of the ocellar triangle.

The genitalia and subgenital plate of a male paratype were removed and cleared using 10% potassium hydroxide solution, and mounted in glycerol on slides, when examined and photographed. Images and measurements were made using Nikon SMZ25 microscope with a Nikon DS-Ri 2 digital camera system. Images were post-processed with Adobe Photoshop 2022.

DNA extraction, amplification, and sequencing

In total, 7 specimens of 4 morphospecies were used for DNA acquisition (see Table 1). Collecting information of the studied specimens are available in the material examined section by the associated codes. Genomic DNA was extracted from entire specimens using a DNeasy Blood & Tissue Kit (QIAGEN, Inc.), following a nondestructive DNA extraction protocol as described in Taekul et al. (2014). Following DNA extraction, the “barcode” region of the mitochondrial cytochrome oxidase subunit 1 (*COI*) and nuclear 28S rRNA D1–2 (*28S*) were amplified using the LCO1490/HCO2198 (Folmer et al. 1994) and D2–3551F/D2–4057R (Gillespie et al. 2005) primer pairs, respectively. Polymerase chain reactions (PCRs) were performed using Tks Gflex DNA Polymerase (Takara), and conducted in a T100 Thermal Cycler (Bio-Rad). Thermo-cycling conditions were: an initial denaturing step at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 50 °C for 30 s, 72 °C for 30s and an additional extension at

Table 1. List of analyzed taxa and accession numbers.

Species	Code	GenBank accession No.	
		28S	COI
Ingroup			
<i>Apenesia</i> sp.1	–	MG760810	MG760759
<i>Apenesia</i> sp.2	–	MG760811	MG760760
<i>Cleistepyris</i> sp.1	–	MG760830	MG760774
<i>Cleistepyris</i> sp.2	–	MG760832	MG760776
<i>Dissomphalus</i> sp.1	–	MG760834	MG760778
<i>Dissomphalus</i> sp.2	–	MG760821	MG760768
<i>Parascleroderma</i> sp.1	–	MG760813	MG760762
<i>Parascleroderma</i> sp.2	–	MG760816	MG760763
<i>Foebethylus emiliacasellae</i>	–	–	MG760815
<i>Foebethylus robusta</i> sp. nov.	SCAU 3042641	–	OL678509
<i>Foebethylus syndesis</i>	SCAU 3042642	OL678115	OL678510
<i>Foebethylus syndesis</i>	SCAU 3042643	OL678116	OL678511
<i>Foebethylus xinglongensis</i> sp. nov.	SCAU 3042638	OL678117	OL678512
<i>Foebethylus xinglongensis</i> sp. nov.	SCAU 3042656	OL678118	OL678513
<i>Foebethylus yunkaishanensis</i> sp. nov.	SCAU 3042639	OL678119	OL678514
<i>Foebethylus yunkaishanensis</i> sp. nov.	SCAU 3042658	OL678120	OL678515
Outgroup			
<i>Prorops nasuta</i>	–	MG760840	MG760784
<i>Sierola gracilis</i>	–	MG760837	MG760781

Note: accession numbers begin with OL are sequences generated in this study.

72 °C for 5 min. Amplicons were directly sequenced in both directions with forward and reverse primers on an Applied Biosystems (ABI) 3730XL by Guangzhou Tianyi Huiyuan Gene Technology Co., Ltd. (Guangzhou, China). Chromatograms were assembled with Geneious 11.0.3. All sequences generated from this study are deposited in GenBank (accession numbers see Table 1). All residual DNAs are archived (–30 °C) in the molecular laboratory of SCBG, Guangzhou, China, and are available for further study upon request.

Molecular species delimitation and phylogenetic analysis

All sequences were blasted in BOLD (Barcode of Life Database, http://www.barcodinglife.org/index.php/IDS_OpenIdEngine, only for *COI*) and GenBank. Sequences were aligned using MAFFT v7.470 by the G-INS-I strategy for 28S and G-INS-I strategy for *COI* (Kato and Standley 2013). Genetic Kimura-2 parameter (K2P) distances of *COI* sequences within and between species were calculated in MEGA 7 with pairwise deletion for gaps (Kumar et al. 2016). For phylogenetic analysis, sequences of specimens of three morphologically similar or phylogenetically close genera, *Apenesia* Westwood, *Cleistopyris* Kiefer, *Dissomphalus* Ashmead and *Parascleroderma* Kieffer, as suggested by previous studies (Alencar et al. 2018; Chen and Azevedo 2020), were extracted from Alencar et al. (2018) (Table 1). The 28S sequence of *Foenobethylus emiliacasellae* Várkonyi and Polaszek was downloaded from Genbank. *Prorops nasuta* (Waterston, 1923) and *Sierola gracilis* Fullaway, 1920 (Hymenoptera, Bethyridae) selected as outgroups as used by Alencar et al. (2018). The concatenated sequences of 28S and *COI* were then analyzed using RAxML as implemented in Geneious 11.0.3 under the GTRGAMMA evolutionary model to generate a maximum likelihood (ML) tree.

Results

This study generated seven sequences of *COI* and six sequences of 28S for seven specimens. These seven voucher specimens were subjected to further morphological examination and four species were recognized, of which three are described as new. The *COI* sequences do not show a high match with sequences in both BOLD and GenBank databases. The closest match is an undetermined species of *Parascleroderma*, with 86.4% identical base pairs. Genetic distances of *COI* sequences among *Foenobethylus* species and representative species of four other morphologically similar or purported phylogenetically close genera and outgroups are in Table 2. Intraspecific distances of the *COI* sequences of *Foenobethylus* are identical. Interspecific distances among *Foenobethylus* species range between 10.3% and 13.6%. Intergeneric distances between *Foenobethylus* and the four potential close genera and the outgroups range between 14.3% and 28.6%, with *Parascleroderma* is the most close genus, which shows 14.8–

18.6% divergence. The morphology-based delimitations of species are congruent with the molecular species identification based on *COI* sequences. Phylogenetic relationships between *Foebethylus* and the studied genera are shown in Fig. 1. *Foebethylus* was recovered as a monophyletic clade, with *Parascleroderma* as a sister group.

Table 2. Genetic distances of *COI* sequences among studied taxa (%).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>Apenesia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2 <i>Apenesia</i> sp2	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-
3 <i>Cleistopyris</i> sp1	20.3	19.4	-	-	-	-	-	-	-	-	-	-	-	-
4 <i>Cleistopyris</i> sp2	19.8	19.4	15	-	-	-	-	-	-	-	-	-	-	-
5 <i>Dissomphalus</i> sp1	27.3	26.9	26.5	25.4	-	-	-	-	-	-	-	-	-	-
6 <i>Dissomphalus</i> sp2	23.4	23.5	27.2	22.6	26.4	-	-	-	-	-	-	-	-	-
7 <i>Parascleroderma</i> sp1	19.8	19.2	19.4	17.4	24.9	21	-	-	-	-	-	-	-	-
8 <i>Parascleroderma</i> sp2	17	16.4	21.1	20.8	26.2	23.4	17.3	-	-	-	-	-	-	-
9 <i>Foebethylus robusta</i> sp. nov.	18.7	18.7	20.9	18.6	25	23.5	14.3	18.6	-	-	-	-	-	-
10 <i>Foebethylus syndesis</i>	21.4	21.2	22.5	19.9	25.2	24.6	15.4	17.4	11.3	-	-	-	-	-
11 <i>Foebethylus xinglongensis</i> sp. nov.	20.1	19.6	20.9	17.7	24.8	24.7	14.6	16.4	13.1	13.6	-	-	-	-
12 <i>Foebethylus yunkaishanensis</i> sp. nov.	19.8	19.6	21.2	19.4	31.5	23.9	14.8	16.7	10.8	10.3	12.3	-	-	-
13 <i>Sierola gracilis</i>	25.2	24.7	27.1	27	28.6	27.4	24.7	25.5	27	28.6	27.8	27.5	-	-
14 <i>Prorops nasuta</i>	25	24.7	26.2	25.5	25.5	27	23.7	25.5	25.3	27.5	26.4	25.2	27.2	-

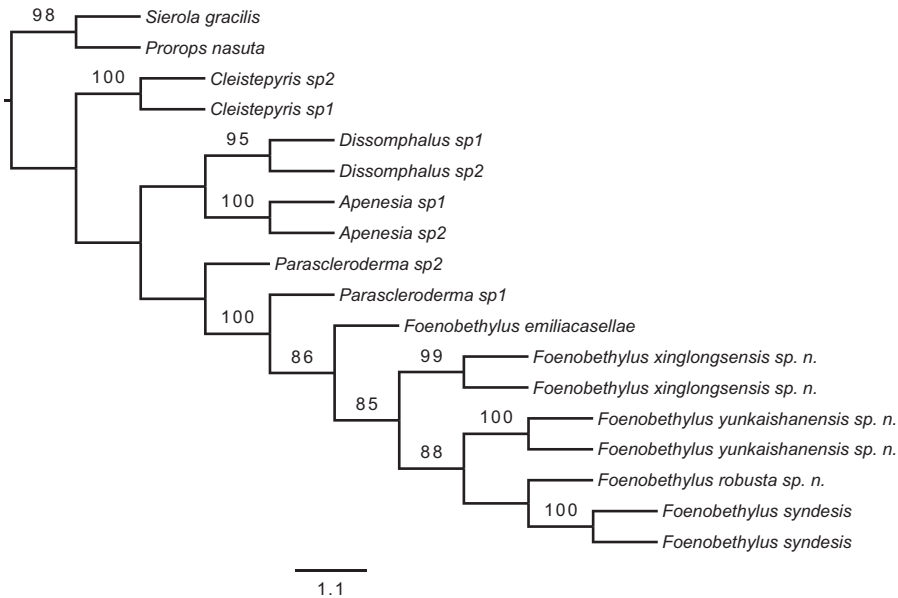


Figure 1. Maximum likelihood tree demonstrating the clustering of *Foebethylus* and related genera based on concatenated sequences (*COI* and *28S*).

Species treatment

Foenobethylus robusta Li & Chen, sp. nov.

<http://zoobank.org/B2F138C5-2376-458B-9488-D2E965C42744>

Figures 2, 3

Diagnosis. Male. Head rectangular and elongate (Fig. 2B). Clypeus with median lobe truncate, median carina incomplete, not reaching anterior clypeal margin, and straight in dorsal profile. Eye glabrous (Fig. 2B). Notaulus very weakly converging posteriorly, complete and deep (Fig. 2C). Propodeum polished (Fig. 2C). Pterostigma broad, about 0.4× as wide as long (Fig. 2F). Metatrochanter without spine (Fig. 3G). Metafemur with only one acute spine in ventral midline, 0.26× as long as metafemoral width, touching apical margin of metatrochanter, and with one small, broad and dentate protuberance ventrally, 0.04× metafemoral width, located on second quarter of metafemur (Fig. 3G). Posterior hypopygeal margin strongly incurved, lateral lobe without conical protuberance (Fig. 3E). Basivolsella large, 0.6× as long as gonostipe, basal half about as wide as apical half, basal margin incurved (Fig. 3C, D).

Description. Male holotype. Body length 4.52 mm. Forewing length 3.10 mm.

Colors. Head, mesosoma, metasoma, antenna and apex of mandible dark castaneous; palpi, base of mandible, all tibiae and tarsi castaneous; wings subhyaline, fore wing somewhat infusate medially.

Head. Head (Figs 2B, 3A) rectangular and elongate, 1.2× as long as wide. Mandible with five apical sharpened teeth, posterior tooth largest, middle three teeth smaller, anterior tooth smallest. Clypeus with median lobe truncate, median carina incomplete, not reaching anterior clypeal margin, and straight in dorsal profile. Eye glabrous, almost touching mandible base at anterior corner. Malar space reduced. Frons weakly coriaceous, almost polished, punctures very sparse and small. WH 0.84× LH. WF 0.66× WH. WF 1.63× HE. OOL 1.44× WOT. Frontal angle of ocellar triangle obtuse. Anterior ocellus far posterior to supra-ocular line. Temple divergent anterad, corner rounded. Vertex badly outcurved. First four antennomeres in ratio of about 25:12:11:11 (Fig. 2E). All flagellomeres distinctly longer than wide, pubescence erect, about 0.48× as long as flagellomeral width. Maxillary palpus with five palpomeres (Fig. 3A). Labial palpus with two palpomeres (Fig. 3A). Occipital carina complete. Medioccipito-genal carina complete. Hypostomal carina thick, almost straight, angled medially.

Mesosoma (Figs 2C, D, 3B). Mostly polished and weakly coriaceous. Pronotal flange short, exposing propleuron dorsally. Dorsal pronotal area short, without anterior carina strongly progressively narrowing anterad, lateral surface concave. Notaulus very weakly converging posteriorly, complete, deep, and progressively more evident posteriorly. Parapsidal signum sinuous, absent anteriorly. Mesoscutellum shorter than anteromesoscutum. Mesoscutum-mesoscutellar sulcus deep, arched, sides wider than middle. Metanotum conspicuous, metascutellum wide and short, metanotal trough not trabeculate, metanotal fovea outlined. Metapectal-propodeal disc polished, metapostnotal median carina complete, although weak posteriorly,

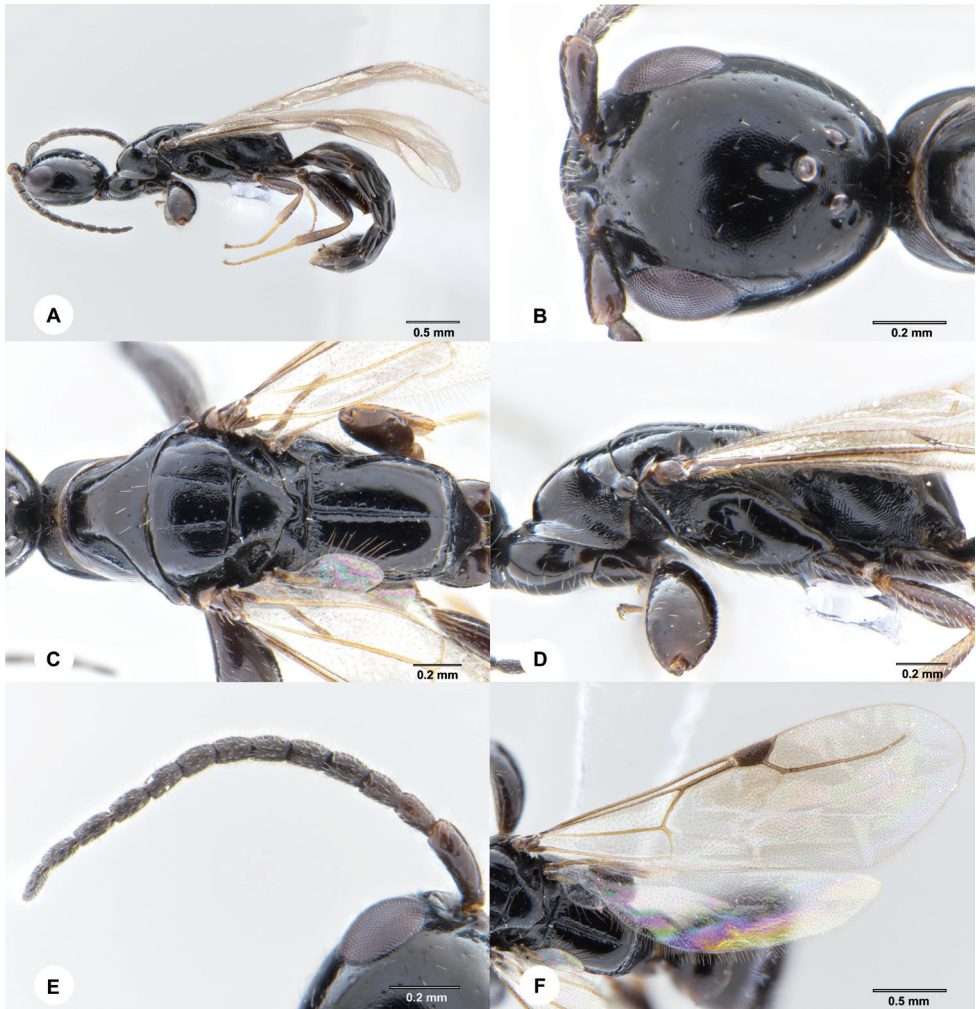


Figure 2. *Foenobethylus robusta* Li & Chen, sp. nov., male, holotype (SCAU 3042645) **A** lateral habitus **B** head, dorsal view **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** antenna **F** wings.

lateral and transverse posterior carinae complete; propodeal spiracle circular, located on lateral surface of propodeum, ventral to lateral carina. Propodeal declivity transverse sculptured, without median carina. Mesopleuron with mesopleural pit large and well defined. Pleurosternum small, triangular, with vertex directed posterad. Prepectus with epicnemial medial projection complete, posterior prepectal flange thick. **Wings** (Fig. 2F). Forewing with three closed cells (Costal, Radial and First Cubital); pterostigma about 0.4× as wide as long, anterior board outcurved; 2r-rs&Rs sector vein long; Rs&M reaching Sc+R far from pterostigma. Hind wing with one straight hamulus, and four distal hamuli equally distant, and strongly curved. **Legs**. Profemur swollen, 2.7× as long as wide, apical half of ventral margin serrulate. Metatrochanter

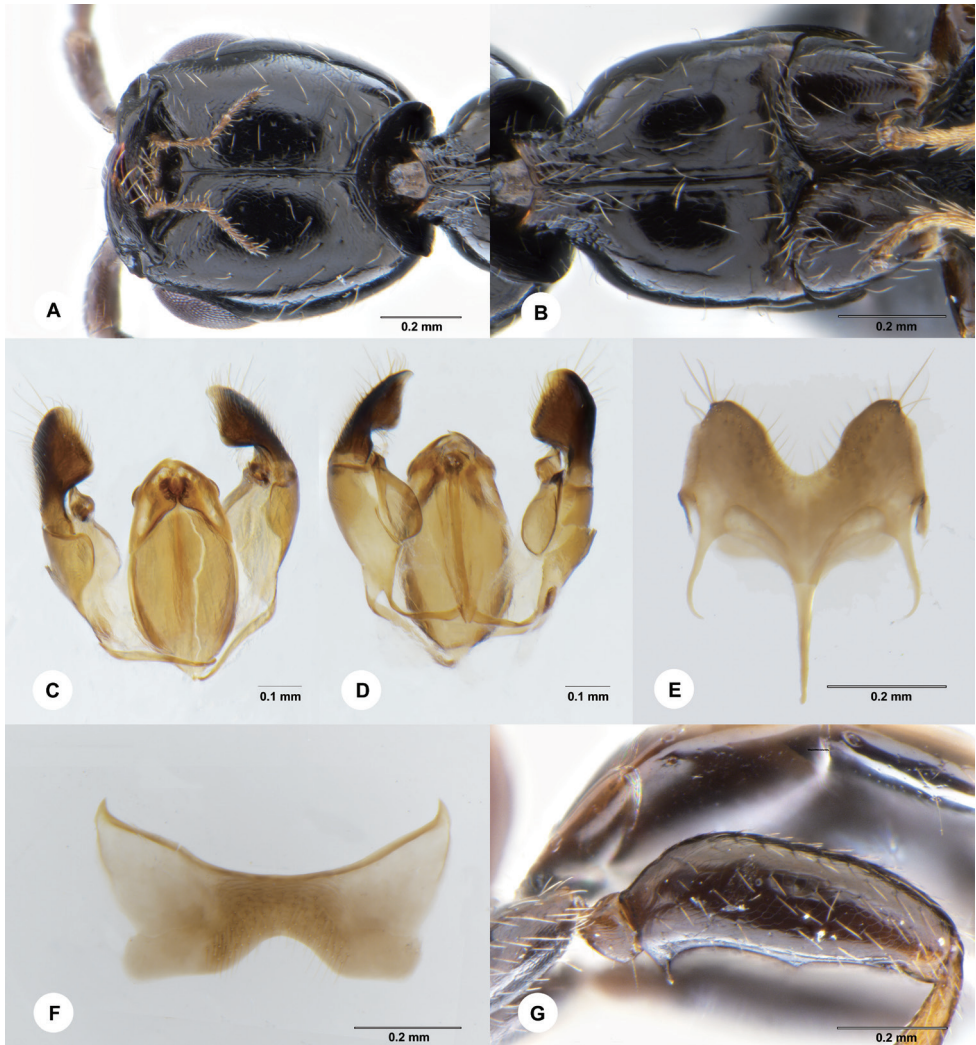


Figure 3. *Foenobethylus robusta* Li & Chen, sp. nov., male, **A, B, G** holotype (SCAU 3042645) **C–F** paratype (SCAU 3042641) **A** head, ventral view **B** mesosoma, ventral view **C** genitalia, dorsal view **D** genitalia, ventral view **E** subgenital plate **F** 7th sternite **G** metaleg, lateral view.

(Fig. 3G) without spine. Metafemur (Fig. 3G) with one acute spine in ventral midline, $0.26\times$ as long as metafemoral width, touching apical margin of metatrochanter, and with one small, broad and dentate protuberance ventrally, $0.04\times$ metafemoral width, located on second quarter of metafemur.

Metasoma. Weakly longer than mesosoma. Seventh sternite (Fig. 3F) with posterior margin incurved at about middle third. Hypopygium (Fig. 3E) with spiculum longer than median length of hypopygium, and $1.3\times$ longer than anteromedial apodeme, latter strongly curved mesad apically; posterior margin strongly incurved, lateral lobe

obtuse rounded. **Genitalia** (Fig. 3C, D). Harpe shorter than gonostipe; aedeagus slightly wide, 2.32× as long as wide, apex aedeagus posterior to posterior margin of gonostipe, 0.6× as long as gonostipe; basivolsella large, 0.6× as long as gonostipe, basal half about as wide as apical half, basal margin incurved.

Variation. Mesosoma more polished, especially pronotum and propodeum.

Etymology. The specific epithet derived from the Latin word for robust, and refers to the robust body of this species.

Material examined. *Holotype*, male, CHINA: Yunnan, Dali, Yunlong County, 2608 m, 25°50'57.94"N, 99°14'30.58"E, 27.xiii–12.ix.2020, MT, SCAU 3042645 (SCBG). *Paratypes*: 2 males. 1 male, same collecting data as holotype, SCAU 3042641 (SCBG); 1 male, CHINA: Yunnan, Dali, Yunlong County, 2537 m, 25°50'49.91"N, 99°14'22.95"E, 28.v–14.vi.2020, MT, SCAU 3042657 (SCBG).

Distribution. Oriental region, China, Yunnan Province.

Remarks. This new species is very similar to *F. syndesis* Chen & Azevedo [Yunnan and Hainan, China], but can be separated from the latter by the following characters: median carina of clypeus incomplete (complete in *F. syndesis*); notaulus complete and deep (incomplete and shallow in *F. syndesis*); declivity of propodeum without median carina (with median carina in *F. syndesis*); metafemur with only one acute spine in ventral midline (with two acute spines in *F. syndesis*); lateral lobe of hypopygium without conical protuberance (with conical protuberance in *F. syndesis*).

Foenobethylus syndesis Chen & Azevedo, 2020

Foenobethylus syndesis Chen & Azevedo, 2020: 1241–1246 (diagnosis, description, distribution, key).

Material examined. Other material. 1 male, CHINA: Hainan, Mt. Diaoluoshan, 18°40'2.4"N, 109°54'32.09"E, 31.x–30.xi.2020, MT, Long-long Chen, SCAU 3042642 (SCBG); 1 male, CHINA: Hainan, Mt. Jianfengling, 18°41'42.37"N, 108°51'36.11"E, 688.01m, 30.iv–10.v.2020, MT, Chun-yang Xu, SCAU 3042643 (SCBG).

Distribution. Oriental region, China, Yunnan and Hainan Provinces.

Foenobethylus xinglongensis Wang & Chen, sp. nov.

<http://zoobank.org/ABD5BAD9-35DB-4466-B782-94B367020F84>

Figures 4, 5

Diagnosis. Male. Head rectangular and elongate (Fig. 4B). Clypeus with median lobe obtuse rounded, median carina complete, reaching anterior clypeal margin, high, straight in lateral profile. Eye glabrous (Fig. 4B). Frons almost polished (Fig. 4B). Notaulus converging posteriorly, incomplete and shallow (Fig. 4C). Metapostnotal median carina incomplete, posterior third absent. Declivity of propodeum transversely

rugulose (Fig. 4D). Metatrochanter without spine (Fig. 5F). Metafemur with only one proximal acute spine in ventral midline, $0.19\times$ as long as metafemoral width, touching apical margin of metatrochanter (Fig. 5F). Posterior hypopygeal margin strongly incurved, lateral lobe with conical protuberance (Fig. 5B). Basivolsella large, $0.6\times$ as long as gonostipe, basal half about as wide as apical half, basal margin incurved (Fig. 5C, D).

Description. Male holotype. Body length 2.32 mm. Forewing length 1.67 mm.

Colors. Head, mesosoma (but pronotum and propleura castaneous), metasoma castaneous; base of scape, flagellomeres, apex of mandible, all coxae, all trochanter, all femora, basal half of all tibiae and claws pale castaneous; apex of scape, pedicel, base of mandible, palpi, protibia, apical half of all tibiae and tarsi yellow; wings subhyaline.

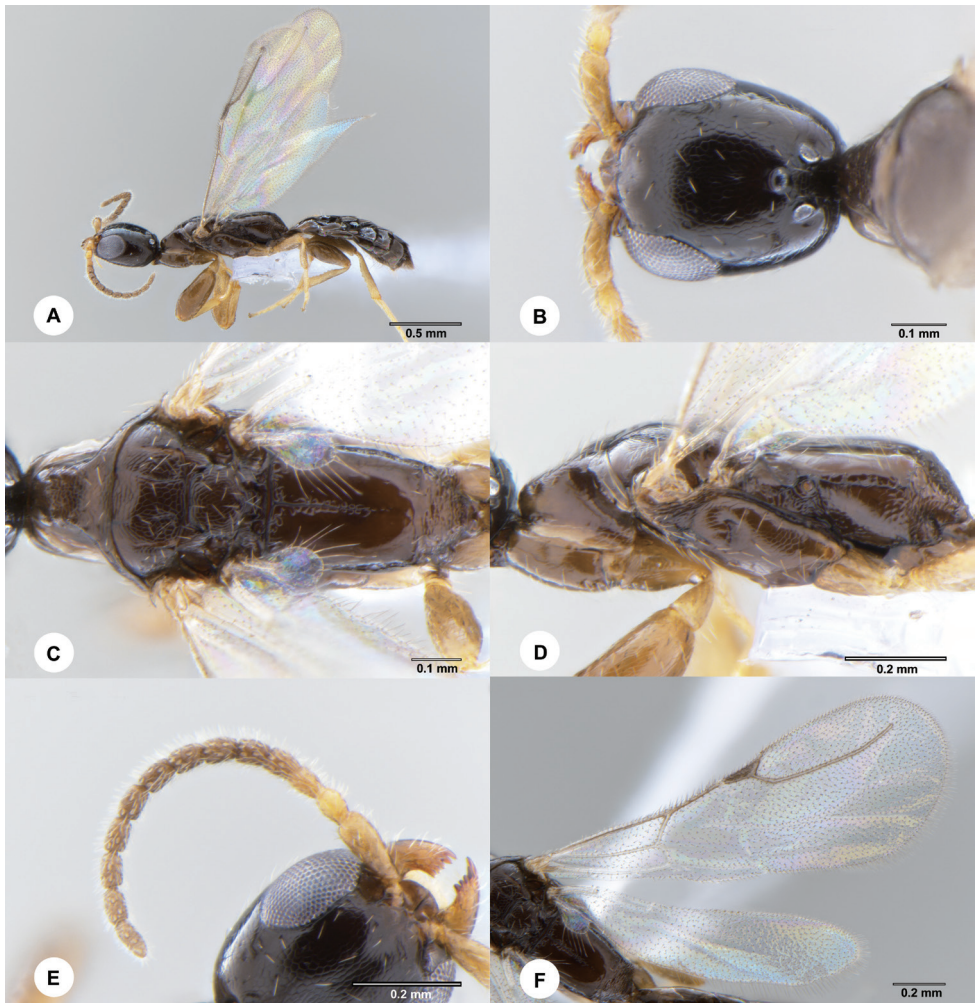


Figure 4. *Foenobethylus xinglongensis* Wang & Chen, sp. nov., male, holotype (SCAU 3042798) **A** lateral habitus **B** head, dorsal view **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** antenna **F** wings.

Head. Head (Figs 4B, 5A) rectangular and elongate, $1.2\times$ as long as wide. Mandible with five apical sharpened teeth, posterior tooth largest, middle three teeth smaller, anterior tooth smallest. Clypeus with median lobe obtuse rounded, median carina complete, reaching anterior clypeal margin, high, straight in lateral profile. Eye glabrous, almost touching mandible base at anterior corner. Malar space reduced. Frons very weakly coriaceous, almost polished, punctures very sparse and small. WH $0.86\times$ LH. WF $0.62\times$ WH. WF $1.35\times$ HE. OOL $1.19\times$ WOT. Frontal angle of ocellar triangle obtuse. Anterior ocellus far posterior to supra-ocular line. Temple divergent anterad, corner rounded. Vertex badly outcurved. First four antennomeres in ratio of about 35:15:14:13 (Fig. 4E). All flagellomeres distinctly longer than wide, pubescence erect, about $0.63\times$ as long as flagellomeral width. Maxillary palpus with five palpomeres (Fig. 5A). Labial palpus with two palpomeres (Fig. 5A). Occipital carina complete. Medioccipito-genal carina complete. Hypostomal carina thick, almost straight, angled medially.

Mesosoma (Figs 4C, D, 5A). Mostly polished and weakly coriaceous. Pronotal flange short, exposing propleuron dorsally. Dorsal pronotal area short, without anterior carina strongly progressively narrowing anterad, lateral surface concave. Notaulus converging posteriorly, incomplete, shallow, faint, but progressively more evident posteriorly. Parapsidal signum almost straight, absent anteriorly, but wide and deep posteriorly. Mesoscutellum slightly shorter than anteromesoscutum. Mesoscutum-mesoscutellar sulcus deep, arched, sides wider than middle. Metanotum conspicuous, metascutellum wide and short, metanotal trough trabeculate, metanotal fovea outlined. Metapectal-propodeal disc polished, metapostnotal median carina incomplete, absent posteriorly, lateral and transverse posterior carinae complete; propodeal spiracle circular, located on lateral surface of propodeum, ventral to lateral carina. Propodeal declivity transversely rugulose, without median carina. Mesopleuron with mesopleural pit large and well defined. Pleurosternum small, triangular, with vertex directed posterad. Prepectus with epicnemial medial projection complete, posterior prepectal flange thick. **Wings** (Fig. 4F). Forewing with three closed cells (Costal, Radial and First Cubital); pterostigma about $0.24\times$ as wide as long, anterior board outcurved; 2r-rs&Rs sector vein long; Rs&M reaching Sc+R far from pterostigma. Hind wing with one straight hamulus, and four distal hamuli equally distant, and strongly curved. **Legs.** Profemur swollen, $2.4\times$ as long as wide, apical half of ventral margin serrulate. Metatrochanter (Fig. 5F) without spine. Metafemur (Fig. 5F) with only one proximal acute spine in ventral midline, $0.19\times$ as long as metafemoral width, touching apical margin of metatrochanter.

Metasoma. Weakly longer than mesosoma. Seventh sternite (Fig. 5E) with posterior margin incurved at middle two fifths. Hypopygium (Fig. 5B) with spiculum about as long as median length of hypopygium, and $1.5\times$ longer than anteromedial apodeme, latter slightly curved mesad apically; posterior margin strongly incurved, lateral lobe with conical protuberance. **Genitalia** (Fig. 5C, D). Harpe shorter than gonostipe; aedeagus wide, $2.26\times$ as long as wide, apex aedeagus posterior to posterior margin of gonostipe, $0.6\times$ as long as gonostipe; basivolsella large, $0.6\times$ as long as gonostipe, basal half about as wide as apical half, basal margin incurved.

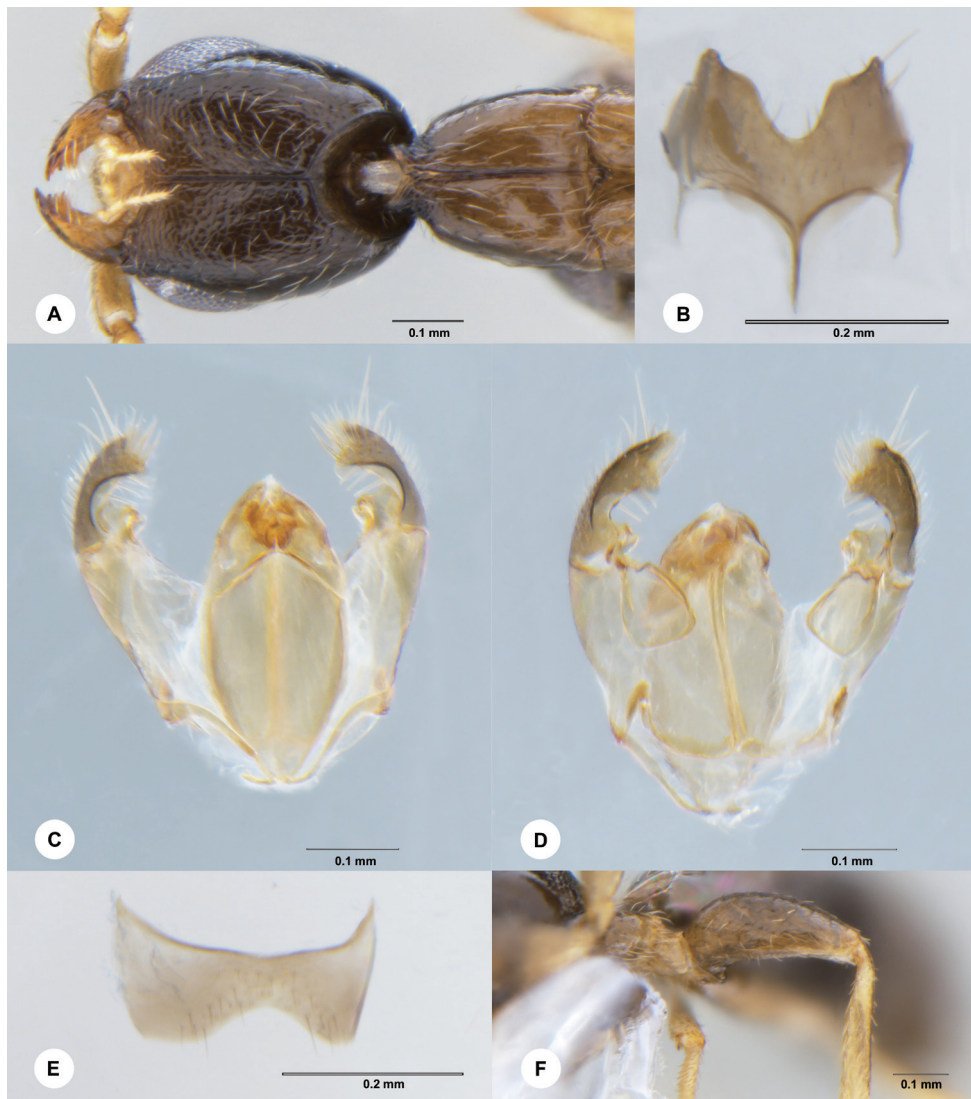


Figure 5. *Foenobethylus xinglongensis* Wang & Chen, sp. nov., male, **A, F** holotype (SCAU 3042798), **B–E** paratype (SCAU 3042638). **A** head and mesosoma, ventral view **B** subgenital plate **C** genitalia, dorsal view **D** genitalia, ventral view **E** 7th sternite **F** metaleg, lateral view.

Variation. Notauli are more well impressed; metapostnotal median carina slightly longer.

Etymology. The specific epithet refers to the locality (Xinglong Tropical Botanical Garden) where the type specimens were collected.

Material examined. *Holotype*, male, CHINA: Hainan, Wangning, Xinglong Tropical Botanical Garden, 18°44'24"N, 110°11'38"E, 30.i–30.ii.2021, MT, Zheng Wang, SCAU 3042798 (deposited in SCBG). *Paratypes*: 2 males. 1 male, CHINA:

Hainan, Wangning, Xinglong Tropical Botanical Garden, 18°43'52"N, 110°11'30"E, 18.vii–25.viii.2020, MT, Zheng Wang, SCAU 3042638 (SCBG); same data as holotype, but 9.vi–18.vii.2020, SCAU 3042656 (SCBG).

Distribution. Oriental region, China, Hainan Province.

Remarks. This new species is very similar to *F. sharkeyi* Savergnini & Azevedo [Thailand], but can be separated from the latter by the following characters: frons almost polished (coriaceous in *F. sharkeyi*); metapostnotal median carina incomplete, posterior third absent (complete in *F. sharkeyi*); declivity of propodeum transversely rugulose (areolate-rugose in *F. sharkeyi*); profemur 2.4× as long as wide (1.2–1.3× in *F. sharkeyi*).

***Foenobethylus yunkaishanensis* Chen & Luo, sp. nov.**

<http://zoobank.org/F57CCCF3-51B8-4137-82A4-55325A4C10B7>

Figures 6, 7

Diagnosis. Male. Head rectangular and elongate (Fig. 6B). Clypeus with median lobe truncate, median carina incomplete, not reaching anterior clypeal margin, but high and straight in lateral profile. Eye glabrous (Fig. 6B). Distance between posterior margin of compound eye and occipital carina longer than length of compound eye in dorsal view. Notaulus converging posteriorly, almost complete except the apex (Fig. 6C). Metatrochanter without spine (Fig. 7G). Metafemur with acute spine in ventral midline, proximal one 0.35× as long as metafemoral width, touching apical margin of metatrochanter, distal one 0.14× metafemoral width, located on basal two fifth of metafemur (Fig. 7G). Posterior hypopygeal margin strongly incurved, lateral lobe with conical protuberance (Fig. 7E). Basivolsella large, 0.6× as long as gonostipe, basal half distinctly wider than apical half, basal margin incurved (Fig. 7C, D).

Description. Male holotype. Body length 3.14 mm. Forewing length 2.08 mm.

Colors. Head, mesosoma, metasoma, base of scape, all flagellomeres, apical half of mesotibia and metatibia, all trochanter, and claws dark castaneous; apex of scape, pedicel, palpi, protibia, basal half of mesotibia and metatibia, and tarsi castaneous; wings subhyaline.

Head. Head (Figs 6B, 7A) rectangular and elongate, 1.2× as long as wide. Mandible with five apical sharpened teeth, posterior tooth largest, middle three teeth smaller, anterior tooth smallest. Clypeus with median lobe truncate, median carina incomplete, not reaching anterior clypeal margin, but high and straight in lateral profile. Eye glabrous, almost touching mandible base at anterior corner. Malar space reduced. Frons very weakly coriaceous, almost polished, punctures very sparse and small. WH 0.86× LH. WF 0.61× WH. WF 1.19× HE. OOL 1.20× WOT. Frontal angle of ocellar triangle obtuse. Anterior ocellus far posterior to supra-ocular line. Temple divergent anterad, corner rounded. Vertex badly outcurved. First four antennomeres in ratio of about 21:8:8:7 (Fig. 6E). All flagellomeres distinctly longer than wide, pubescence erect, about 0.67× as long as flagellomeral width. Maxillary palpus with five palpomeres (Fig. 7A). Labial palpus with two palpomeres (Fig. 7A). Occipital carina complete. Medioccipitogenal carina complete. Hypostomal carina thick, almost straight, not angled medially.

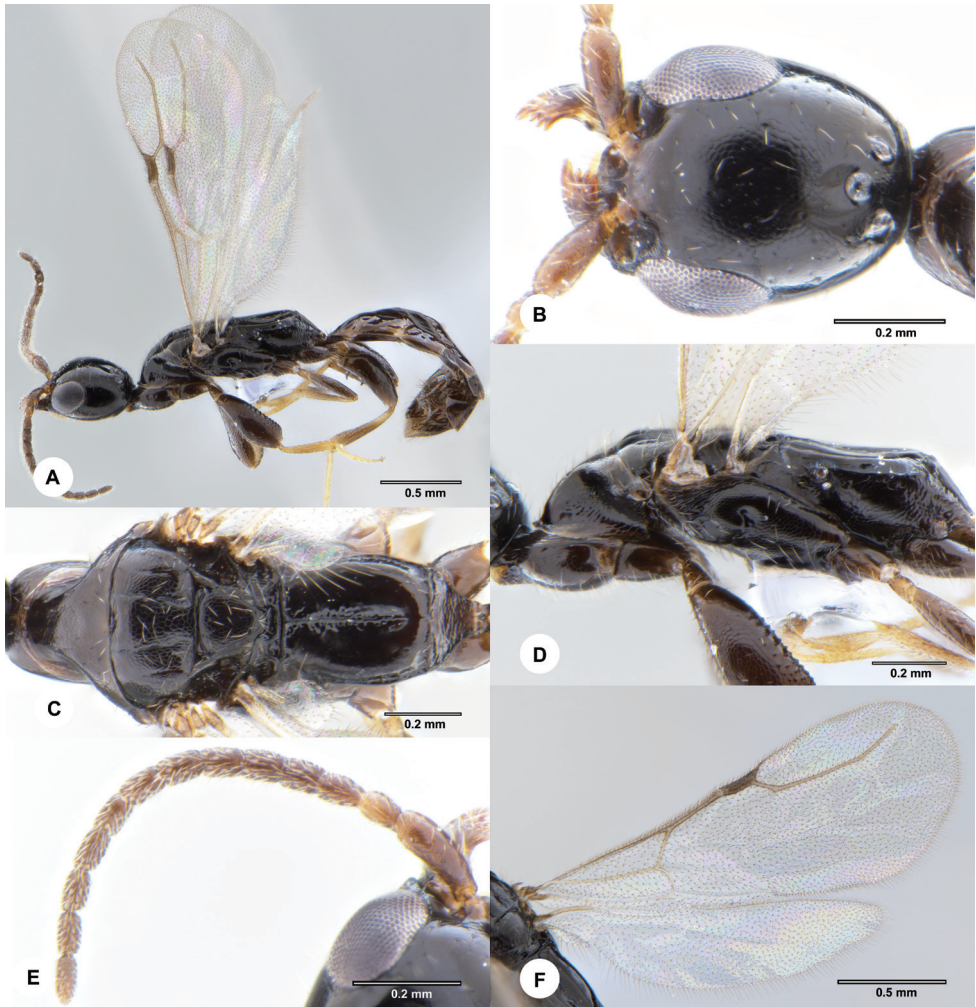


Figure 6. *Foenobethylus yunkaishanensis* Chen & Luo, sp. nov., male, holotype (SCAU 3048315) **A** lateral habitus **B** head, dorsal view **C** mesosoma, dorsal view **D** mesosoma, lateral view **E** antenna **F** wings.

Mesosoma (Figs 6C, D, 7B). Mostly polished and weakly coriaceous. Pronotal flange short, exposing propleuron dorsally. Dorsal pronotal area short, without anterior carina strongly progressively narrowing anterad, lateral surface concave. Notaulus converging posteriorly, almost complete except the apex, deep, distinct, and progressively more evident posteriorly. Parapsidal signum sinuous, absent anteriorly. Mesoscutellum shorter than anteromesoscutum. Mesoscutum-mesoscutellar sulcus deep, arched, sides wider than middle. Metanotum conspicuous, metascutellum wide and short, metanotal trough trabeculate, metanotal fovea outlined. Metapectal-propodeal disc polished, metapostnotal median carina incomplete, absent posteriorly, lateral and transverse posterior carinae complete; propodeal spiracle circular, located



Figure 7. *Foenobethylus yunkaishanensis* Chen & Luo, sp. nov., male **A, B, G** holotype (SCAU 3048315), **C–F** paratype (SCAU 3042639) **A** head, ventral view **B** mesosoma, ventral view **C** genitalia, dorsal view **D** genitalia, ventral view **E** subgenital plate **F** 7th sternite **G** metaleg, lateral view.

on lateral surface of propodeum, ventral to lateral carina. Propodeal declivity transverse sculptured, and without median carina. Mesopleuron with mesopleural pit large and well defined. Pleurosternum small, triangular, with vertex directed posterad. Prepectus with epicnemial medial projection complete, posterior prepectal flange thick. **Wings** (Fig. 6F). Forewing with three closed cells (Costal, Radial and First Cubital); pterostigma about 0.3× as wide as long, anterior board outcurved; 2r-rs&Rs sector vein long; Rs&M reaching Sc+R far from pterostigma. Hind wing with one straight hamulus, and four distal hamuli equally distant, and strongly curved. **Legs**. Profemur swollen, 2.6× as long as wide, apical half of ventral margin serrulate. Metatrochanter (Fig. 7G)

without spine. Metafemur (Fig. 7G) with acute spine in ventral midline, proximal one 0.35× as long as metafemoral width, touching apical margin of metatrochanter, distal one 0.14× metafemoral width, located on basal two fifth of metafemur.

Metasoma. Much longer than mesosoma. Seventh sternite (Fig. 7F) with posterior margin incurved at middle third. Hypopygium (Fig. 7E) with spiculum much longer than median length of hypopygium, and 1.2× longer than anteromedial apodeme, latter distinctly curved mesad apically; posterior margin strongly incurved, lateral lobe with conical protuberance. **Genitalia** (Fig. 7C, D). Harpe shorter than gonostipe; aedeagus wide, 1.93× as long as wide, apex aedeagus posterior to posterior margin of gonostipe, 0.65× as long as gonostipe; basivolsella large, 0.6× as long as gonostipe, basal half distinctly wider than apical half, basal margin incurved.

Variation. Body size maller and color lighter.

Etymology. The specific epithet refers to the locality (Mt. Yunkaishan) where the type specimens were collected.

Material examined. *Holotype*, male, CHINA: Guangdong Yunkaishan National Nature Reserve, 1480 m, 22°17'40.72"N, 111°12'37.97"E, 29.v–4.vii.2020, MT, Long-long Chen, SCAU 3048315 (deposited in SCBG). **Paratypes:** 2 males. 1 male, CHINA: Guangdong Yunkaishan National Nature Reserve, 22°16'22.67"N, 111°11'38.7"E, 30.vi–23.vii.2020, MT, Long-long Chen, SCAU 3042639 (SCBG); 1 male, CHINA: Guangdong Yunkaishan National Nature Reserve, 22°17'40"N, 111°12'37.97"E, 1480 m, 9.v–4.vii.2020, MT, Long-long Chen, SCAU 3042658 (SCBG).

Distribution. Oriental region, China, Guangdong Province.

Remarks. This new species is very similar to *F. bidentatus* Várkonyi & Polaszek [Brunei, Thailand], but can be separated from the latter by the following characters: distance between posterior margin of compound eye and occipital carina longer length of compound eye in dorsal view (as long as in *F. bidentatus*); seventh sternum with distal margin strongly emarginated (narrowly emarginated in *F. bidentatus*); posterior margin of hypopygium strongly incurved (broadly and almost evenly emarginate in *F. bidentatus*).

Key to males of *Foenobethylus*

- 1 Metatrochanter with one ventral spine or tooth 2
- Metatrochanter without ventral spine or tooth..... 5
- 2 Metafemur with one long proximal spine, 0.5× as long as metafemur width 3
- Metafemur with one short proximal spine, 0.6× as long as metafemur width... 4
- 3 Pronotum with anterior horizontal flange medially very narrow; metatrochanter with one needle-like long spine ventrally; metafemur with a ventral oblique furrow *F. emiliacasellae* Várkonyi & Polaszek
- Pronotum with anterior horizontal flange medially as broad as laterally; metatrochanter with one tooth or broad spine; metafemur ventrally flattened, without oblique furrow *F. elongatus* Várkonyi & Polaszek

- 4 Hypopygium with posterior margin strongly concave, base of paramere with triangular protuberance on dorsal margin *F. pyramidis* Savergnini & Azevedo
- Hypopygium with posterior margin weakly concave, base of paramere without triangular protuberance on dorsal margin *F. thomascokeri* Várkonyi & Polaszek
- 5 Metafemur with one spine 6
- Metafemur with two spines 8
- 6 Middle of metafemur with one small, broad and dentate protuberance ventrally *F. gracilis* Kieffer
- Middle of metafemur without protuberance ventrally 7
- 7 Frons almost polished; metapostnotal median carina incomplete, posterior third absent; declivity of propodeum transversely rugulose *F. xinglongensis* Wang & Chen, sp. nov.
- Frons coriaceous; metapostnotal median carina complete; declivity of propodeum areolate-rugose *F. sharkeyi* Savergnini & Azevedo
- 8 Proximal spine locates at basal 1/3 of metafemora and close to distal spine, and tips of two spines slightly convergent 9
- Proximal spine locates on very base of metafemora and distantly separated from distal spine, and tips of two spines almost parallel 10
- 9 Aedeagus wide, 2.0× as long as wide *F. hainanensis* Liu, Chen & Xu
- Aedeagus narrower, 1.2× as long as wide *F. thaianus* (Terayama)
- 10 Distal spine locates before midpoint of metafemora and close to proximal spine 11
- Distal spine locates at or after midpoint of metafemora and distantly separated from proximal spine 12
- 11 Distance between posterior margin of compound eye and occipital carina as long as length of compound eye in dorsal view; seventh sternum with distal margin narrowly emarginated; posterior margin of hypopygium broadly and almost evenly emarginate *F. bidentatus* Várkonyi & Polaszek
- Distance between posterior margin of compound eye and occipital carina longer than length of compound eye in dorsal view; seventh sternum with distal margin strongly emarginated; posterior margin of hypopygium strongly incurved *F. yunkaishanensis* Chen & Luo, sp. nov.
- 12 Distal spine obtuse 13
- Distal spine acute *F. syndesis* Chen & Azevedo
- 13 Lateral lobe of hypopygium without conical protuberance; propodeum polished; pterostigma broad, about 0.4× as wide as long *F. robusta* Li & Chen, sp. nov.
- Lateral lobe of hypopygium with conical protuberance; propodeum coriaceous, areas along metapostnotal median carina rugose; pterostigma relatively slender, about 0.3× as wide as long *F. zhejiangensis* Liu, Chen & Xu

Discussion

Based on a preliminary phylogenetic analysis using morphological data, Várkonyi and Polaszek (2007) first assigned *Foenobethylus* to the subfamily Pristocerinae. However, the phylogenetic position of *Foenobethylus* within Pristocerinae was still unclear in their study. According to Azevedo and Lanes (2007), *Afgoiogfa*, *Foenobethylus* and *Parascleroderma* are closely related genera. However, currently no molecular sequences of *Afgoiogfa* are available for phylogenetic analysis. From the results of Alencar et al. (2018), the clade of *Foenobethylus* + *Parascleroderma* + *Cleistopyris* was recovered as the sister-group of *Apenesia*. In the light of the first discovery of *Foenobethylus* female, Chen and Azevedo (2020) suggested that *Foenobethylus* might be a synonym under *Parascleroderma* due the extreme similarity they share in females. *Foenobethylus* also shares some similar characters with *Apenesia* and *Dissomphalus* (Chen and Azevedo 2020), although *Dissomphalus* was never found close to *Foenobethylus* in any phylogenetic analyses (Alencar et al. 2018). The molecular data seem to support the relatedness between *Foenobethylus* and *Parascleroderma*, as suggested by their similar morphology. In the present study, all of the five studied *Foenobethylus* species form a monophyletic clade, with *Parascleroderma* as a sister group (Fig. 1). This result is congruent with that of Alencar et al. (2018), in which *Parascleroderma* is sister to *Foenobethylus*. The intergeneric distances between *Foenobethylus* and *Parascleroderma* ranged between 14.8–18.6%, generally higher than interspecific distances within *Foenobethylus*. This high genetic distance suggests that *Foenobethylus* is likely a distinct genus, as similar intergeneric distances have been found in Epyrinae of Bethylinidae (Colombo et al. 2020). However, given that the two *Parascleroderma* species together with all the *Foenobethylus* also form a monophyletic group in this study, the possibility that these two genera are synonymous cannot be ruled out. The precise taxonomic delimitation of both genera could be resolved by accumulating molecular data of more *Parascleroderma* taxa for phylogenetic analyses.

The relatively high interspecific genetic distances (10.3%–13.6%) indicate that the use of DNA barcoding for delimitating morphologically similar species of *Foenobethylus* may be promising. For example, *F. robusta* is very similar to *F. syndesis*, but the genetic distance between them is up to 11.3% and they are well supported as different species. Future comprehensive taxon sampling and molecular analyses should be able to test the power of DNA barcoding in delimitating morphologically similar species.

With the three newly described species, the total number of *Foenobethylus* is raised from 11 to 14 (Table 3). Species of *Foenobethylus* mainly occur in tropical forests (Savergnini and Azevedo 2013). All of the three new species described in this study were also collected in tropical or subtropical forests, indicating that species diversity of *Foenobethylus* from tropical and subtropical forests of Southeast Asia is still undersampled and intensive study is required. The wingless feature of the females allows these parasitoids to adapt to the restricted environments such as tunnels under the tree bark, where the females look for preys (Chen and Azevedo 2020). However, the host of *Foenobethylus* species is still unknown. As other members of Pristocerinae,

Table 3. List of the world species of *Foenobethylus* (updated from Chen and Azevedo 2020).

Species	Distribution	
	Country	Region
<i>F. bidentatus</i> Várkonyi & Polaszek, 2007	Brunei, Thailand	Oriental
<i>F. elongatus</i> Várkonyi & Polaszek, 2007	Malaysia, Indonesia	Oriental
<i>F. emiliacasellae</i> Várkonyi & Polaszek, 2007	Thailand	Oriental
<i>F. gracilis</i> Kieffer, 1913	Philippines, Thailand	Oriental
<i>F. hainanensis</i> Liu, Chen & Xu, 2011	China	Oriental
<i>F. pyramidis</i> Savernini & Azevedo, 2013	Thailand	Oriental
<i>F. robusta</i> Li & Chen, sp. nov.	China	Oriental
<i>F. sharkeyi</i> Savernini & Azevedo, 2013	Thailand	Oriental
<i>F. syndesis</i> Chen & Azevedo, 2020	China	Oriental
<i>F. thaianus</i> (Terayama, 1998)	Thailand	Oriental
<i>F. thomascokeri</i> Várkonyi & Polaszek, 2007	Malaysia, Thailand	Oriental
<i>F. xinglongensis</i> Wang & Chen, sp. nov.	China	Oriental
<i>F. yunkaishanensis</i> Chen & Luo, sp. nov.	China	Oriental
<i>F. zhejiangensis</i> Liu, Chen & Xu, 2011	China	Oriental

species of *Foenobethylus* are likely ectoparasitoids of beetle larvae in concealed habitat (Terayama 2006). Searching for wood boring beetle larvae in tropical and subtropical forests should be a promising direction in finding the hosts of these parasitoids.

Acknowledgements

Thanks to Dr. Yan-Qiong Peng (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences) for providing some of the fresh specimens. We thank the subject editor Dr. Michael Ohl and the two reviewers, Dr. Colombo and Dr. Azevedo for their valuable suggestions. This material is based upon work supported in part by the Program of Ministry of Science and Technology of China (2018FY100406), the Foundation of Chengdu Normal University Talent Introduction Research Funding (YJRC202009, No. 111/111158701), and the Agricultural Ecology and Green Food Development Project (CSCXTD2020B11).

References

- Alencar IDCC, Waichert C, Azevedo CO (2018) Opening Pandora's box of Pristocerinae: molecular and morphological phylogenies of *Apenesia* (Hymenoptera, Bethyridae) reveal several hidden genera. *Systematic Entomology* 43: 481–509. <https://doi.org/10.1111/syen.12295>
- Azevedo CO, Lanes GO (2007) Rediscovery of Oriental *Foenobethylus* Kieffer, 1913 with discussion of allied genus (Hymenoptera, Bethyridae). *Mittelugen des Internationalen Entomologischen Vereins* 32: 133–141.
- Brito CD, Lanes GO, Azevedo CO (2021) Anatomic glossary of mesopleural structures in Bethyridae (Hymenoptera: Chrysidoidea). *Papéis Avulsos de Zoologia* v.61: e20216152. <http://doi.org/10.11606/1807-0205/2021.61.52>

- Chen HY, Azevedo CO (2020) Discovery of a couple of *Foenobethylus* (Hymenoptera, Bethylidae) in copulation suggests a synonym under *Parascleroderma*. *Journal of Asia-Pacific Entomology* 23: 1241–1247. <https://doi.org/10.1016/j.aspen.2020.10.001>
- Colombo WD, Waichert C, Azevedo CO (2020) Molecular and morphological species delimitation of Epyrinae (Hymenoptera: Bethylidae) from Papua New Guinea. In: Robillard T, Legendre F, Villemant C, Leponce M (Eds) *Insects of Mount Wilhelm, Papua New Guinea – volume 2*. Muséum national d'Histoire naturelle, Paris, 209–319.
- Folmer O, Black M, Hoch W, Lutz R, Vrijenoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Gillespie JJ, Munro JB, Heraty JM, Yoder MJ, Owen AK, Carmichael AE (2005) A Secondary Structural Model of the 28S rRNA Expansion Segments D2 and D3 for Chalcidoid Wasps (Hymenoptera: Chalcidoidea). *Molecular Biology and Evolution* 22: 1593–1608. <https://doi.org/10.1093/molbev/msi152>
- Harris RA (1979) A glossary of surface sculpturing. *Occasional Papers in Entomology* 28: 1–31. <https://doi.org/10.1371/journal.pone.0140051>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lanes GO, Kawada R, Azevedo CO, Brothers D (2020) Revisited morphology applied for Systematic of flat wasps (Hymenoptera, Bethylidae). *Zootaxa* 4752(1): 1–127. <https://doi.org/10.11646/zootaxa.4752.1.1>
- Liu J, Chen H, Xu Z (2011) Two new species of genus *Foenobethylus* Kieffer, 1913 (Hymenoptera, Bethylidae) from China with a key to the known species. *Zootaxa* 2806: 53–59. <https://doi.org/10.11646/zootaxa.2806.1.4>
- Savergnini JR, Azevedo CO (2013) Taxonomy of *Foenobethylus* Kieffer (Hymenoptera, Bethylidae) with description of two new species. *Journal of Asia-Pacific Entomology* 16: 433–441. <https://doi.org/10.1016/j.aspen.2013.06.004>
- Taekul C, Valerio AA, Austin AD, Klompen H, Johnson NF (2014) Molecular phylogeny of telenomine egg parasitoids (Hymenoptera: Platygasteridae s.l.: Telenominae): evolution of host shifts and implications for classification. *Systematic Entomology* 39: 24–35. <https://doi.org/10.1111/syen.12032>
- Terayama M (2006) *The Insects of Japan. Vol. I, Bethylidae* (Hymenoptera). Fukuoka, (Japan): Entomological Society of Japan, 319 pp.
- Várkonyi G, Polaszek A (2007) Rediscovery and revision of *Foenobethylus* Kieffer, 1913 (Hymenoptera, Bethylidae). *Zootaxa* 1546: 1–14. <https://doi.org/10.11646/zootaxa.1546.1.1>