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Most northern Oriental distribution of *Zethus* Fabricius (Hymenoptera, Vespidae, Eumeninae), with a new species from China

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Abstract

The distribution of *Zethus* Fabicius, 1804, in the Oriental and Palaearctic regions is discussed, with special reference to the northeastern Oriental species. A newly discovered species, *Z. velamellatus* Tan, **sp. n.** from China (Zhejiang), is described and illustrated. The first key to species of *Zethus* Fabricius from China is presented. *Zethus nigerrimus* Gusenleitner, 2001 is recorded for the first time from China and redescribed.

Keywords

Zethus, China, key, new record, new species

Introduction

Zethus Fabricius, 1804, is the largest eumenine genus with 272 valid species of which the majority (230 spp.) occurs in the New World (Carpenter 2011, Lopes et al. 2015, 2017, Cooper 2016, Nguyen and Carpenter 2016, Nguyen and Xu 2017, Selis 2017, Yeh and Lu 2017). The genus is characterized by having propodeum with orifice elongate, acutely pointed dorsally, propodeal valvula elongate and quadrate, separate from propodeal lamella; labial palp four-segmented; mid-tibia usually with two spurs (Bohart and Stange 1965, Nguyen and Carpenter 2016, Tan et al. 2018, submitted).

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Although they are widespread in the tropics, with 25 species occurring in the Oriental Region (Nguyen and Carpenter 2016, Nguyen and Xu 2017, Yeh and Lu 2017), only few species and specimens are known from China. Lee (1985) was the first to record a *Zethus* sp. from China: *Z. dolosus* Bingham, 1897. Unfortunately, the record by Lee (1985) was overlooked by Zhou et al. (2011) and Nguyen and Xu (2017). Up to the present, there are only four species recorded from China (Lee 1985, Nguyen and Xu 2017, Yeh and Lu 2017, Tan et al. 2018, submitted). In this paper, two additional species, *Z. velamellatus* Tan, sp. n. and *Z. nigerrimus* Gusenleitner, 2001, rec. n., are added to the Chinese fauna. A key to species of the genus *Zethus* from China is included.

Material and methods

Specimens were collected by hand net. The studied specimens are deposited in the Hymenoptera Collection of the College of Life Sciences, Northwest University, Xi'an (**NWUX**). Morphological terminology follows Yeh and Lu (2017) and Nguyen and Xu (2017). Nomenclature of mesopleural sulci and sutures is shown in Figure 1. Length of body is measured from anterior margin of the head to the apex of the second metasomal tergum; length of first metasomal tergum is measured from the posterior margin of the tendon to the apex of the tergum medially, its height is the maximum height in lateral view. Observations and descriptions were made with an Olympus SZX11 stereomicroscope and fluorescent lamps. Photographic images were made with a Keyence VHX-5000 digital microscope and Photoshop CS 6 was used to make the plates.

Abbreviations: approx., approximately; id., idem; F, antennal flagellomere; S, metasomal sternum; T, metasomal tergum; ecc, epicnemial carina; eps, epipleural sulcus; ess, episternal sulcus; mps, mesopleural suture.

Table 1. List of *Zethus* spp. recorded from Oriental and Palaearctic fauna.

Oriental species	Distribution
Zethus albopilosus Giordani Soika, 1995	India
Zethus angulatus Nguyen & Carpenter, 2016	Vietnam
Zethus bakeri Giordani Soika, 1995	Singapore
Zethus celebensis Giordani Soika, 1960	Indonesia
Zethus ceylonicus de Saussure, 1867	India, Sri Lanka
Zethus dolosus Bingham, 1897	China (Guangdong), Bhutan, India, Myanmar, Thailand, Vietnam
Zethus fulgens Gusenleitner, 2007	Malaysia
Zethus improcerus Giordani Soika, 1995	Malaysia
Zethus indicus Giordani Soika, 1960	India (Sikkim)
Zethus luzonensis Giordani Soika, 1941	Philippines
Zethus malabaricus Giordani Soika, 1995	India
Zethus malayanus Gusenleitner, 2010	China (Guangdong), Malaysia, Vietnam

Oriental species	Distribution
Zethus mandibularis Giordani Soika, 1995	Indonesia
Zethus nanlingensis Nguyen & Xu, 2017	China (Guangdong)
Zethus nigerrimus Gusenleitner, 2001	China (Jiangxi), Vietnam, Laos, Malaysia
Zethus planiclypeus Gusenleitner, 1988	Thailand
Zethus propodeus Nguyen & Carpenter, 2016	Vietnam
Zethus puehringeri Gusenleitner & Gusenleitner, 2013	Laos
Zethus quadridentata Cameron, 1902	Borneo
Zethus soikai Selis, 2017	Philippines
Zethus tansoneus Nguyen & Carpenter, 2016	Vietnam
Zethus trimaculatus Cameron, 1904	India, Laos, Vietnam
Zethus tumidus Nguyen & Carpenter, 2016	Vietnam
Zethus varipunctatus Cameron, 1902	Malaysia
Zehtus velamellatus Tan, sp. n.	China (Zhejiang)
Palaearctic species	**Distribution**
Zethus asiaticus Gusenleitner, 2011	Kyrgyzstan
Zethus favillaceus Walker, 1871	Saudi Arabia, Djibouti, Sudan, Kenya, Tanzania, Burundi, Zimbabwe, South Africa

Key to species of the genus *Zethus* from China

1 First metasomal segment short and stout: 2.0–2.2× as long as its maximum width in dorsal view and approx. 2.5× as long as high in lateral view **2**

– First metasomal segment long and slender: 2.5–3.5× as long as its maximum width in dorsal view and 3.3–6.0× as long as high in lateral view **4**

2 Propodeal lamella almost invisible as the submarginal carina is not produced above propodeal valvulae; mesopleuron reticulate-rugose; first metasomal tergum punctate; clypeus of ♀ punctate-reticulate and depressed space between apical teeth without median ridge; second tergum with apical yellow band. China (Zhejiang) ..... ***Z. velamellatus* Tan, sp. n.**

– Propodeal lamella well-developed as the submarginal carina is produced into a distinct lamella above propodeal valvulae; mesopleuron sparsely punctate; first metasomal tergum reticulate-rugose; clypeus of ♀ punctate and depressed space between apical teeth with a median ridge; second tergum completely black..... **3**

3 Leg yellowish brown; clypeus of ♀ tri-dentate, clypeus of ♂ with apical notch 1/5 as wide as clypeus; mandible of ♂ with basal tooth forming a rectangular plate and separated from middle tooth by a broad notch. China (Taiwan) ....***Z. taiwanus* Yeh & Lu, 2017**

– Leg black; clypeus of ♀ minutely bi-dentate, clypeus of ♂ with apical notch 1/6 as wide as clypeus; mandible of ♂ with two small basal teeth, similarly shaped and not separated by a broad notch. China (new record; Jiangxi); Laos; Malaysia; Vietnam .....***Z. nigerrimus* Gusenleitner, 2001**

4 First metasomal tergum long and slender, approx. 3.5× as long as wide, densely and coarsely punctate, and with median carina; propodeum shiny and with lateral carinae. China (Guangdong); Bhutan; India; Myanmar; Thailand; Vietnam ..... ***Z. dolosus*** **Bingham, 1897**

– First metasomal tergum relatively short and wider, approx. 2.5× as long as wide, finely punctate, and without median carina; propodeum dull and without lateral carinae..... **5**

5 First metasomal tergum in dorsal view nearly parallel-sided; second metasomal segment relatively long, 1.2× as long as wide; China (Guangdong); Malaysia; Vietnam .....***Z. malayanus*** **Gusenleitner, 2010**

– First metasomal tergum in dorsal view gradually widening from base to basal one-sixth of tergum, then gradually narrowed apically; second metasomal segment relatively short, 1.4× as long as wide; China (Guangdong) .... ***Z. nanlingensis*** **Nguyen & Xu, 2017**

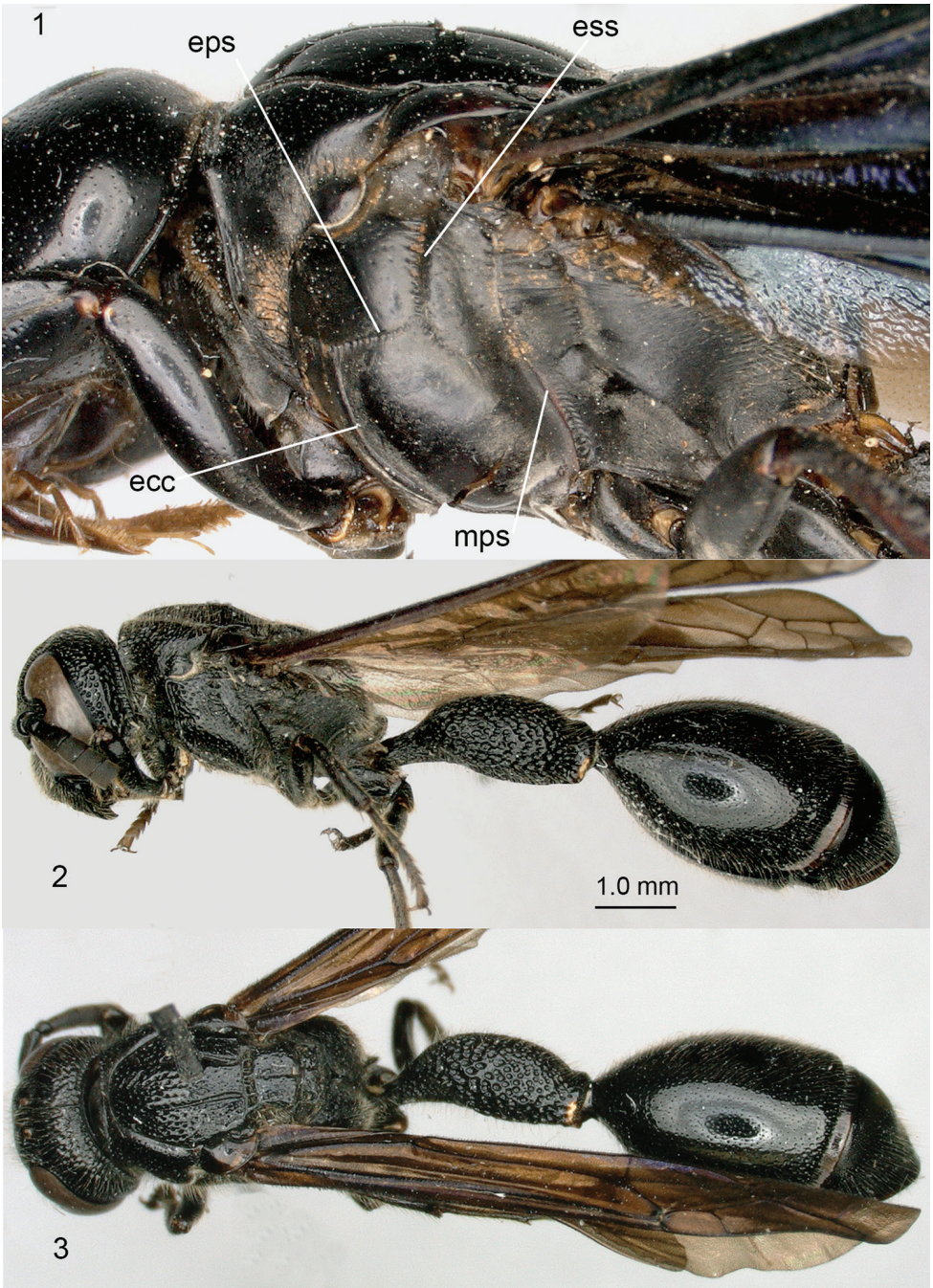
Taxonomy

Zethus nigerrimus **Gusenleitner, 2001, rec. n.**
Figs 2–13

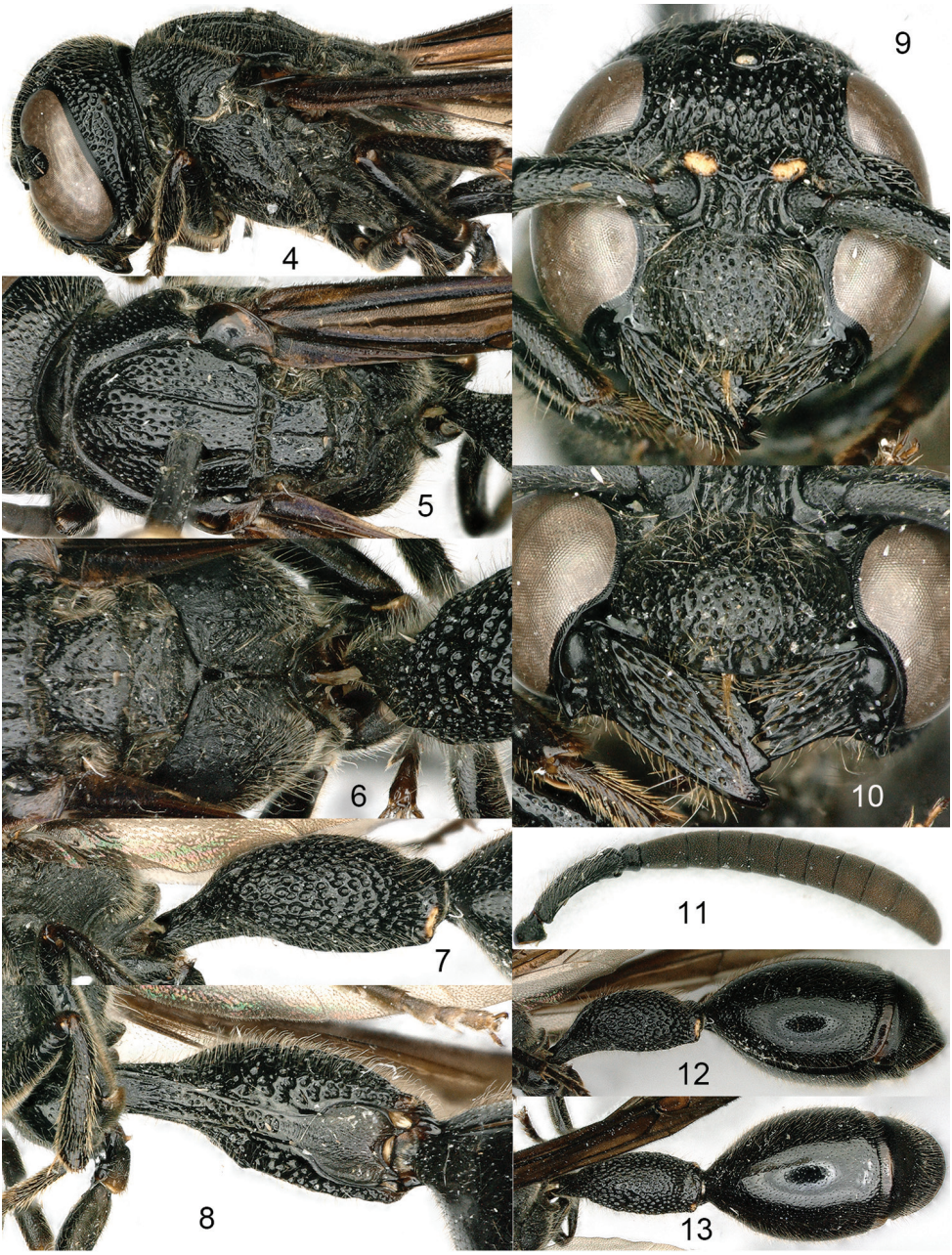
Zethus nigerrimus Gusenleitner, 2001: 659 (♀, N. Vietnam, Naturhistorisches Museum Wien); 2017: 101; 2012: 1050; Gusenleitner and Gusenleitner 2013: 138; Yeh and Lu 2017: 536.

Material examined. 1♀ (NWUX): "CHINA: Jiangxi, Fuzhou, Zixi, 7.vi.2010, N27.70°, E117.05°, Meijuan Lou".

Diagnosis. Body about 13.1 mm, almost entirely black, except a pair of yellow spots near dorso-inner margin of antennal sockets, and a pair of transverse yellow lateral spots on apical margin of TI (Figs 2, 3, 9). Clypeus of ♀ densely and shallowly foveate, minutely bi-dentate apically, depressed space between teeth with a median ridge (Fig. 10). Anterior half of mesoscutum strongly punctate-rugose, posterior half of mesoscutum, mesoscutellum and metanotum sparsely punctate with distance between punctures much longer than diameter of puncture. Epicnemial carina (Fig. 1, ecc) strong and raised, bordered posteriorly by narrow sulcus; episternal sulcus (Fig. 1, ess) wide, distinctly crenulate and depressed (Fig. 3), epipleural sulcus (Fig. 1 eps) indistinct; mesopleura (episternum) sparsely punctate below episternal and epipleural sulci, epicnemium and posterior part of episternum coriaceous (Fig. 3). Propodeum coriaceous with strong striae laterally; posterior depression very shallow, almost flat and finely transversely striate, submedian carina indiscernible; propodeal lamella well developed and protruding upward (Figs 6, 7). TI short, approx. 2.2× as long as wide in dorsal view and reticulate-rugose (Fig. 6); anterior half of SI reticulate-rugose and foveolate, posterior half densely transversely striate (Fig. 8). TII approx. 1.4× as long as wide in dorsal view, sparsely micro-punctate (Figs 12, 13); TII, TIII and SII with



Figures 1–3. 1 *Zethus coeruleopennis* (Fabricius), mesosoma, lateral aspect **2–3** *Z. nigerrimus* Gusenleitner, ♀ **2** Habitus, lateral aspect **3** id., dorsal aspect. Abbreviations: ecc = epicnemial carina; eps = epipleural sulcus; ess = episternal sulcus; mps = mesopleural suture.



Figures 4–13. *Zethus nigerrimus* Gusenleitner, ♀. **4** Head and mesosoma, lateral aspect **5** mesosoma dorsal aspect **6** propodeum, dorsal aspect **7** propodeum and TI, lateral aspect **8** SI, ventral aspect **9** head, anterior aspect **10** clypeus, anterior aspect **11** antenna **12** metasoma, lateral aspect **13** metasoma, dorsal aspect.

well-developed apical lamella, flat (about 0.25 mm, 0.4 mm and 0.17 mm long respectively); SII in lateral view smoothly curved from base to apical margin (Fig. 12).

Distribution. China (Jiangxi); Vietnam, Laos; Malaysia. It is a new record for China.

Zethus velamellatus **Tan, sp. n.**
http://zoobank.org/DBA926D0-5F9C-44CC-B9C1-C39C4E8BA572
Figs 14–24

Material examined. Holotype, ♀ (NWUX): "CHINA: Zhejiang, Hangzhou, Lin'an, Qingliangfeng, Shunxi, N30.06° E118.94°, 23.viii.2013, Jiangli Tan".

Diagnosis. Clypeus of ♀ punctate-reticulate and depressed space between apical teeth without median ridge; mesopleuron reticulate-rugose; propodeal lamella almost invisible as the submarginal carina is not produced above propodeal valvulae; T1 unevenly punctate and approx. twice as long as its maximum width in dorsal view and approx. 2.4× as long as high in lateral view; SI densely striate and sparsely punctate; TI with apical yellow band.

Description. Length of body 13.0 mm; fore wing length 11 mm; width of mesonotum (including tegulae) 3.1 mm.

Head. Head transversely oblong, approx. 1.3× wider than high in anterior view (Fig. 20), about 2.2× wider than long in dorsal view, coarsely punctate-reticulate and with long setae. Temple contracted behind eyes, approx. 1.2× wider than eye in dorsal view. Occipital carina developed, with crenulae in front of it. Clypeus gently convex, slightly less than twice as wide as long, emarginated at basal margin; apex minutely bidentate, depressed space between both teeth without median ridge (Fig. 21); clypeus punctate-reticulate with dense yellowish brown long setae (more than three times ocellar diameter); width of apical depression about a quarter width of clypeus. Mandible with four teeth, coarsely punctate-rugose, third and fourth teeth truncated. Antennal scape punctate, 2.7× as long as its maximum width; FI 1.9× as long as its maximum width, FII as long as wide, FIII–IX wider than long, FX bullet-shaped, as long as its basal width (Fig. 22).

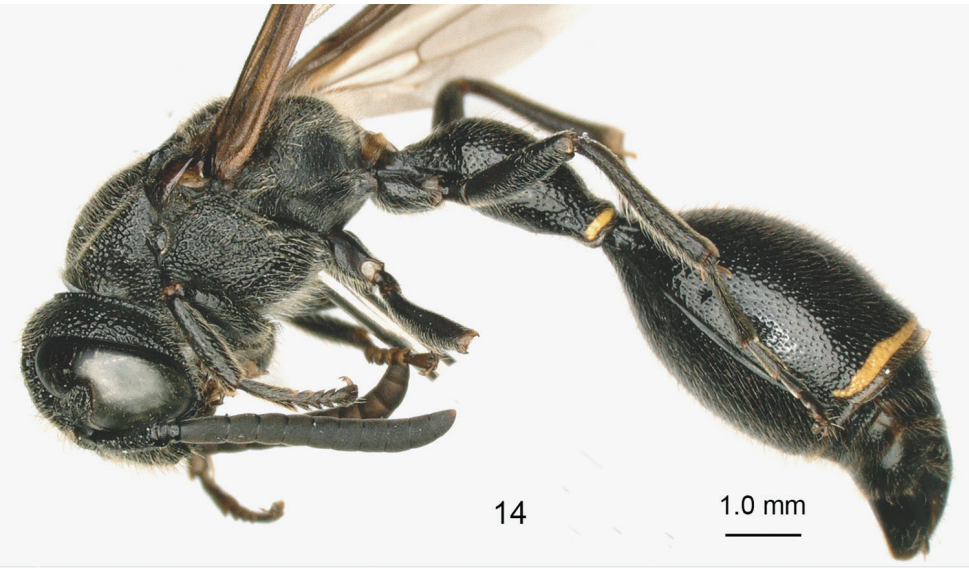
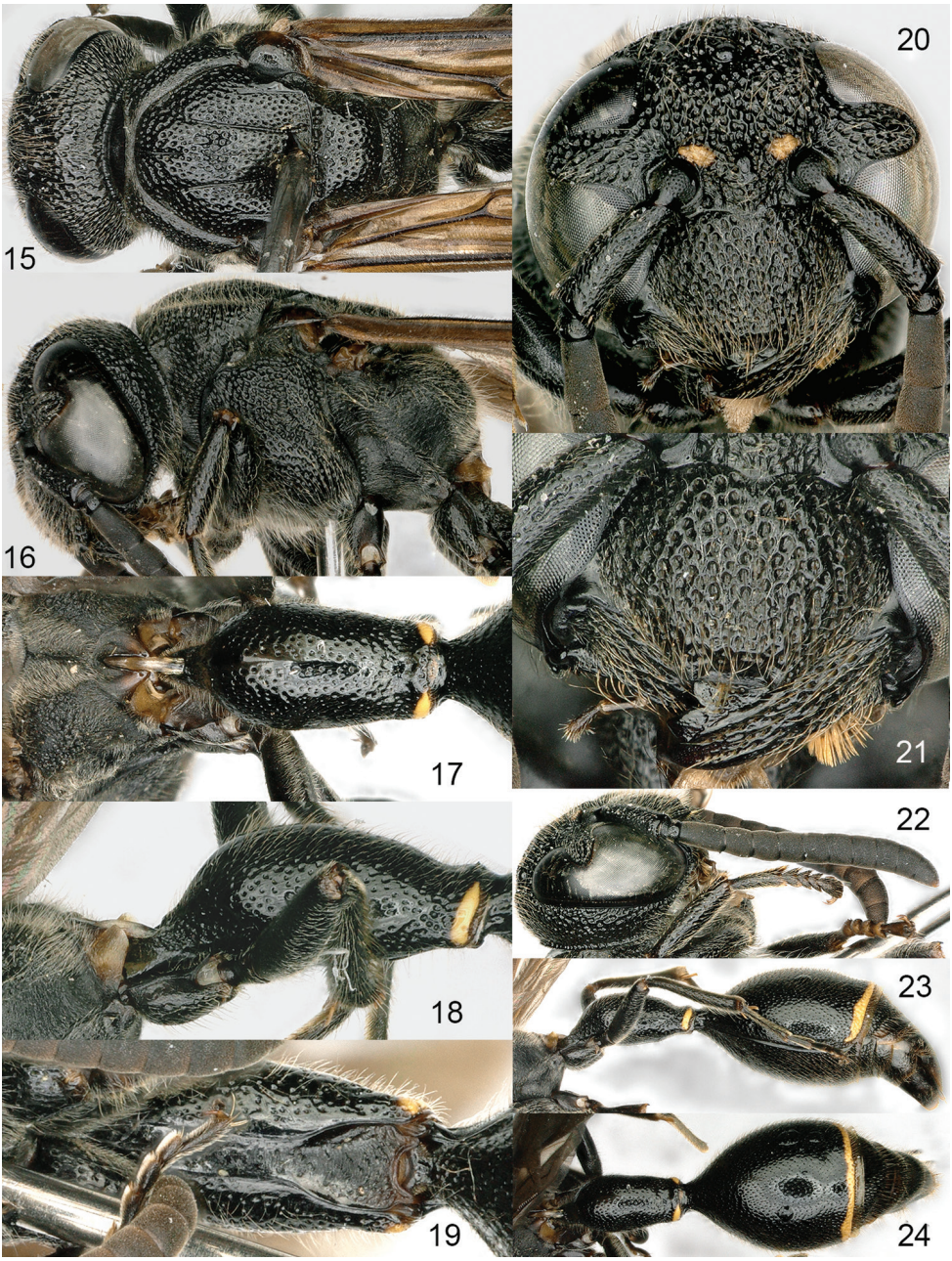


Figure 14. *Zethus velamellatus* Tan, sp. n., holotype, ♀, habitus, lateral aspect.



Figures 15–24. *Zethus velamellatus* Tan, sp. n., holotype, ♀. **15** Head and mesosoma, dorsal aspect **16** head and mesosoma, lateral aspect **17** propodeum and TI, dorsal aspect **18** propodeum and TI, lateral aspect **19** SI, ventral aspect **20** head, anterior aspect **21** clypeus, anterior aspect **22** antenna **23** metasoma, lateral aspect **24** metasoma, dorsal aspect.

Mesosoma. Pronotum reticulate-punctate dorsally with ventro-lateral area punctate-rugose (Fig. 15–16). Mesoscutum coarsely rugose-punctate to densely punctate (Fig. 15); mesoscutellum and metanotum coarsely punctate with distance between punctures less than diameter of puncture. Epicnemial carina distinct, bordered posteriorly by a narrow sulcus; episternal sulcus indistinctly developed as a crenulate depression, epipleural suture indistinct; mesopleuron (episternum) coarsely punctate-rugose (Fig. 16), below pleural and epipleural sulci densely punctate-rugose with epicnemium and posterior part of episternum coriaceous (Fig.16). Propodeum coriaceous-aciculate laterally and without lateral carina (Fig. 17), coriaceous-reticulate postero-laterally and oblique punctate-rugose along each side of median carina and with dense setae (Fig. 17); submarginal carina not produced into a lamella resulting in absence of propodeal lamella above propodeal valvula (Fig. 17).

Metasoma. TI short, about twice as long as wide in dorsal view, gradually widened from base to basal one third, then slightly narrowed toward apex, with maximum width 3.1× its basal width (Fig. 17); in lateral view smoothly curved between basal stem and apical part; strongly convex dorsally, about 2.4× as long as high (Fig. 18); TI unevenly punctate; SI densely striate and sparsely punctate (Fig. 19). TII sparsely punctate with rather short petiole basally, about 1.4× as long as wide in dorsal view (Figs 23, 24); SII in lateral view smoothly curved from base to apical margin (Fig. 23); TII and SII with raised apical lamella of approx. 0.2 mm and 0.1 mm long, respectively, apical lamella of TIII flat and approx. 0.25 mm long.

Colour (Figs 14–19). Body black, except a yellow spot near dorso-inner margin of antennal socket, a pair of transverse yellow lateral spots on apical margin of TI, TII with a narrow yellow subapical band and propodeal valvula yellowish brown. Wings yellowish brown tinged.

Remarks. *Zethus velamellatus* sp. n. fits well into the *trimaculatus*-group (Giordani Soika 1958, Yeh and Lu 2017) in sharing the main character of a short and stout first metasomal segment. The new species is easily to separate because of the missing submarginal lamella of the propodeum, the punctate sculpture of SI and smoothly curved profile of SII in lateral view.

Distribution. China (Zhejiang).

Etymology. This species is named "velamellatus ("ve" is Latin for "without") because the propodeal lamella is invisible in this species.

Discussion of Oriental and Palaearctic distribution of *Zethus* Fabricius

Zethus Fabricius, 1804, is the most speciose genus of the Vespidae. It consists of 272 valid species, mainly occurring in the pantropical area with most species in the Neotropical region (230 species); the numbers are much lower for the other regions Afrotropical (15), Oriental (26), and Palaearctic (2) (Giordani Soika 1940, Bohart and Stange 1965, Gusenleitner 2011, Carpenter et al. 2010, Carpenter and Madl 2011,

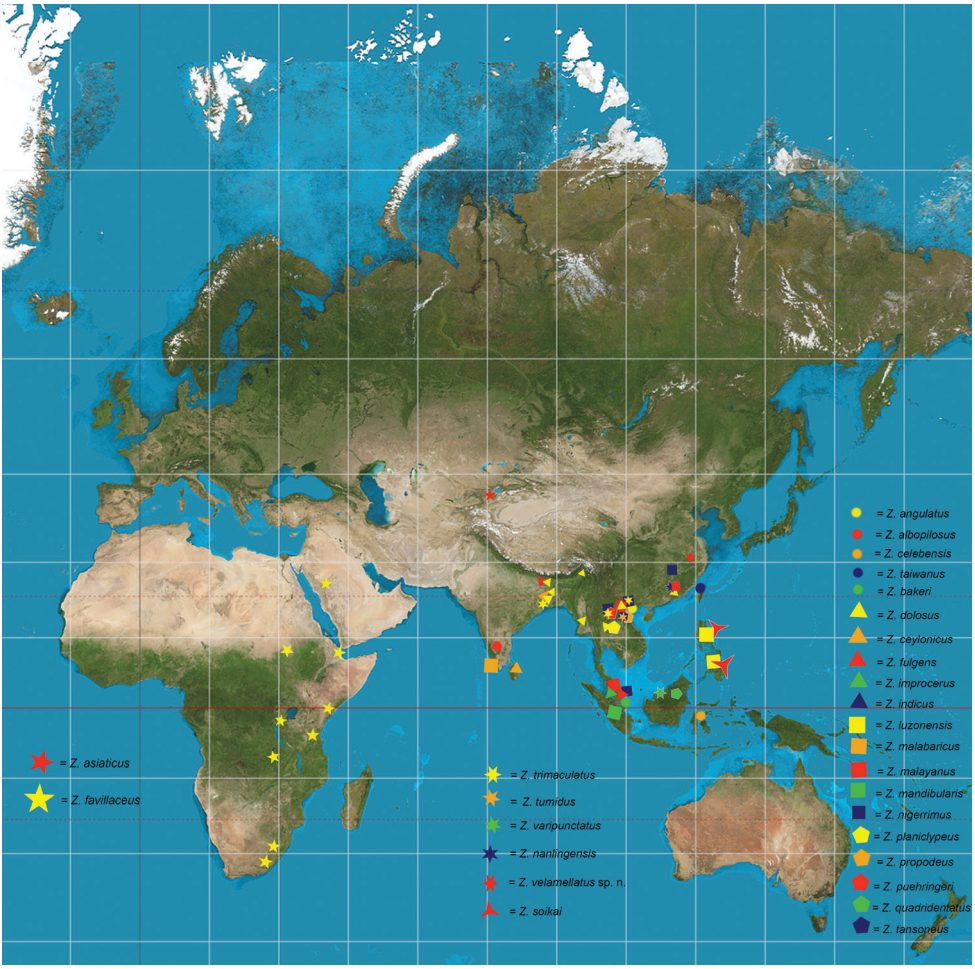


Figure 25. Zoogeographical map illustrating *Zethus* spp. recorded from Oriental and Palaearctic regions; *Z. favillaceus* is included as borderline species. Map from: http://blogs.discovermagazine.com.

Nugroho et al. 2012, Nidup et al. 2016, Nguyen and Carpenter 2016, Carpenter, unpublished). In addition, Bohart and Stange (1965) reported one undescribed species from Australia. Compared with its Oriental congeners, *Z. velamellatus* is the most northern (30°N) species known so far. The type locality (Fig. 25) lies within the boundaries of the Palaearctic-Oriental transitional zone as defined for mammals (between 33°N and 28°N; Hoffmann 2001).

A widespread but sporadic distribution may suggest a relict group (Tan et al. 2010). Hermes et al. (2014) recovered Zethini sensu lato as the sister-lineage to the remaining Eumeninae. The fossil and phylogeny of the genus is still unclear (Bohart and Stange 1965). The genus has been divided into four subgenera: *Zethoides* Fox and *Zethusculus* de Saussure, are restricted to the Western Hemisphere, *Madecazethus* Giordani Soika is endemic in Madagascar, but *Zethus* Fabricius s. str. is pantropical (Bohart and Stange

1965, Giordani Soika 1979). This distribution pattern fits well with "classic Indian Ocean (Gondwanic)" pattern (de Jong and van Achterberg 2007; especially the example of the genus *Celaenorrhinus* (Lepidoptera)). The research on Cretaceous fossil Vespidae reveals two basal groups (Priorvespinae and Euparagiinae) indicating that the time of subfamily-level division of Vespidae could be traced back to about 120–65 Ma (Carpenter and Rasnitsyn 1990). The connection between Africa and South America was severed during Late Cretaceous, at least 80 Ma (Hallam 1994). The minimum age of the Eumeninae is estimated to be approx. 90 Ma (Perrard et al. 2017) and the origin of the genus *Zethus* could be estimated between 90–80 Ma, allowing for the Gondwanic distribution pattern.

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Flower associations and nesting of the pollen wasp *Quartinia major* Kohl, 1898 (Hymenoptera, Vespidae, Masarinae) in Morocco

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Abstract

Females of *Quartinia major* Kohl were observed to visit flowers of *Pulicaria mauritanica* Batt., *Cladanthus arabicus* (L.) Cass. and *Asteriscus graveolens* (Forssk.) Less., (all Asteroideae Asteraceae) at two localities in southern Morocco. Pollen in the provisions of two brood cells was more than 99% *Aster*-type (Asteroideae), indicating broad oligolecty. During pollen uptake from *P. mauritanica*, the females of *Q. major* employed a hitherto undescribed harvesting technique: They used their mouthparts to squeeze pollen from the corolla tubes of early male phase disc florets. Pollen was ingested immediately after it had been extracted. The nest was a multicellular subterranean burrow excavated in friable soil and surmounted by a turret. The nest walls were stabilized with self-generated silk.

Keywords

Palaearctic, Asteroideae, flower visiting behaviour, pollen uptake, oligolecty, nest construction, silk

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Introduction

The pollen wasp genus *Quartinia* is comprised of more than 140 species, occurring either in the Afrotropical or the Palaearctic region (Carpenter 2001, 2003, Gess and Gess 2010, Gess 2011a, 2011b, Gusenleitner 2010a, 2010b, 2012a, 2012b, Schmid-Egger 2015). The members of *Quartinia* are small in comparison with other taxa of the Masarinae, ranging from ± 2–7 mm in length (Richards 1962, Gess 2007, Gess and Gess 2010). Knowledge of the bionomics of the Palaearctic species of *Quartinia* is still very limited and mainly restricted to flower visitation records for fourteen species published by Kohl (1898), Morice (1900), Saunders (1905), Benoist (1929), Bequaert (1940), Popov (1948), Gusenleitner (1973, 1990), Hohmann et al. (1993), and Carpenter (2003). Recently Mauss and Müller (2016) and Mauss and Mauss (2016) investigated in more detail flower visiting, nesting and mating behaviour of two allied *Quartinia* species endemic to the Canary Islands. Both species were found to be polylectic, using pollen from at least two different plant families with very different flower architecture. In contrast, most of the other Palaearctic *Quartinia* species have been recorded from only Asteraceae, suggesting oligolecty, though the actual degree of their pollen specialisation is still unknown. In the same way, Popov (1948) classified *Quartinia shestakovi* Kostylev and two undescribed taxa of *Quartinia* as oligolectic as they were observed to exclusively visit Chenopodiaceae.

Quartinia major was described by Kohl in 1898 based on four specimens collected by Otto Schmiedeknecht in Oran. Since then it has been recorded from several localities in Algeria and Morocco (Richards 1962, Carpenter 2001). The imagines have been observed to visit only flowers of various Asteraceae belonging to the subfamily Asteroideae, namely *Calendula* sp. (Kohl 1998), *Pallenis maritima* (L.) Greuter (Saunders 1905 as *Asteriscus maritimus* Moench) and *Coleostephus myconis* (L.) Rchb. f. (Bequaert 1940 as *Chrysanthemum myconis* L.). Further information about the bionomics of the species was until now lacking.

In the following study data concerning flower associations, flower visiting behaviour and nesting of *Quartinia major* are presented for the first time. A comparison is made with published bionomic characters of other species of the genus.

Material and methods

Investigations were carried out on four days between 13 and 17 April 2017 at two localities in the Anti Atlas in southern Morocco [I Ruderal road side 0.6 km NW Tizourgane, 20 km N Tafraout, 29°53.416'N, 09°00.399'W, 1240 m a.s.l.; II Wadi 2.75 km SW Ifrane Atlas Saghir, 29°12.178'N, 09°30.323'W, 750 m a.s.l.]. Geographic coordinates (WGS 84) were measured using a Garmin GPS 12. Most observations were made at locality I. Dry specimens of *Quartinia major* from both localities were identified using the key by Richards (1962) and compared with the holotype at the Natural History Museum Vienna.

For all documentation of observations the local time (= Greenwich Mean Time) was used. Observations were made with a close-up binocular (Pentax Papilio 8.5×21) and documented by using a Canon EOS 70D camera with a 180 mm macro lens and a 25 mm extension tube (scale more than 1:1, resolution 20 mega pixel) and macro flash-lights. The behaviour at flowers was also recorded and analysed by short video movies taken with a Canon EOS 70D camera with a 100 mm macro lens.

Specimens of all plant species that were visited by pollen wasps were collected and preserved dried. The material was placed in the herbarium of the State Museum of Natural History in Stuttgart (Herbarium STU). The plant taxa were identified following Fennane et al. (1999, 2007); the nomenclature follows the African Plant Database (version 3.4.0). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals at the flowering plant species independent of the number of flowers or plants visited by an individual during a single observed foraging incident. Sightings of flower visiting individuals were either counted while walking randomly along flowering plants across the area at locality I (random transect, total investigation time 120 min) or during unsystematic, random observations at localities I and II (total investigation time 360 min). Flower visiting behaviour of *Quartinia major* at *Pulicaria mauritanica* Batt. was observed at various patches of the plant at locality I (point observation, total investigation time 90 min). In addition, various other flowers were randomly scrutinized for visitors in a parallel study on bees (Müller et al. in prep.). Pollen samples from two brood cell provisions from a single nest were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were identified under a light microscope at magnifications of times 400 or 1000 and determined to the subfamily level taking genus types into account. For characterizing the degree of host-plant association, the categories defined by Müller and Kuhlmann 2008 (based on Cane and Sipes 2006) were used.

Nests were marked in the field with little ice-cream national flags and named after the country code of the flag used. Female behaviour at the nest was only observed at nest CH for approximately 180 min in total from the discovery of the nest at 12h50 on 14 April until 11h20 on April 15 when the female was collected. The nest GB was already abandoned on its discovery on 13 April. Both nests were excavated on 15 April using a combination of two reading glasses that provided a sufficient magnification. In the field, nest dimensions were measured using a calliper rule (accuracy 0.01 mm). The cells along with their contents were separately stored in small vials in a freezer until they were investigated under a Wild M3 stereomicroscope (maximum magnification times 60) on 7 August 2017.

Results

Habitat

At locality I *Quartinia major* was found on a richly flowering ruderal area along a roadside and on the adjacent broad embankment which changed onto a weakly grazed

stony hillside covered with widely spaced trees, namely *Argania spinosa* (L.) Skeels (Sapotaceae) (Fig. 1). The climate is arid with a mean annual precipitation of 235 mm and a mean annual temperature of 16.6 °C (data from Tafraout, AM ONLINE Project). The vegetation type could be categorized as degraded *Argania spinosa* scrub forest and bushland (sensu White 1983) comprised of at least 13 flowering plants from 9 families, including *Pulicaria mauritanica* and *Cladanthus arabicus* (L.) Cass. from Asteraceae.

At locality II *Quartinia major* inhabited a dry riverbed with adjacent plains and slopes (Fig. 2). The climate is arid with a mean annual precipitation of 170 mm and a mean annual temperature of 17.3 °C (data from Ifrane Atlas-Saghir, AM ONLINE Project). The ground surface was densely strewn with many stones of variable size and sparsely covered with several species of richly flowering dwarf shrubs as well as chamaephytes and therophytes, including *Cladanthus arabicus* and *Asteriscus graveolens* (Forssk.) Less. The vegetation type was Succulent sub-Mediterranean scrubland (sensu White 1983).

Flower associations

At locality I the females of *Quartinia major* were observed to visit only flowers of *Pulicaria mauritanica* and *Cladanthus arabicus*, which were the only plants in flower belonging to the Asteroideae (Table 1). During the random transect investigation 87 % of the sightings were recorded at *P. mauritanica* and 13 % at *C. arabicus* (n= 31 sightings). At locality II females of *Q. major* were recorded exclusively at flowers of *Asteriscus graveolens* (Table 1).

During a flower visit a female of *Quartinia major* would stand on the capitula (»heads«) of the composites with her longitudinal body axis orientated in a more or less radial manner, her head facing outwards (Fig. 3). In this radial position she moved sideways from disc floret to disc floret in a circle around the central axis of the inflorescence (Fig. 3). For nectar uptake a female moved her head downwards and protruded her proboscis into the corolla tube of a disc floret (Figs 9, 10). After a moment she raised her head again, removed and retracted her proboscis from the disc floret, moved her body slightly sideways, starting the whole process again, by inserting her proboscis into the next disc floret.

Pollen collection was observed only at flowers of *Pulicaria mauritanica*. During pollen uptake a female rapidly moved her head and mesosoma characteristically downward and horizontally forward, clasping the base of the corolla tube of a disc floret that had just started flowering with her mandibles. The female would then move her head and mesosoma forward-upwards, thereby pressing pollen out of the corolla tube with her mouthparts (Figs 12, 13a). On several occasions her fore tarsi came into contact with the corolla tube closely below her mandibles in addition. The extruded pollen mass was quickly ingested with the mouthparts, aided by movements of the fore tarsi (Fig. 13b). Pollen would also gradually accumulate on the surface of the head and the mesosoma during nectar or pollen uptake. This was removed from time to time by very fast alternating forward grooming movements of the fore legs (Fig. 14) and eventually brought between the mouthparts where the pollen grains were ingested (Fig. 11).

Figures 1–2. Habitat of *Quartinia major*. **1** Locality I, ruderal road side 20 km to the north of Tafraout, with yellow flowering dwarf shrubs of *Pulicaria mauritanica*. Two nests were found close to the little white flag in the foreground on the left **2** Locality II, wadi 2.75 km to the south-west of Ifrane Atlas Saghir, with yellow flowering plants of *Asteriscus graveolens* that were visited by females of *Q. major*.

Table 1. Sightings of flower visiting females of *Quartinia major* at the flowers of various plant taxa at two localities in Morocco. Sightings were made during random transect investigations, point observations and unsystematically recording.

Plant taxon	Sightings ♀
Asteraceae	
Pulicaria mauritanica Batt.	92
Cladanthus arabicus (L.) Cass.	6
Asteriscus graveolens (Forssk.) Less.	6
other plant taxa	
more than 10 flowering species from 8 families	0

Female brood care

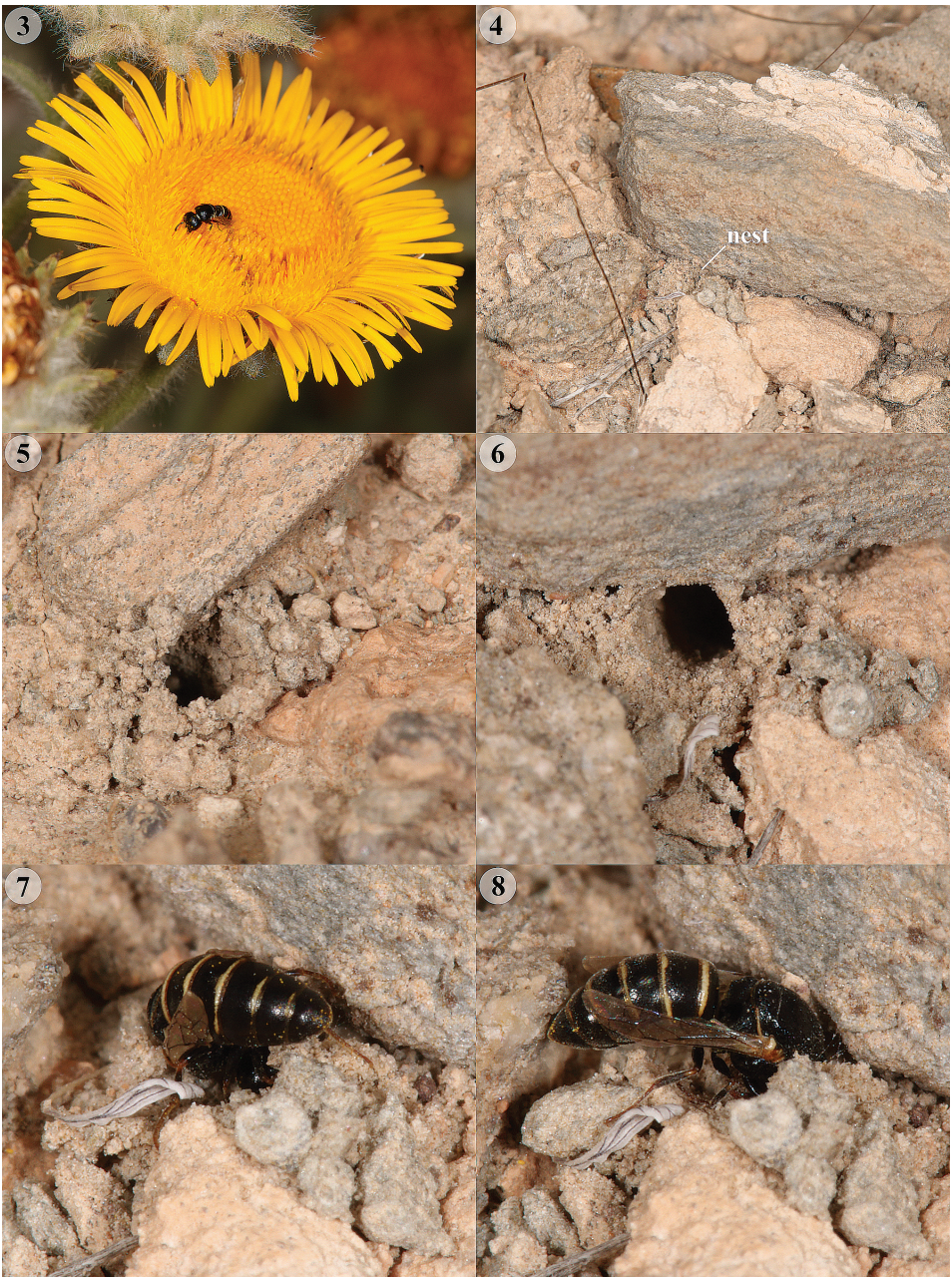
Nest site: Two nests were situated in horizontal ground on a terrace at the upper edge of the embankment (Fig. 1). The ground consisted of gravel mixed with friable soil sparsely covered by plants including *Pulicaria mauritanica* and in a distance of about 20 m also *Cladanthus arabicus*. The distance between the nests was 43 cm, the distance from the nest to the next plant of *P. mauritanica* measured 65 cm in nest CH and 28 cm in nest GB.

Nest structure: The nest consisted of a subterranean burrow with the entrance surmounted by a short oblique turret with an outer diameter of about 4.5 mm (Figs 5, 6). The inner diameter of the turret measured 2.0 mm at its base, which corresponded to the diameter of the shaft, but measured towards the opening was slightly greater in nest CH. The height of the turret varied between 1-2 mm. Both nests had the entrance to one side of a little stone (Figs 4, 15). The burrow of nest GB consisted of a subvertical shaft ending blindly at a depth of 10 mm just above a little underground stone (Fig. 15). In nest CH the shaft continued in a slope of about 20 degrees beneath the adjacent little stone, where it turned downwards more sharply and continued at about 75 degrees to the surface till it reached a depth of 20 mm, where it turned again into a more horizontal direction for 3–4 mm. Then the shaft turned obliquely downwards again and continued into an open brood cell with the opening orientated obliquely upwards (Fig. 15, cell No. 1). A second cell was situated at a distance of 18 mm from the shaft (Fig. 15, cell No. 2). The depth of the cells below the ground was 20 mm and 24 mm respectively (Table 2).

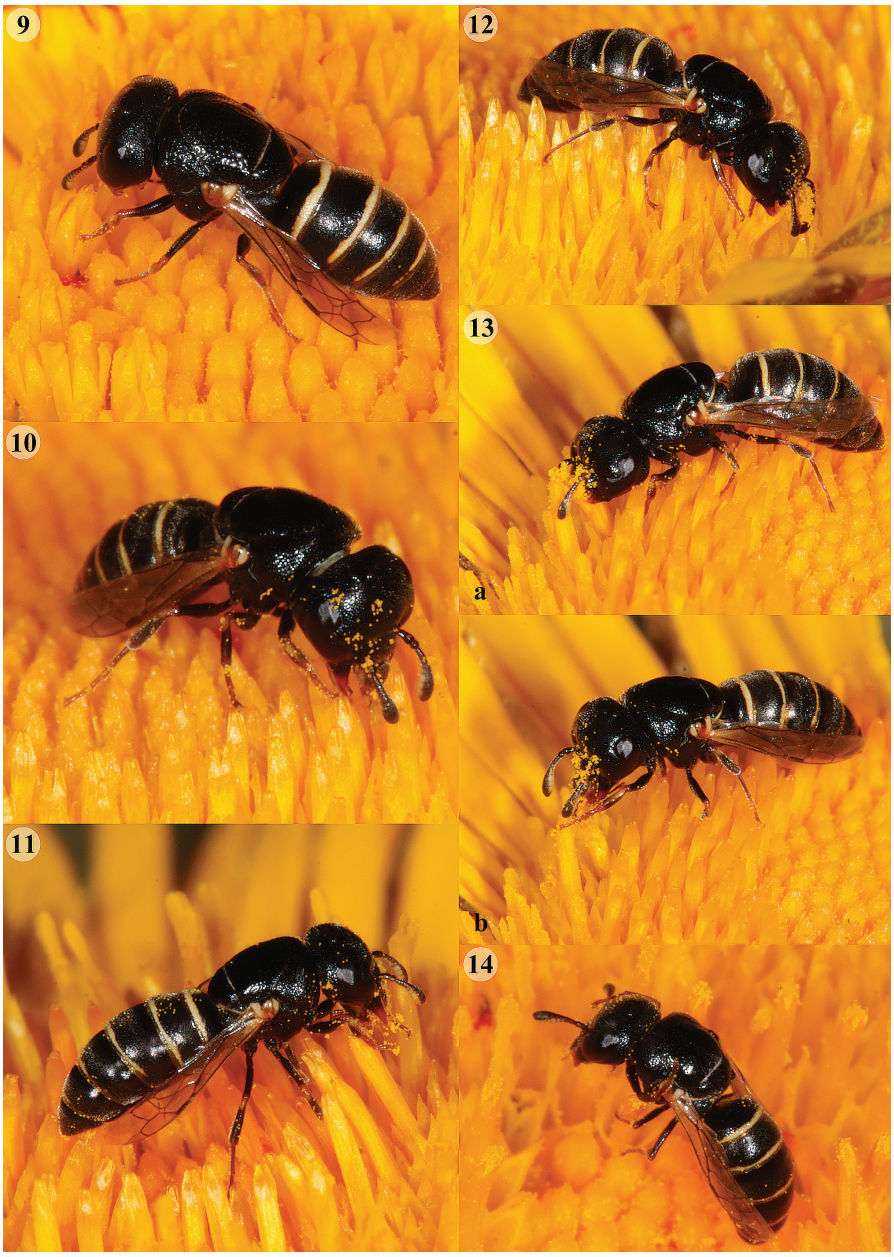
The delicate, non-rigid walls of the turret, the shaft and the brood cells consisted of little particles of the friable soil bonded together with a continuous lining of silk[1]. The silken lining of the shaft continued into the lining of the terminal cell.

Brood cell content: The content of the brood cells is summarized in Table 2. The provision consisted of an orange-yellow, moistly shining, rather sticky pollen loaf. The loaf was well separated from the cell wall and had a papillate surface. The provision

[1] The term silk is used in a generic sense in accordance with Gess and Gess 1992, while the chemical constitution of the »silk« filaments is unknown.



Figures 3–8. 3 Female of *Quartinia major* visiting disc florets on a capitulum of *Pulicaria mauritanica*. The proterandric disc florets open from the outer ones inwards. The mouthparts of the female are situated in the zone where disc florets are in an early male phase of anthesis **4** Location of nest CH of *Q. major* at locality I **5** Nest entrance of nest GB (viewed at an angle) **6** Nest entrance of nest CH (viewed from above) **7** Female of nest CH partly backed out of the turret moving slightly around her longitudinal axis with her mouthparts orientated towards the inner surface of the turret wall **8** Female of nest CH backing out of the nest carrying a load of soil particles with her mouthparts (visible between fore and mid femur).



Figures 9–14. Flower visiting behaviour of females of *Quartinia major*. **9** Nectar uptake from disc florets on capitulum of *Asteriscus graveolens* **10** Female with protruded proboscis taking up nectar from disc florets of *Pulicaria mauritanica* **11** Ingestion with the mouthparts of pollen grains that had accumulated on the fore legs **12** Female pressing pollen out of the corolla tube of a disc floret of *P. mauritanica* with her mouthparts, while the pollen grains accumulate above the corolla in front of her head surrounded by her antennae **13** Pollen uptake from disc floret of *P. mauritanica* **a** Female pressing pollen out of the corolla tube **b** female immediately afterwards ingesting pollen supported by her fore legs **14** Female brushing pollen from her exoskeleton with rapid alternating movements of her fore legs.

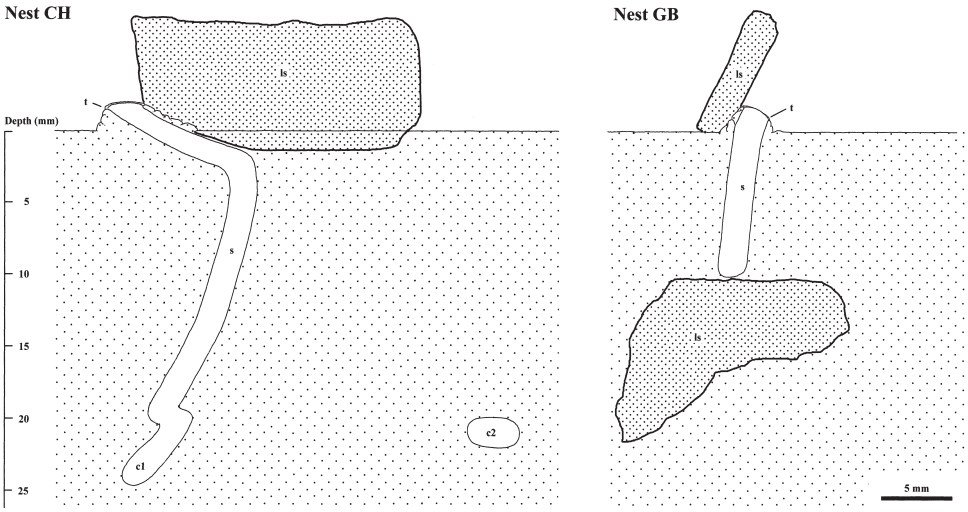


Figure 15. Schematic vertical cross sections of the nest architecture and brood cell arrangement of nest CH and nest GB of *Quartinia major* investigated on 15 April, 2017 at locality I (c = brood cell with cell number, ls = little stone, s = main shaft, t = turret).

Table 2. Details of the brood cells of nest CH of *Quartinia major* investigated on 15 April, 2017 at locality I.

Cell No.	Orientation to the north (°)	Depth below ground surface (mm)	Condition	Content	Pollen composition
1	330	24	open	pollen loaf, egg	Asteraceae Asteroideae, *Aster*-type: >99% Cichorioideae, *Taraxacum*-type: single grains
2	?	20	sealed	pollen loaf [egg or larva probably artificially lost, as cell had been damaged during excavation]	Asteraceae Asteroideae, *Aster*-type: >99% Asteroideae, *Anthemis*-type: single grains Cichorioideae, *Taraxacum*-type: single grains

consisted nearly exclusively of pollen of the *Aster*-type of Asteroideae, while pollen of the *Anthemis*-type of Asteroideae and from flowers of Cichorioideae was present only in single grains.

Behaviour at the nest: The female always entered the nest head first and left the nest backwards. At the beginning of a short period of nest building behaviour the female appeared a few times backwards in the nest entrance and remained for a few seconds with her head and parts of her mesosoma inside of the turret moving slightly around her longitudinal axis with her mouthparts orientated towards the inner surface of the turret wall (Fig. 7) before she moved downwards again into the nest shaft. After that the female backed out of the shaft and performed a typical orientation flight with

several ever-widening arcs until she was approximately 50 cm away from the nest entrance, returned straight forward to the nest and re-entered it head first. After a short time she reappeared and backed a bit further out of the turret carrying a load of small soil particles with her mouthparts (Fig. 8). Then she stopped, probably discharged the load and moved rapidly forwards and re-entered the nest head first again. She repeated this process a few times.

On her last return to the nest in the afternoon at 15h57, the female entered the nest directly head first and remained in the nest until the end of the observation period at 16h27. In the morning the female appeared backwards in the nest shaft at 10h09, 18 min after the onset of the nest observation period, backed out of the entrance immediately afterwards and remained for 7 s on the nest with her head above the turret before she flew off. During the following section of the observation period the female was absent from the nest three times probably performing provisioning flights, as indicated by the condition of brood cell No. 1 of the nest that was in the provisioning phase (Table 2). These potential provisioning flights lasted between 13 min and 18 min (median 16 min, n = 3).

Activity

The median diurnal activity of the females at flowers lasted for 6.6 h (n = 2) with the first activity recorded at 9h55 and the last at 16h36. Males were not observed at any time during the observation period.

Discussion

Flower associations

At both study sites the females of *Quartinia major* were observed to visit only flowers of three different species from three genera of Asteroideae, a subfamily of the Asteraceae. This is in congruence with the flower visiting records published by Kohl (1898), Saunders (1905) and Bequaert (1940) that are also all for members of the Asteroideae. Moreover, the brood cell provisions contained nearly exclusively pollen from flowers of Asteroideae. These findings suggest that *Q. major* is broad oligolectic (sensu Müller and Kuhlmann 2008) with regard to its pollen source, using exclusively pollen of Asteroideae for brood cell provisioning but from more than one genus of Asteroideae. Association with Asteraceae seems to be widespread within *Quartinia* as 79 % of 14 Palaearctic species (Benoist 1929, Bequaert 1940, Carpenter 2003, Gusenleitner 1973, Gusenleitner 1990, Hohmann et al 1993, Morice 1900, Popov 1948, Saunders 1905) and 55 % of 42 Afrotropical species (summarized by Gess and Gess 2010) for which flower-visiting records are available have been recorded from this plant family. In the Palaearctic eight species have been exclusively recorded from Asteraceae. However, *Q. major* is the first Palaearctic species for which oligolecty has been demonstrated by pollen analysis from brood cell provisions. In

the Afrotropical region ten species were exclusively recorded from Asteraceae (cf. Gess and Gess 2010), indicating specialization on this plant family as the single pollen source, even though the oligolectic use of pollen of Asteraceae for brood cell provisioning has been demonstrated solely for *Quartinia vagepunctata* von Schulthess (Gess and Gess 1992).

At locality I the brood cell provisions contained nearly exclusively pollen of the *Aster*-type suggesting that pollen was actively collected only from *Pulicaria mauritanica*. This is also supported by the fact that pollen uptake by females of *Quartinia major* was observed only at this plant. In contrast pollen from *Cladanthus arabicus*, which is of the *Anthemis*-type, was probably only included in the provisions as a result of passive contamination either due to pollen grains adhering to the exoskeleton of the female wasp during nectar visits to *C. arabicus* or due to pollen transfer from disc florets of *C. arabicus* to the capitula of *P. mauritanica* by other flower visitors. A preference for flowers of *P. mauritanica* over flowers of *C. arabicus* by *Q. major* females is also suggested by the results of the random transect walks since more than 85 % of the females were recorded from *Pulicaria*. However, since both investigated brood cells originated from the same nest, the presumed preference for taxa having pollen of the *Aster*-type over taxa possessing pollen of the *Anthemis*-type should be confirmed with larger sample sizes.

The distinct technique of *Quartinia major* females during pollen uptake from disc florets of *Pulicaria mauritanica* has not been reported before for any other pollen wasp or bee species. Other *Quartinia* species ingest pollen either directly from the anthers or they brush pollen with their fore legs from the anthers or the body surface towards the mouth where it is ingested (Gess 1996, Gess and Gess 2010, Mauss and Müller 2016, Mauss and Mauss 2016). Squeezing out pollen from the corolla of disc florets in the early male phase with the mouthparts probably enables the females of *Q. major* to remove the pollen efficiently before it becomes available for other flower visitors. In this context it is of note that during cell provisioning, probable combined pollen and nectar collection flights of the female of *Q. major* from nest CH lasted for only 16 min in the median which is at the lower end of the range observed for some other pollen wasp species (17.3 min in *Celonites abbreviatus* (Villers), Bellmann 1984; 41.9 min in *Celonites fischeri* Spinola, Mauss and Müller 2014; 31.5 min in *Pseudomasaris phaceliae* Rohwer, Neff and Hook 2007; 31.3 min in *Pseudomasaris edwardsii* (Cresson) Torchio 1970). The comparatively short duration of the potential provisioning flights of *Q. major* may be associated with the derived technique of pollen uptake in this species. This is supported by the fact that *C. abbreviatus*, that also performs comparatively short provisioning trips (cf. Bellmann 1984), also uses a highly derived method for pollen uptake (Schremmer 1959, Bellmann 1984, Müller 1996, Mauss 2006).

Female brood care

Quartinia major was found nesting in friable soil close to its main forage plant. This is similar to the nesting situation in *Quartinia canariensis* Blüthgen (Mauss and Müller 2016), the Afrotropical *Quartinia vagepunctata* (Gess and Gess 1992), nesting in a metre

square area clear of plants that was surrounded by the forage plants, and *Quartinia poecila* von Schulthess (Gess and Gess 2010), nesting on the mound formed around the forage plant, a situation suspected by Gess and Gess (2010) to be common to some other Afrotropical species of *Quartinia*. Each nest of *Q. major* had its entrance to one side of a little stone, slightly embedded in the substrate, offering some protection to and a somewhat stable substrate for the burrow descending beneath it and which is identical with the nest location next to a stone or an earth clod, recorded for *Q. vagepunctata* (Gess and Gess 1992) whereas the nests of other species were found on bare ground (Gess 2009, Gess and Gess 2010, Mauss and Müller 2016) and those of seven species in sand-filled snail shells (Gess and Gess 1999, Gess and Gess 2008).

The walls of the burrow and the newly provisioned cells of *Quartinia major* were non-rigid soil particle and silk structures with a silk lining, the silk being produced by the nest building female. This character occurs in all *Quartinia* species for which nesting is known (Gess and Gess 1992, 1999, Gess and Gess 2010, Mauss and Müller 2016) and is unique among the Masarinae (Gess and Gess 1992, Mauss 2007). Therefore it can be regarded as an outstanding apomorphic trait of *Quartinia* that enabled the members of the stem-line of *Quartinia* to inhabit ecosystems with friable, sandy soil (Mauss and Müller 2016).

A short more or less vertical turret surmounting the nest entrance as in *Quartinia major* is also present in nests of *Q. canariensis* (Mauss and Müller 2016) and most Afrotropical *Quartinia* species (Gess and Gess 2010). The existence of a turret at the nest entrance is probably a plesiomorphic trait of *Quartinia* adopted from the ground pattern of the Masarinae (Mauss 2007). A probably derived turret form exists in *Q. vagepunctata* that builds a horizontal, bag-like turret (Gess and Gess 1992).

As in *Quartinia canariensis* (Mauss and Müller 2016) there is no evidence that females of *Q. major* are able to turn inside the nest, as the focally observed female always entered the nest head first and reappeared backwards. This was also the case in the earliest observed appearance in the morning and on the last return to the nest in the evening. Therefore females of *Q. major* probably spend the night in the burrow head downwards. This is in contrast to the behaviour of females of *Q. canariensis* that spend the night inside the nest with their head orientated upwards towards the nest entrance, so that they appear head first in the morning (Mauss and Müller 2016). This is the result of a characteristic behaviour of the females of *Q. canariensis* that reappear backwards in the nest entrance after the last return to the nest in the afternoon, back out a few steps from the nest entrance, move forward on top of the turret and re-enter the nest metasoma first with the dorsal side orientated downwards (Mauss and Müller 2016). This distinct behaviour seems to be absent in *Q. major*.

The nest of *Quartinia major* consisted of a subterranean burrow terminated by a cell, which is principally similar to the nest architecture of *Q. vagepunctata* (Gess and Gess 1992) and *Q. canariensis* (Mauss and Müller 2016). The depths of the brood cells of *Q. major* below the ground surface were also within the range of these species measuring 20–24 mm in *Q. major*, 25–30 mm in *Q. vagepunctata* (Gess and Gess 1992) and 15–23 mm in *Q. canariensis* (Mauss and Müller 2016). Like the nest of

Q. canariensis (Mauss and Müller 2016) the nest CH of *Q. major* is believed to have been multicellular and this was also suggested for nests of *Q. vagepunctata* (Gess and Gess 1992). Moreover, in all *Quartinia* species nesting in snail shells the nest is multicellular with up to 20 or even more cells (Gess and Gess 2010). The distant and isolated position of cell No. 2 in nest CH of *Q. major* is remarkable and resembles the situation in the nest of *Q. canariensis* (Mauss and Müller 2016). The isolated position of the sealed cell No. 2 demonstrates that it was excavated and provisioned by the female previous to the cell No. 1. As in the nest of *Q. canariensis* a connection from this isolated cell to the main shaft was no longer perceptible during nest excavation, indicating that it had been build at the end of a separate long secondary shaft that was either filled with soil by the female or that just collapsed after the brood cell had been sealed.

During nest excavation the female of *Quartinia major* backed out of the shaft carrying soil particles with her mouthparts, which is similar to the behaviour of *Q. canariensis* (Mauss and Müller 2016) and all other primarily ground nesting masarine wasps (cf. Gess 1996, Gess and Gess 2010, Mauss 2007). Therefore, these elements of the behaviour are probably plesiomorphic. As in other species of *Quartinia* (Gess and Gess 1992, Gess and Gess 2010, Mauss and Müller 2016) no observable liquid was used by *Q. major* during nest excavation.

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Supplementary material 1

***Quartinia major* female nectar uptake from disc flowers on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae) I**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

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Supplementary material 2

***Quartinia major* female nectar uptake from disc flowers on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae) II**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

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Supplementary material 3

***Quartinia major* female indirect pollen uptake from the exoskeleton with brushing movements of the fore legs on capitulum of *Pulicaria mauritanica* (Asteraceae, Asteroideae)**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

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Supplementary material 4

***Quartinia major* female pressing pollen out of the corolla tube of the disc flowers of *Pulicaria mauritanica* (Asteraceae, Asteroidea) with her mouthparts**

Authors: Volker Mauss, Andreas Müller, Rainer Prosi

Data type: Video file

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Cavities in bromeliad stolons used as nest sites by *Euglossa cordata* (Hymenoptera, Euglossini)

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Abstract

Herein, we describe nests of the orchid bee *Euglossa cordata* that were constructed in cavities of *Aechmea distichantha* (Bromeliaceae) stolons. We present data about nest and cell size, number of adults and brood, and analyses of larval provisions. The presence of *E. cordata* carcasses embedded in the resin of nest partitions indicates that these nests were used by multiple generations. Based on larval provisioning, *E. cordata* is polylectic and relies heavily on a few plant species.

Keywords

island, larval provision, natural cavity, nesting biology, orchid bees

Introduction

Orchid bees (Apidae: Euglossini) are important pollinators in the Neotropical region, as they pollinate hundreds of plant species from many families (Ramírez et al. 2002), including orchids. Previous research indicates a large degree of variation in Euglossini nesting substrates, including soil, termite nests, bamboo canes, orchid roots, and man-made cavities (Bodkin 1918, Sakagami et al. 1967, Garófalo et al. 1993, Gonzales and Gaiani 1990, respectively). Among the five different genera and ~200 species of orchid

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bees (Roubik and Hanson 2004), some species build freestanding nests with a resin involucre (Eberhard 1988, Wcislo et al. 2012), while other species search for empty cavities (Garófalo 1985, Gonzales and Gaiani 1990). Dressler (1982) hypothesized that species nesting inside cavities may develop sociality, whereas species building aerial nests would be solitary. Although aerial nest with multiple adult females have been described for *Euglossa*, the study did not clarify the degree of sociality (Eberhard 1988).

Besides sociality, the nesting biology of many orchid bee species is still unknown because females are rarely observed in nature and only males are known for some species (Roubik and Hanson 2004). Human-made cavities in bamboo canes or wooden boxes have increased the knowledge of the nesting biology and social organization of orchid bees (Zucchi et al. 1969, Augusto and Garófalo 2009, Boff et al. 2015, 2017, Andrade et al. 2016). However, such methods are limited to cavity nesting species, with little information regarding natural nesting cavities (Wcislo et al. 2012), even for common species such as *Euglossa cordata* Linnaeus. *Euglossa cordata* is an orchid bee species that is widely distributed in South America (Nemésio and Silveira 2007) and abundant in Southeastern Brazil (Cordeiro et al. 2010, Aguiar and Gaglianone 2012).

This species is primitively eusocial, with a single dominant female who has full reproductive skew towards subordinates (Freiria et al. 2017). Studies about population genetics of *Euglossa cordata* indicate large population sizes and that environmental discontinuity does not play a strong role on genetic diversity in this species (Cerântola et al. 2010, Rocha-Filho et al. 2013, Boff et al. 2014). Herein we report females of *E. cordata* using cavities in stolons of the bromeliad *Aechmea distichantha* Lem. as nest sites. We also describe the pollen included in the larval provisions of this bee. This is the first study to describe orchid bees using bromeliads as nesting sites.

Material and methods

Natural nests were found on the Ilha da Vitória (45°01'W, 23°45'S), a small island (221 ha) in the state of São Paulo, Brazil ca. 40 Km away from the mainland (Figure 1) in November 2009. Ilha da Vitória is covered with plants commonly found in the Atlantic Forest, but has less floral diversity than the neighboring islands: Ilhabela, and Ilha de Búzios (Ângelo 1989). Ilha da Vitória has only rocky shores, where plant species that are adapted to this extreme habitat grow.

One such species is the bromeliad *Aechmea distichantha* which grows over the rocks at the edge of the island. These bromeliads are fixed to the rocks by very thin, root-like structures that arise from the plants' stolons. Typically, stolons are solid structures that emerge from plant rhizophora and grow parallel to the rocky substrate. Close to their termini they turn upward, grow vertically, and lead to the next generation bromeliad (pup). An *Aechmea* stolon presents three layers: a coat (consisting of the lignified epidermis and/or a stratified layer of cork), a cortex, and vascular cylinder (Proença and Sajo 2008). All together the stolon forms a bridge linking two individual plants (Suppl. material 1: Figure S1a–b).

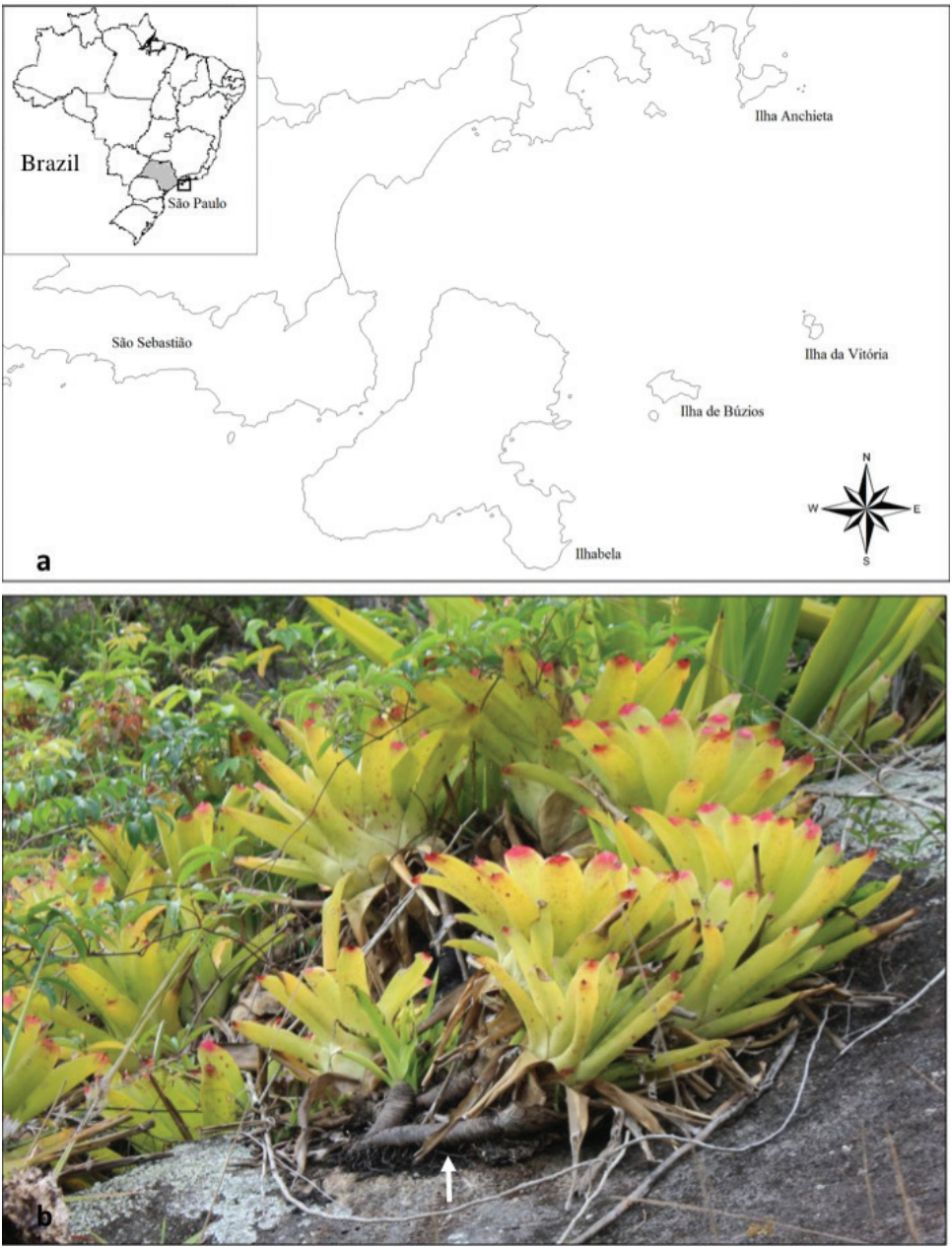

Figure 1. Location of study site. **a** The data was sampled on Ilha da Vitória, archipelago of Ilhabela, in São Paulo state **b** The habitat of the bromeliad on the rocks of the board, arrow highlights stolon of *A. distichantha*.

We sampled a total of seven stolons, either from the foliage or on the bare rock. Five of them were old (dry) stolons and two were living stolons. All stolons were carefully removed and brought to the Bee Laboratory at the University of São Paulo. In the lab,

all the old stolons were dissected and found to contain cavities. In 2018, we dissected living stolons, which linked two living plants. Living stolons presented no cavities, but instead were filled with aqueous white tissues (Suppl. material 1: Figure S1c–d).

We found nests of *Euglossa cordata* in the dry stolons of *Aechmea distichantha* (Suppl. material 1: Figure S2a–b), with three nests in two different stolons. These stolons were similar to a "clean gallery", with little or no plant tissue left inside. After opening stolons and exposing the cavities, adult and immature individuals were fixed in ethanol. Adult bees found with undamaged wings were considered newly emerged, while bees with damaged wing ends were classified as not newly emergent. Nest architecture was described, brood cells were measured with a digital vernier caliper, and larval provisions were analyzed using brood feces ($n_{cel\ l}$ = 10) and fresh pollen content (n_{cell} = 1). In the laboratory, we analyzed pollen samples from nests 1 and 3 following acetolysis. We were unable to determine pollen from nest 2 since open cells were empty and the closed cell was undisturbed. Microscope slides were mounted and pollen grains were identified by a specialist (CFP Luz). We estimated pollen type frequencies using 300 pollen grains per slide (n = 2 slides per cell) (see Boff et al. 2011). We used the package bipartite in R to visualize network-level analyses (Dormann et al. 2009).

Vouchers of bee specimens were deposited in the entomological collection "Paulo Nogueira-Neto" in the Ecology Department at the University of São Paulo. Pollen slides were deposited in the Palynology Collection at the Institute of Botany of São Paulo state.

Results

We found a total of 25 cells in three nests. Nests 2 and 3 were found inside the same stolon, but the nest cavities were not connected to each other. In nests 1 and 2 we found ten brood cells each. In nest 3 we found five cells. In the closed cells of all nests we observed a cell collar. The brood cells (n = 13) were 9.04 mm (±0.98) wide and 12.3 mm (±2.62) long. In nest 1 we found two living adults (one male and one female) classified as recently emerged brood. We also found the carcass of another female. In the laboratory two other individuals (a female and a male) emerged. Additionally, we found fresh pollen inside an open cell (Figure 2).

A mixture of resin and carcasses acted as a barrier between the two nests in connected stolons. In nest 2 we found one dead female with damaged wings, a dead male inside a brood cell, and a fragmented bee carcass whose body parts were embedded in resin and unable to sex. In nest 3 we found two open and three closed brood cells. In the lab, two bees (one male, one female) emerged from the closed cells and one non-sexed dead larva was extracted from their cell (Table 1). In nests 1 and 2 the cells were aligned inside the cavities, with each cavity length about 13 cm (see Figure 2). In nest 3, cells were built in a single cluster inside a smaller cavity with 5.5 cm length (Figure 3). For all nests resin was only used in the brood cells and around the nest entrance.

Figure 2. Details of two nests found inside stolons of bromeliads. In nest 1 only a part of the cell is shown. On the left side of nest 1 it is possible to see an open brood cell with fresh pollen in caramel color.

Table 1. Snapshot of intranidal data of *Euglossa cordata*. Details of three nests found inside the stolons of *A. distichantha*. No = Non-observed.

	Nest 1	Nest 2	Nest 3
Resident female alive	1	0	1
Males alive	1	1	No
Brood cell with fresh provision	1	0	0
Closed cells	4	1	3
Cell under construction	0	0	1
Old open cells	6	9	1
Emerged individuals	2 ♀/ 2 ♂	1 ♂	1 ♀/ 1 ♂
Dead bee(s) or carcass(es)	1	3	1
Pollen types (n)/cells (n)	16/7	No	9/4

We found several pollen types associated with the diet of immature *Euglossa cordata*. We determined 21 pollen types, corresponding to species from seven families (Figure 4). The frequency of pollen types varied from two to nine in one single brood cell. Four plant species (*Centrosema* sp., *Dalechampia* sp2, *Myrcia* sp. and *Solanum* sp1)

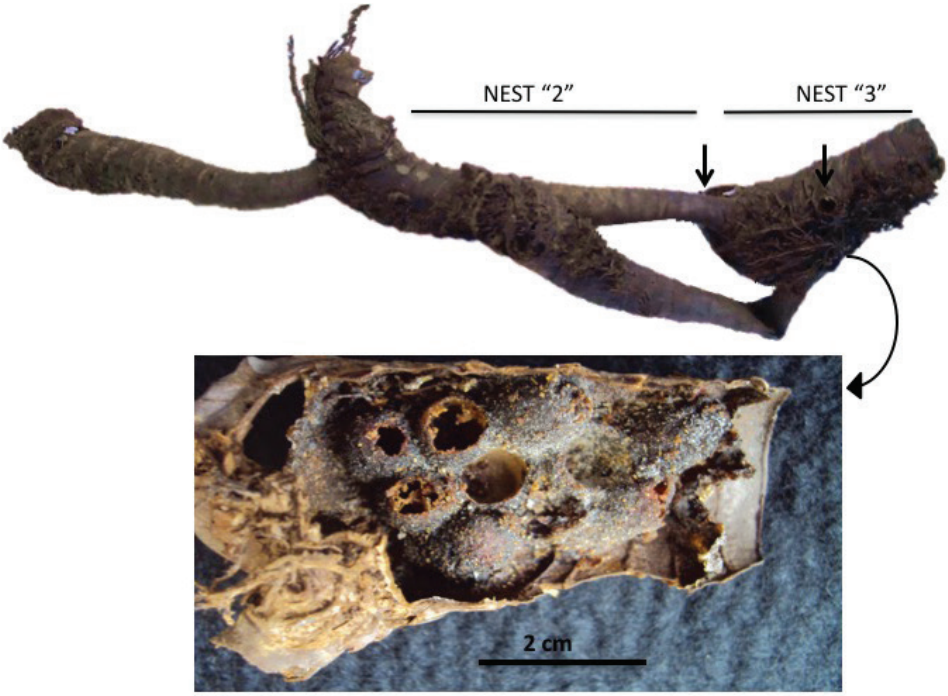

Figure 3. Stolon of *A. distichantha* with two connected nests of *Euglossa cordata*. Nest 2 and 3 were separated by resin and bee carcasses (arrow between nest 2 and nest 3; see details in Suppl. material 1: Fig. S1c). The entrance of nest 3 is indicated (arrow) and nest 3 is in detail after dissection (with scale, 2 cm).

were found in both nests. In five brood cells, we found that at least 80% of all pollen grains came from a single plant species. Species with the highest pollen frequencies were *Myrcia*, *Solanum*, *Baccharis*, *Genipa americana,* and *Eucalyptus* (Figure 4).

Discussion

Euglossa cordata females build nests in empty cavities. Even though their nests have been documented in bamboo canes or observation boxes, this species is not restricted to such substrates. Herein, we report that *E. cordata* uses naturally lignified cavities, specifically stolons of the bromeliad *Aechmea distichantha*, as nesting sites. The cavities inside the stolons seem to be an efficient site to build nests. We found carcasses of old *Euglossa* females in all nests, which may indicate that nests were reused by multiple generations.

We observed that internal cavities in the stolon may be due to drying of moist internal tissues after plant death. However, we found one stolon that was occupied by an unidentified species of termite. In this stolon, we presume that the termites were foraging in the internal tissue, since we did not find termite eggs, or a queen or king in the cavity (characteristics of a termite nest) (personal communication T Carrijo 2018). Therefore, although cavities occupied by the orchid bees may have been caused by

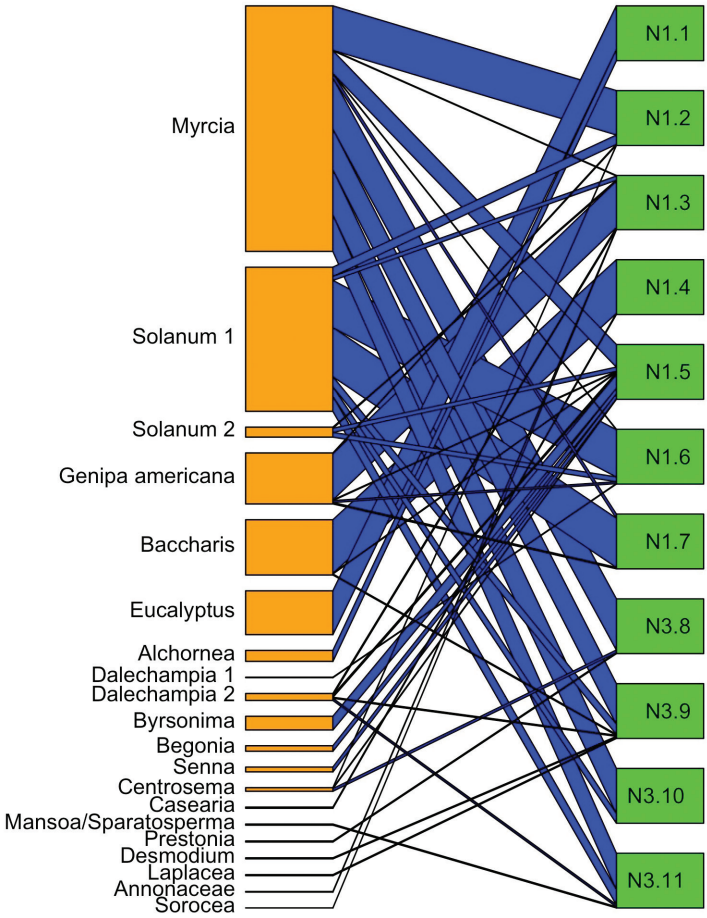

Figure 4. Network-level analysis of larval provision of *Euglossa cordata*. Each orange rectangle represents the pollen type found in the brood cells. The green rectangles represent individual brood cell. The first number inside each green rectangle corresponds to the nest identity and the second number to the brood cell itself. The connection between rectangles (blue) shows the pollen types used as food for immature *E. cordata*. The width of each blue link corresponds to the frequency of pollen grains inside each brood cell. The content from brood cell N1.7, correspond to open cell in the nest 1 (see Fig. 2).

drying of internal tissues after plant death, *E. cordata* may benefit from prior foraging/cleaning activity of termites in the tissues of the stolon.

Furthermore, we found nests inside empty galleries, where rare roots pieces remained (see the bottom of nest 2, Figure 2). Females of *Euglossa cordata* built their cells in two different ways inside the cavities. In long and narrow cavities, brood cells were linear, while in wider and shorter cavities, cells were arranged in a cluster. Besides that, nest size seemed to be dependent on the dimensions of the stolon. Zillikens et al. (2001) reported that *Augochlora esox* (Halictidae: Augochlorini) nested in the rosettes of *Aechmea* plants, and that rosette size limited the nest architecture of the sweat bees. Similar findings have

been documented for other bee species nesting in human made cavities (Alonso et al. 2011, Seidelmann et al. 2016). We assigned *E. cordata* as a heteromorphic bee species because nest size and structure is dependent on the cavity (see Michener 2007, p.25). This behavioral plasticity of *E. cordata* may indicate that there is no single nest architecture or substrate for this species. Instead, females of *E. cordata* seem to optimize the size of a cavity when building their nests, and search for cavities in different substrates.

The nesting biology of *Euglossa*, including *E. cordata* (Garófalo 1985, Gonzales and Gaiani 1990), is documented for circa 20% of the species (see Wcislo et al 2012). Interestingly, this group of neotropical bees seems to either build nests in cavities or build aerial nests. Cavity users, as their name suggests, use cavities to build nests, as we observed herein. Other *Euglossa* species build aerial nests made of plant resources, such as resin that anchors the steam or leaf of a plant (see video in Wcislo et al. 2012). Such remarkable differences in nesting behavior within a genus may extend to other bee genera, such as *Centris*, who either nest in empty cavities or excavate nests underground (Vinson et al. 2010, Sabino et al. 2017, respectively).

Larval provision

Studies suggest that *Euglossa* species are polyletic species (Ramírez et al. 2002, Cortopassi-Laurino et al. 2009, Villanueva-Gutierrez et al. 2013, Silva et al. 2016), which means that the pollen diet of the brood consists of multiple plant families. However, it seems as though *Euglossa* bees collect higher amounts of pollen grains from a few species of plants in the same family. In the current study 10 out of 11 brood cells had one single plant species with pollen frequency higher than 70 %. From the same ten brood cells, 80 % had pollen from either Myrtaceae (n = 6) or Solanaceae (n = 2). Similar findings have been reported for *E. annectans* Dressler and *E. townsendi* Cockerell (eg. Cortopassi-Laurino et al. 2009, Silva et al. 2016, respectively).

Directly comparing studies about *Euglossa* diet is difficult because these studies are not uniform, with study areas distributed across the Neotropical region in different habitats and vegetation. Furthermore, studies are based on many different *Euglossa* species with different nest numbers (and brood cells) [*ie.* Arriaga and Hernandez (1998), (n_{nests} = 57); Cortopassi-Laurino et al. (2009), (n_{nests} = 12); Villanueva-Gutierrez et al. (2013) (n_{nests} = 27); Silva et al. (2016) (n_{nests} = 6)]. However, the most frequently reported pollen grains are from Melastomataceae, Myrtaceae, and Solanaceae species. We analyzed the pollen content of 11 cells and found the same amount of pollen types that were reported for *Euglossa townsendi* (Silva et al. 2016) (50+ brood cells were analyzed).

Besides nesting sites, *Aechmea distichantha* may also offer food resources to *Euglossa* species. Pollen grains of several species of *Aechmea* have been reported in brood cells of *E. annectans* (Cortopassi-Laurino et al. 2009), but were not found in the samples we analyzed. Asteraceae pollen in the bees´ diet seems to be novel for *Euglossa* species. We found *Baccharis* (Asteraceae) pollen in three different brood cells, and in one cell it ac-

counted for more than 95 % of all pollen grains. This may indicate that either broods differed in their pollen need or that brood cells were filled in different seasons, when flower availability changed.

Conclusion

Given the importance of orchid bees as pollinators of Neotropical plants, aspects related to their maintenance, such as nesting sites, deserve priority in conservation, especially on islands where nesting habitats are less common than in other continuous environments. Previous studies on Ilha da Vitória showed low diversity of orchid bees on this island (Cordeiro et al. 2010) and, at the molecular level, there is lower genetic diversity than compared to bigger islands and the mainland (Boff et al. 2014). Due to the fact that stolons of *Aechmea distichantha* are suitable cavities for nests of *Euglossa cordata*, this plant may be an important resource for sustaining the population of orchid bees on this small island. Thus, *E. cordata* on the island may regularly use stolons for multiple generations. Lastly, they are polylectic but rely heavily on a few species of plants.

Acknowledgment

To Rafaela Forzza and Silvana Buzato for identifying *Aechmea distichantha*, to Cynthia FP Luz and the Institute of Botany of São Paulo state for identification of pollen types. To Anna Friedel, Antonella Soro, and Corey Smith for their comments on previous versions of the manuscript for which we thank them and the referees. The "Fundação de Amparo á Pesquisa do Estado de São Paulo" (FAPESP) for supporting our field activities.

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Supplementary material 1

Figure S1. Stolon of living bromeliads

Authors: Samuel Boff, Isabel Alves-dos-Santos

Data type: species image

Explanation note: The internal moist tissues of stolons from living plants.

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Link: https://doi.org/10.3897/jhr.62.22834.suppl1

Supplementary material 2

Figure S2. Details of *Euglossa cordata* nests

Authors: Samuel Boff, Isabel Alves-dos-Santos

Data type: species image

Explanation note: Nests were found inside stolons of bromeliads (*Aechmea distichantha*) on Ilha da Vitória, in Brazil.

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RESEARCH ARTICLE

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Morphology and review of the odd genus *Rhadinoscelidia* Kimsey, 1988 (Hymenoptera, Chrysididae, Loboscelidiinae)

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Abstract

The small chrysidid genus *Rhadinoscelidia* Kimsey, 1988, is reviewed and the new species *Rh. chaesonensis* **sp. n.** is described. Peculiar deformations of the head are documented in a large series of one species, *Rh. malaysiae* Kimsey, 1988, from Thailand.

Keywords

Loboscelidia, Oriental Region, Thailand, Hainan, Laos, Java, Malaysia

Introduction

The subfamily Loboscelidiinae contains two genera *Loboscelidia* Westwood, 1874, and *Rhadinoscelidia* Kimsey, 1988 (Kimsey and Bohart 1991). Loboscelidiines are characterized by the antennae inserting horizontally on a shelf-like projection mid face, the vertex is prolonged posteriorly into a neck-like projection; the pronotum has a short line of ribbon-like setae along the anterolateral corner; the tegula is very large, covering

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both wing bases and is held in place by a mesopleural ridge; the mesopleuron is smooth without sculpturing, the propodeum has an ear-like lateral projection, and the forewing lacks a stigma, costal and subcostal veins. *Rhadinoscelidia* can be characterized by further reductions of some of these features and a different arrangement of the patches of ribbon-like setae seen in *Loboscelidia*.

The chrysidid genus *Rhadinoscelidia* is rarely collected and is the most oddly modified of the chrysidid wasps. To date the genus is only known from Hainan Island (China), Thailand, Laos, West Java (Indonesia) and Malaysia (mainland) (Fig. 1). However, *Rhadinoscelidia* species probably occur throughout Southeast Asia, including Cambodia, Viet Nam, southern mainland China and Myanmar.

Male and female *Rhadinoscelidia* are difficult to separate. Although the number of external metasomal segments is sexually dimorphic in *Rhadinoscelidia* as it is in *Loboscelidia* the segments are difficult to distinguish using simple stereomicroscopy, and exserting the genitalia is generally necessary to determine the sex of a specimen.

Nothing is known about the biology of *Rhadinoscelidia* species. Unlike the situation in *Loboscelidia* where museum specimens are predominantly male, there are far more female *Rhadinoscelidia* than males among the small number of specimens in collections.

There are some unusual features in this group in addition to the odd structural modifications that characterize the genus. A large series of specimens from Thailand shows marked and inconsistent asymmetry of the head as shown in Figs 2–8. The reason for this asymmetry is not clear. However, it may affect the value of species distinctions based on facial dimensions, facial sculpturing, presence or absence of carinae, and the shape and position of emarginations or projections on the back of the head.

In addition, these wasps have what appear to be a number of secretory sites on the meso- and metasoma. All specimens examined had clusters of white, crystalline material in three sites, a fovea at the base of each forecoxa, surrounding the petiolar insertion on the propodeum, and on the apex of metasomal sternum I (as in Fig. 10a–c).

Materials and methods

Specimens were borrowed from the following museums, and repositories are indicated by the acronyms: CNC – Canadian National Insect Collection, Ottawa, Ontario; QSBG – Chiang Mai Royal Botanical Garden, Chiang Mai, Thailand; ROM – Royal Ontario Museum, Toronto, Canada; SCAU – Hymenoptera Collection, South China Agricultural University, Guangzhou; and UCRC – Entomological Research Museum, University of California, Riverside, USA; USU – Utah State University, (American Entomological Institute collection), Logan, Utah, USA.

Morphological terminology follows that used by Kimsey and Bohart (1991). The hindwing lacks venation, so wing vein characters are only for the forewing. Wing veins are given in the text as abbreviations: Cu = cubital vein, cu-a = cubital-anal cross vein,

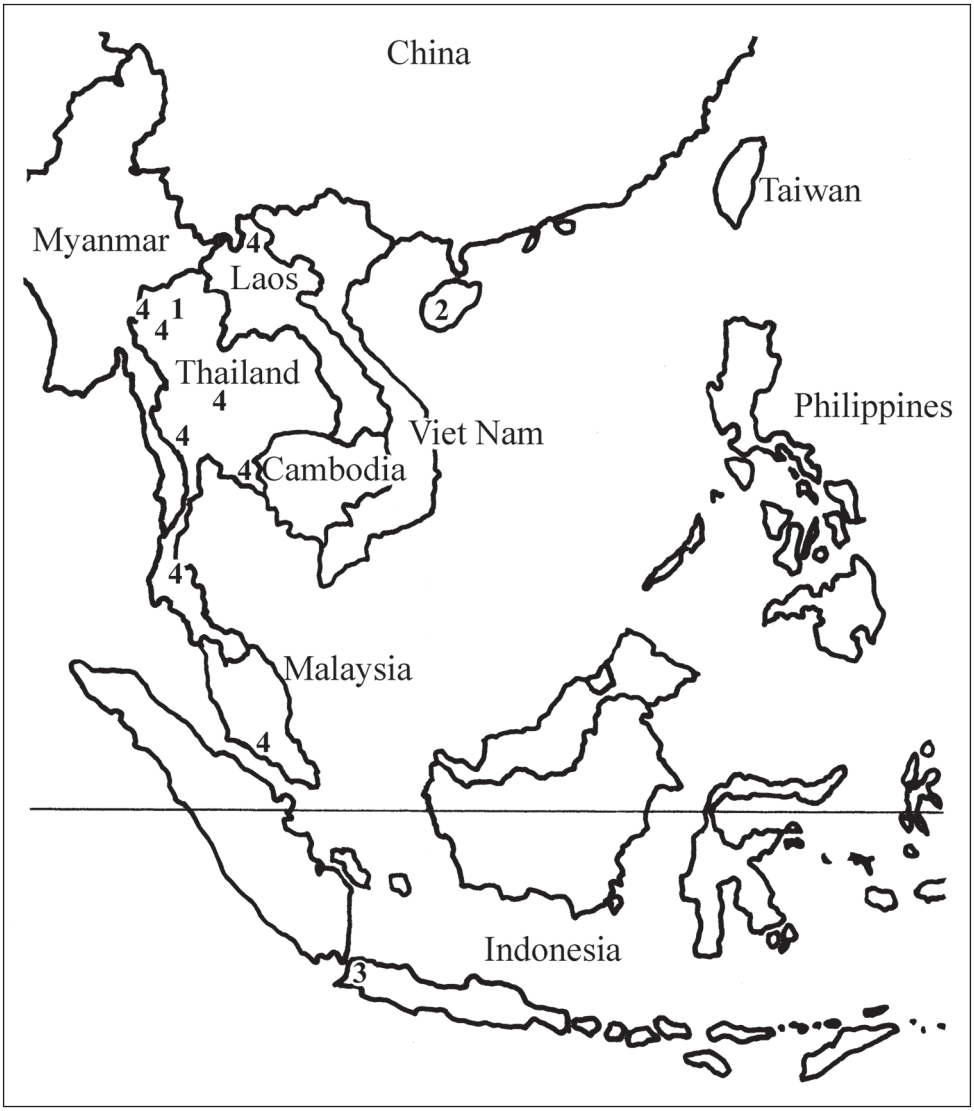


Figure 1. Distribution map of *Rhadinoscelidia* species. **1** *Rh. chaesonensis* **2** *Rh. delta* **3** *Rh. halimunensis* **4** *Rh. malaysiae*.

M = medial vein, R = radial vein, Rs = radial sector, R1 = first radial branch. Head length versus width is measured from the apex of the cervical extension to the furthermost point of the frontal projection and across the widest part of the head in lateral view. Antennal articles are measured at the point of greatest breadth and compared with the total length of the article. Wing veins are compared relative to the length of R1. Pronotal dimensions are measured from the medial length of the pronotum in dorsal view to the distance between the apices of the posterolateral angles.

Systematics

Genus *Rhadinoscelidia* Kimsey

Rhadinoscelidia Kimsey, 1988:77. Type species: *Rhadinoscelidia malaysiae* Kimsey, 1988: 78. Monobasic and original designation.

Diagnosis. *Rhadinoscelidia* is distinguished from *Loboscelidia* by the extreme reduction of the wing venation, short male flagellomeres, slender legs, and, in particular, the strongly constricted postocellar area of the head.

Description. Vertex strongly arched dorsally, with ocelli at apex and sharply declivous posteriorly; genal fringe short, not extending onto cervical plate, separated from ventral surface by carina or flange, with separate anterolateral fringe; male scape length twice or more eye height, without transparent flange; male F-II-X less than twice as long as broad, apical flagellomeres about as long as broad; pronotum narrowed medially in dorsal view, broadly rounded laterally and dorsally, anterior fringe located on anterolateral angle or tubercle, less than 0.25× eye height; mesopleuron with omaulus and without indication of scrobal sulcus; scutum with notauli; scutellum as long as scutum; metanotum narrow and parallel-sided; forewing without A or cu-a, venation occupying less than one-fifth of wing; membrane evenly stained, wing 0.2–0.3× as long as broad; femora with small apical flanges; tibiae without transparent flange.

Distribution. The genus is known from Hainan Island (China) (Liu and Xu 2011), Thailand, Laos (Kimsey1988), Indonesia (West Java) (Kojima, Ubaidillah 1988) and Malaysia (mainland) (Kimsey 1988).

Key to species of *Rhadinoscelidia*

1 Hindtarsal claw edentate; eye small, separated by more than half its diameter from ocelli in lateral view (Figs 9, 10); vertex rounded without carina or line posterior to or laterad of hindocelli (Fig. 10)..... ***chaesonensis*** **Kimsey, sp. n.**

– Hindtarsal claw with one small subsidiary tooth; eye larger, separated by half its diameter or less from ocelli in lateral view (as in Fig. 11); vertex angulate and/or with carina or line posterior to and/or laterad of hindocelli **2**

2 Flagellomere I twice as long as broad; frons with Y-shaped carina extending ventromedially from midocellus; West Java ..... ***halimunensis*** **Ubaidillah**

– Flagellomere I 1.3–1.6× as long as broad; frons with wrinkles or fine carinae radiating ventrally from midocellus..... **3**

3 Vertex without transverse carina or sharp angle behind ocelli; flagellomere XI 1.9× as long as broad; Hainan Is., China..... ***delta*** **Liu, Yao & Xu**

– Vertex with transverse carina or sharp angle behind ocelli; flagellomere XI 1.6–1.7× as long as broad; Laos, Malaysia, Thailand ..... ***malaysiae*** **Kimsey**

Species descriptions

Rhadinoscelidia chaesonensis sp. n.

http://zoobank.org/18CF799F-6494-4426-B3DA-6D6F903F04B3
Figs 9, 10

Diagnosis. This species has distinctively small eyes, in lateral view the eye is separated from the vertex apex by more than half its diameter. In addition, the hindtarsal claw is edentate and the vertex is rounded without a transverse ridge or line.

Female description. Body length 2 mm; forewing length 2.3 mm. *Head:* length 1.8–1.9× height in side view; frontal projection shape rectangular in front view, strongly projecting horizontally; frons with shallow wrinkles radiating ventrally from midocellus (Fig. 10); vertex elevated, but rounded across hindocelli, without low ridge extending from vertex along inner eye margin, cervical expansion broadly curved in profile, with anterolateral patch of longer, dense ribbon-like setae (Figs 9, 10); occiput laterally with low ridge behind eye backed by short row of broad ribbon-like setae; eye separated from hindocellus by more than 0.5 eye length in lateral view; gena without scale-like setae; scape length 5× breadth, 0.9–1.0× head length in side view; flagellomere I length 1.8–2.0× breadth; flagellomere II length 1.2× breadth; flagellomere XI length 1.8× breadth. *Mesosoma*: highly polished and impunctate; pronotal length 1.5× breadth; fore and midfemur with short, erect, apically spatulate setae on dorsal surface; hindtibia nearly asetose; hindtarsal claw edentate; forewing venation 0.13× wing length; R 0.5× as long as Rs; Cu 0.8× as long as M (Fig. 10). *Color*: reddish brown; forewing membrane transparent to brown in bands, veins brown.

Male. Unknown.

Type material. Holotype female: Thailand: Lampang, Chae Son NP, campground/lavatory, 18°49.894'N, 99°28.354'E 467m, Malaise trap, 1-7/v/2008, B. Kwannui & A. Sukpeng leg., T5309 (QSBG). Paratype female: same data as holotype, except 21-30/v/2008, T5305 (BME).

Distribution. Thailand: Lampang Prov.

Etymology. The species is named after the collection site in Chae Son National Park.

Rhadinoscelidia delta Liu, Yao & Xu

Rhadinoscelidia delta Liu, Yao & Xu, 2011: 13. Holotype female; China: Hainan, Mt. Wuzhishan (SCAU).

Diagnosis. The most distinctive features of this species are the rounded vertex, frons with fine carinae radiating ventrally from midocellus and flagellomere I less than twice as long as broad.

Female description. Body length 2.3 mm; forewing length 2.5 mm. *Head:* length twice height in side view; frontal projection rectangular in front view; frons smooth, not microstriate, with low ridge extending from vertex along inner eye margin; vertex without foveae, with transverse carina or fold behind hindocelli; cervical expansion strongly curved in profile, with anterolateral patch of longer, dense ribbon-like setae; occiput laterally with low ridge behind eye backed by short row of broad ribbon-like setae; eye separated from hindocellus by 0.2 eye length in lateral view; gena without scale-like setae; scape length 5× breadth, 0.9–1.0× head length in side view; flagellomere I length 1.3× breadth; flagellomere II length 1.2× breadth; flagellomere XI length 1.9× breadth. *Mesosoma*: integument polished, impunctate; pronotal length 1.2× breadth, apicolateral margin curved; forefemur without spatulate or expanded erect setae on dorsal surface; hindfemur with scattered setae dorsally but nearly asetose ventrally; forewing venation restricted to 0.2× wing length; R 0.5× as long as Rs; Cu 0.9× as long as M. *Color*: brown; forewing membrane transparent to brown in bands, veins brown.

Male. Unknown.

Distribution. China: Hainan Prov.; no specimens examined (information provided by Zia-fu Xu).

Rhadinoscelidia halimunensis Ubaidillah

Rhadinoscelidia halimunensis Ubaidillah in Kojima & Ubaidillah, 2003: 200. Holotype male (?); Indonesia: West Java Gn. Halimun National Park (Museum Bogorense, lost?).

Diagnosis. This species can be distinguished from other *Rhadinoscelidia* species by the frons having a Y-shaped carina and flagellomere I twice as long as broad.

Female. Unknown.

Male description (based on the original description). *Body length* 2.7 mm; forewing length 3.5 mm. *Head:* length 1.9× height in side view; frontal projection shape; frons smooth, not microstriate, with low ridge extending from vertex along inner eye margin; vertex without transverse fovea, vertex expansion strongly curved in profile, without low ridge extending from vertex along inner eye margin, cervical expansion broadly curved in profile, with anterolateral patch of longer, dense ribbon-like setae; occiput laterally with low ridge behind eye backed by short row of broad ribbon-like setae; eye separated from hindocellus by 0.4× eye length in lateral view; gena without scale-like setae; scape length 6.7× breadth, 0.8–0.9× head length in side view; flagellomere I length 1.6× breadth; flagellomere II length 1.5× breadth; flagellomere XI length 1.5× breadth. *Mesosoma*: integument smooth, impunctate; pronotal length as long as broad; fore and midfemur without short, erect, apically broadened setae on dorsal surface; hindtibia nearly asetose; forewing venation 0.15–0.16× wing length; R 0.5× as long as Rs; Cu 0.8× as long as M. *Color*: brown, brown; forewing membrane transparent to brown in bands, veins reddish brown.

Distribution. Indonesia: West Java; no specimens were examined.

Discussion. Both authors have been contacted and the type could not be located. The original illustrations of the abdomen and antennae are proportioned similarly to females in this group and it may very well be that the holotype was actually female.

***Rhadinoscelidia malaysiae* Kimsey**
Figs 2–8, 11

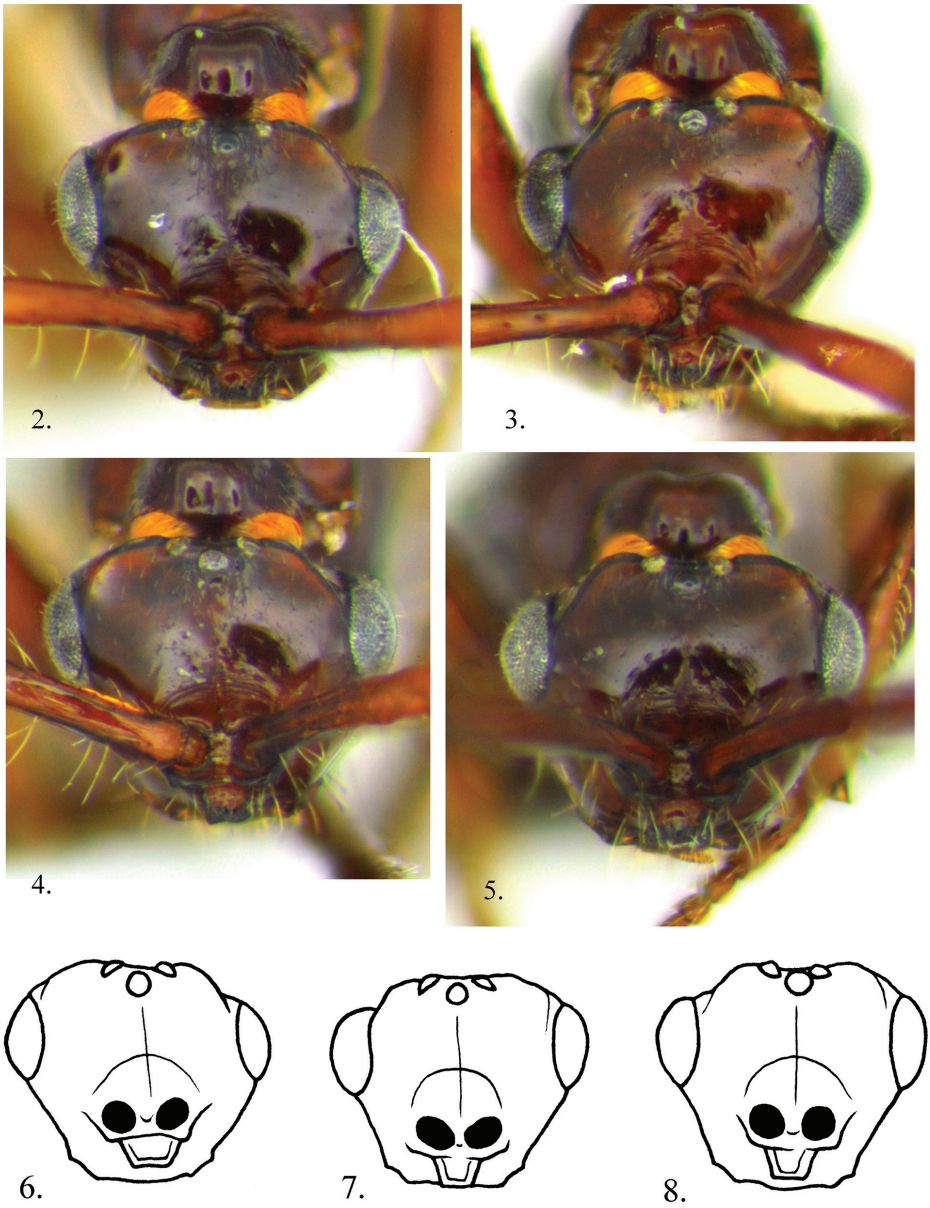
Rhadinoscelidia malaysiae Kimsey, 1988: 78. Holotype male: Malaysia: Pasoh Forest Res., Negri Sembilan (USU).

Diagnosis. This species can be distinguished from the others by the dentate tarsal claw, flagellomere I less than twice as long as broad, the frons smooth without microstriae, and the vertex with a transverse carina or angle.

Female. Unknown.

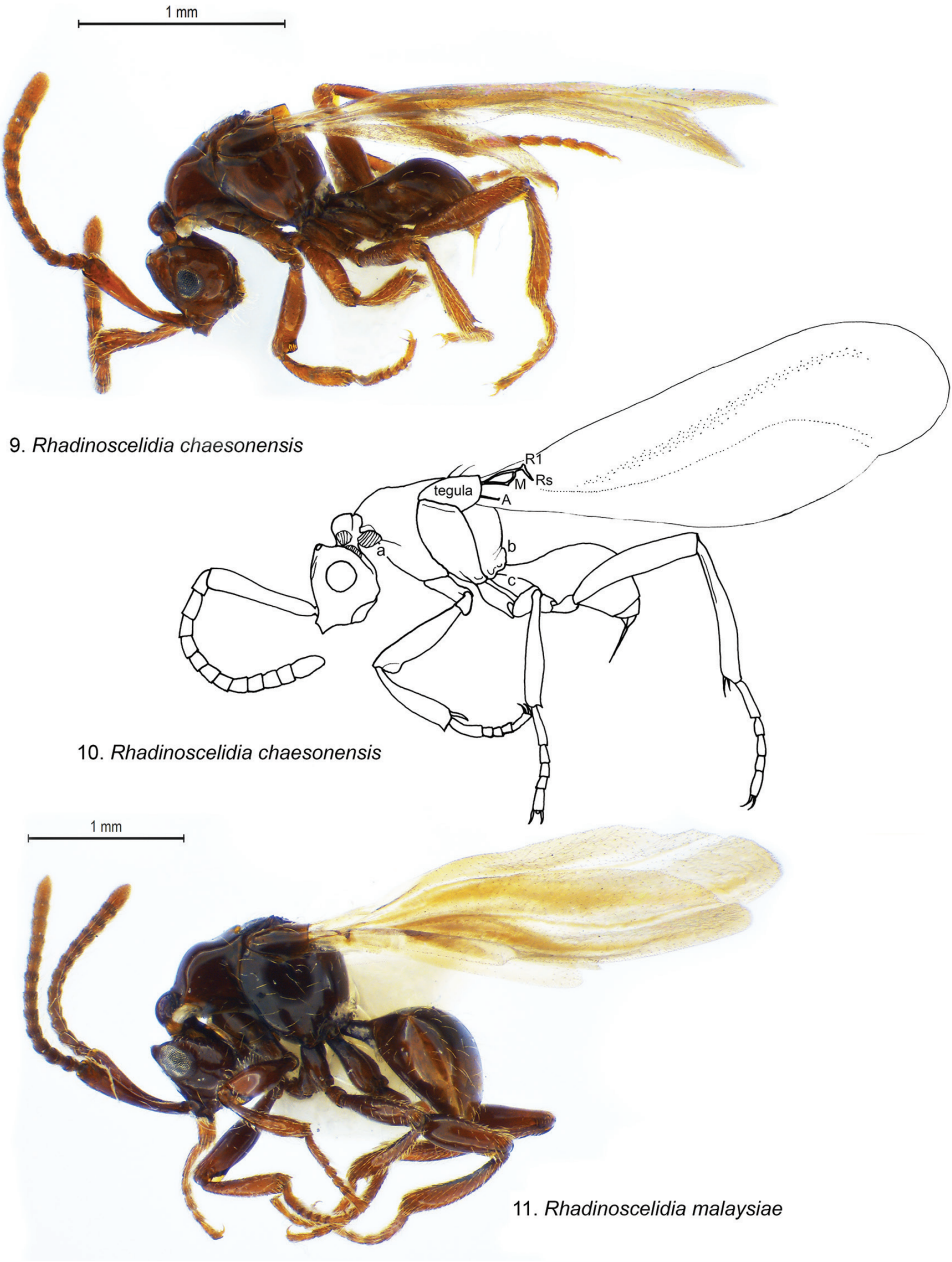
Male description. Body length 2.0–2.5 mm; forewing length 2.3–2.8 mm. *Head:* length 1.8× height in side view; frontal projection rhomboid in front view; frons smooth, not microstriate; vertex without transverse foveae, with low ridge extending from vertex along inner eye margin, cervical expansion strongly curved in profile, with anterolateral patch of longer, dense ribbon-like setae (Fig. 11); occiput laterally with low ridge behind eye backed by short row of broad ribbon-like setae; eye separated from hindocellus by 0.1–0.2 eye length in lateral view (Fig. 11); gena without scale-like setae; scape length 5.4× breadth, 1.0–1.1× head length in side view; flagellomere I length 1.6× breadth; flagellomere II length 1.5× breadth; flagellomere XI length 2.5× breadth. *Mesosoma*: integument smooth, impunctate; pronotal length 1.1× breadth; fore and midfemur with short, erect, apically broadened setae on dorsal surface; hindtibia nearly asetose; forewing venation 0.08–0.10× wing length; R 0.5× as long as Rs; Cu 0.7–0.8× as long as M. *Color*. brown; forewing membrane transparent to brown in bands, veins brown.

Distribution. MALAYSIA: Pasoh Forest Res., Negeri Sembilan. LAOS, **Phongsaly Prov.**: Ban Sano Mai, 21°21'N, 102°03'E, 19–26/v/2004, 1150m, V. Kubáň. THAILAND: **Bangkok**: 180km ne Bangkok, Khao Yei NP, 800m, 10–16/iv/1990, N.T., B.V. Brown; **Chanthaburi Prov.**: Khao Khitchakut NP, Khao Prabaht peak, 12°50.41'N, 102°9.83'E, 875m, Malaise trap, 6–13/iii/2009, Suthida & Charoenchai leg. (T4060); Soi Dao, 14°47.00'N, 101°22.00'E, 7–21/iii/2005, Malaise trap; **Chiang Mai Prov**.: Doi Chiangdao NP Huai Na Lao, 19°24.731'N, 98°55.315'E, 500m, pan trap, 3–8/v/2008, S. Jugsu & A. Watwanich leg. (T5803, T5806, T5809); 19°24.419'N, 98°55.237'E 549m, Malaise trap, 7–14/viii-23–30/ix/2007, S. Jugsu & A. Watwanich leg. (T5668, T5717); 19°24.978'N, 98°54.886'E, 526m, Malaise trap, 18–25/ix/2007, S. Jugsu & A. Watwanich leg. (T5695, T5813); Huai Na Lao, 19°24.731'N, 98°55.315'E, 500m, pan trap, 9–10/v/2008, S. Jugsu & A. Watwanich leg. (T5811); 19°18.803'N, 98°36.395'E, Malaise trap, 13–20/ii/2008, Anuchart & Thawatchai leg.



Figures 2–8. Front view of faces of individual *Rhadinoscelidia malaysiae*. **2–5** Photographs **6–8** Diagrams of Figs 2, 3, 5.

(T5609); **Kanchanaburi Prov.**: Khuean Srinagarindra NP, 14°38.123'N, 98°59.657'E, Malaise trap, 16–23/x/2008, Somboon & Daorueng leg. (T3462); 14°38.312'N, 98°59.643'E, 210m, Malaise trap, 7–14/v/2009, Somboon & Daorueng leg. (T4747); 2–9/iv/2009 (T4788); 14°38.441'N, 98°58.889'E, Malaise trap, 13–20/xi/2008, Som-



Figures 9–11. Lateral view of body. **9, 11** Photographs **10** Diagram. **a–c** possible secretory sites **A** anal vein **M** media **R1** radial vein **Rs** radial sector.

boon & Daorueng leg. (T4423); **Loei Prov.**: Phu Kradueng NP, Nampong/Pong Neep forest unit, 16°56.59'N, 101°41.61'E, 273m, Malaise trap, 26/iv-3/v/2008, Thonghuay Phatai leg. (T5127); **Mae Hong Son Prov.**: Namtok Mae Surin NP, 19°21.593'N,

97°59.254'E, 228m, Malaise trap, 26/viii-2/ix/2007, Manu Namadkum leg. (T5874); **Nakon Si Thammarat Prov.**: Namtok Yong NP, 8°10.434'N, 99°44.508'E 80m, Malaise trap, 2–9/ix/2008, U-prai;K. leg. (T3546); **Phetchabun Prov.**: Nam Nao NP, 16°43.695'N, 101°33.797'E, 921m, Malaise trap, 5–12/v/2007, Leng Janteab, leg. (T2657); 16°43.687'N, 101°33.754'E, 924m, Malaise trap, 19–26/v/2007, Noopean Hongyothi leg. (T2662); Kaeng Krachan NP, 12°47.963'N, 99°27.188'E, Malaise trap, 5–12/ix/2008, Sirichai & Prasit leg. (T4375); 12°49 03'N, 99°21.55'E, Malaise trap, 25–26/vi/2008, B. Brown; **Phitsanulok Prov.**: Thung Salaeng Luang NP, 16°52.64'N, 100°49.44'E, 481m, pan trap, 25–26/iv/2007, Pongpitak leg. (T5205). A total of 28 specimens were examined from BME; CNC, USU , University of California, Riverside, USA; Royal Ontario Museum, Toronto, Canada; Queen Sirikit Botanical Gardens, Thailand), including the holotype.

Discussion. This species probably occurs throughout much of Southeast Asia. Intensive collecting in other regions will probably produce as many specimens as the TIGER project did in Thailand.

Acknowledgements

This study was made possible by the efforts of Michael Sharkey's TIGER project in Thailand and the collaboration of Zai-fu Xu (South China Agricultural University), Doug Yanega (University of California, Riverside) and David Wahl (American Entomological Institute).

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RESEARCH ARTICLE

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Revision of the genus *Hoplocrotaphus* Telenga, 1950 (Hymenoptera, Braconidae, Opiinae)

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Abstract

A revision of the Palaearctic genus *Hoplocrotaphus* Telenga, 1950 (Braconidae, Opiinae) is provided; *H. hamooniae* **sp. n.**, is described and both sexes are illustrated. This genus is recorded for the first time in Iran and Turkmenistan. Illustrated redescriptions of all species are given. An identification key to the species is included.

Keywords

Fly parasitoids, Ichneumonoidea, new species, new records, key, Iran, South Palaearctic

Introduction

The subfamily Opiinae contains more than 2000 described species worldwide (Yu et al. 2016). Opiinae are strictly koinobiont parasitoids of larvae of Diptera – Cyclorrhapha (Wharton 1999) mainly in leaf mines and fruits. The known hosts of about 300 opiine

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species belong predominantly to the families Agromyzidae, Anthomyiidae and Tephritidae (Fischer 1971, 1972, 1977, 1987; Shaw and Huddleston 1991; Yu et al. 2016).

The genus *Hoplocrotaphus* Telenga, 1950 is a small (only three known species) and rarely collected taxon with a South Palaearctic distribution (Yu et al. 2016). The main characters to diagnose the genus are: marginal cell of fore wing very short, vein 1-R1 of fore wing in males thickened, occipital carina widely interrupted dorsally (as in the most part of Opiinae taxa) and far separated from hypostomal carina and not fused with it below near mandible, and face below antennal bases lacking tubercles (Tobias 1986).

According to Telenga (1936) one of the important characters of this genus should be presence of transverse ridge on the temples. However, the revision of the holotype material used for the description of *H. mongolicus* Fischer, 1971, *H. mysteriosus* Fischer, 1971 and *H. pospelovi* Telenga, 1950 showed that only *H. mongolicus* presented such kind of ridge although when type species was checked it looks more as wide subvertical prominence in lower half than a real ridge (Fig. 3E, F). Unfortunately, type specimens of the *H. pospelovi* are without heads (Fig. 7A) and it is impossible to check the real situation with this feature. But according to three conspecific specimens (two males and one female) collected in Turkmenistan in the similar natural condition not far from the species type locality, prominence on temple are completely absent (Fig. 8B, F).

Moreover, it is important to underline the existing incongruence with the species *H. mysteriosus* because of Fischer (1971) included the presence of "ridge" on the temple in the original description. However, when the same specimen used for the description was revised any prominence could be distinguished (Figs 5B–C, 6A).

For the first time *Hoplocrotaphus* is reported from Iran and Turkmenistan. In the present paper a new species, *H. hamooniae* sp. n., is described and illustrated. In addition, illustrated redescriptions of all *Hoplocrotaphus* species and an identification key to species are provided.

Material and methods

The sampling surveys were carried out during 2015 and 2016 around the Hamoon wetlands in the Sistan region (Iran), where *Tamarix stricta* Boiss is the dominant species among the opportunistic salt-tolerant trees and shrubs.

The specimens were collected by light trapping; the trap consists of an incandescent bulb and an actinic fluorescent tube placed on a white sheet. The specimens were sampled by hand and directly emerged in 75% ethanol for subsequent studies. In addition, specimens were collected on *Tamarix* with a modified sweep net. Afterwards, the specimens were chemically treated according to the AXA method (van Achterberg 2009), mounted on triangular cards and labeled.

For the terminology of morphological features, sculpture and measurements see Peris-Felipo et al. (2014); for wing venation nomenclature see van Achterberg (1993). The following abbreviations are additionally used: POL – postocellar line; OOL –

ocular-ocellar line; OD – maximum diameter of lateral ocellus. Material was imaged using a Keyence® VHX-2000 Digital Microscope and Adobe Photoshop® software.

The studied specimens, including the types of *H. hamooniae*, are deposited in the collections of the Entomological Collection at the University of Valencia (Spain; ENV), Department of Plant Protection, Faculty of Agriculture, University of Zabol (Iran; DPPZ), Hungarian Natural History Museum (Budapest, Hungary; HNHM) and Zoological Institute RAS (St Petersburg, Russia; ZISP).

Taxonomy part

Class Hexapoda Blainville, 1816
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Opiinae Leach, 1815
Tribe Opiini Leach, 1815

Genus *Hoplocrotaphus* Telenga, 1950

Type species. *Hoplocrotaphus pospelovi* Telenga, 1950.

Diagnosis. Head (dorsal view) transverse, with rounded temples behind eye. Ocelli weakly enlarged, arranged in triangle with base larger than its sides. Eyes virtually glabrous. Occipital carina widely interrupted dorsally, in the middle and below (lateral view) complete, not fused with hypostomal carina, usually widely separated from hypostomal carinae and independently reached lower margin of head capsule (Figs 1C, 8B). Clypeus moderately narrow and transverse; hypoclypeal cavity present, but narrow. Mandible rather narrow, usually evenly widened towards its base; its upper tooth longer than lower tooth. First flagellar segment of antenna as long as or weakly longer than second segment. Mesosoma short and high. Notauli mainly absent, finely developed on vertical anterior part. Mesoscutal pit always absent. Prescutellar depression (scutellar sulcus) with numerous carinae. Precoxal suture present, smooth, not reaching anterior and posterior margins of mesopleuron. Propodeum completely smooth. Propodeal spiracles relatively small. Hind femur thickened. Hind tibia weakly widened towards apex, shorter than hind tarsus. Pterostigma of fore wing subtriangular, usually rather wide and short. Marginal cell of fore wing strongly shortened, ending far from apex of wing; vein 1-R1 of fore wing thickened (especially in males), not reaching wing apex and shorter than pterostigma length. Vein SR1 of fore wing evenly curved or sometimes sinuate, in male thickened apically. Vein r of fore wing shorter than pterostigma and broad, in male usually thickened. Second submarginal cell of fore wing rather short. Vein m-cu of fore wing distinctly postfurcal, rarely interstitial. First subdiscal cell of fore wing open apically. First metasomal tergite short, widened towards apex, mainly smooth. Ovipositor more or less exerted.

Hoplocrotaphus hamooniae **Peris-Felipo, Belokobylskij & Rakhshani, sp. n.**
http://zoobank.org/CE163734-59B1-437F-B37E-AC63077E0A61
Figures 1, 2

Material examined. Holotype: ♀, IRAN: Sistan-o Baluchestan Province, Zabol- Hamoon wetland, 31°09'03.5"N, 61°20'47.04"E, 477 m, 24.ix.2016, light trap, Nim 245 (H.A. Derafshan leg.) (ENV).

Paratypes. 2♀, same data as holotype (DPPZ); 2♀, same data as holotype but 20.ix.2016, Nim 241 (ZISP) and 13.x.2016 Nim 250 (DPPZ); 1♀, same data as holotype but 31°09'03.5"N, 61°22'46.8"E, 450 m, 19.v.2015, swept on *Tamarix stricta* L., Nim 84 (H.A. Derafshan leg.) (DPPZ); 1♀, same data but, 19.iv.2015, Nim 59 (DPPZ). 1♂, same data as holotype but 20.ix.2016, Nim 101, swept on *Tamarix* sp. (DPPZ).

Comparative diagnosis. This new species resembles *Hoplocrotaphus mongolicus* Fischer, 1971, but differs from it in having the first metasomal tergite 0.6–0.8 times as long as its apical width (1.3 times in *H. mongolicus*), vein 3-SR 0.8 times as long as vein 2-SR (1.3 times in *H. mongolicus*), clypeus 3.7 times as wide as high (6.6 times in *H. mongolicus*), temple in lower half without prominence (Figs 1C, D, 2A) (with distinct prominence on the temple in *H. mongolicus*: Fig. 3B, E, F), occipital carinae widely separated from hypostomal carina (Fig. 1C) (occipital carinae not strongly separated from hypostomal carina in *H. mongolicus:* Figs 3B, 4A), first flagellar segment 2.4 times as long as its maximum width (3.1 times in *H. mongolicus*) and colour of the body light brown (from dark brown to black in *H. mongolicus*).

Description. Female (holotype).

Head. In dorsal view, 1.9 times as wide as median length, 1.1 times as wide as mesoscutum, smooth. Eye in lateral view 1.6 times as high as wide and 1.4 times as wide as temple medially. POL 2.3 times OD; OOL 1.7 times OD. Face 2.4 times as wide as high; inner margins of eyes subparallel. Clypeus 3.7 times as wide as high, slightly curved ventrally. Mandible weakly and evenly widened towards base. Temple in lower half without prominence. Occipital carina ventrally widely separated from hypostomal carinae. Antenna 20-segmented. Scape 1.8 times as long as pedicel. First flagellar segment 2.4 times as long as its apical width, as long as second segment; second segment 2.2 times; third to sixth segments 2.0 times, seventh to ninth segments 1.8 times; 10th to 14th 1.5 times, 15th and 16th 1.3 times; 17th 1.1 times and 18th (apical) segment 2.1 times as long as their maximum width accordingly.

Mesosoma. In lateral view, 1.2 times as long as high. Mesoscutum 0.9 times as long as its maximum width. Posterior mesopleural furrow smooth.

Legs. Hind femur 3.3 times as long as its maximum width. Hind tibia about 6.0 times as long as its maximum subapical width, 0.8 times as long as hind tarsus. First segment of hind tarsus 1.7 times as long as second segment.

Wings. Length of fore wing 2.3 times its maximum width. Marginal cell 3.3 times as long as its maximum width. Vein 1-R1 0.3 times as long as pterostigma, 0.3 times as long as distance between apex of marginal cell and apex of wing. Veins r shorter than

Figure 1. *Hoplocrotaphus hamooniae* sp. n. (**A, C–F** female holotype **B** male paratype) **A–B** Habitus, lateral view **C** Head, lateral view **D** Mandible **E** Antenna **F** Head, frontal view.

pterostigma broad. Vein 3-SR 0.8 times as long as vein 2-SR. Vein m-cu interstitial. Hind wing 3.9 times as long as its maximum width.

Metasoma. First tergite weakly widened towards apex, 0.6 times as long as its apical width. Ovipositor exerted, 0.9 times as long as first tergite, 0.6 times as long as hind femur.

Length. Body 2.1 mm; fore wing 2.1 mm; hind wing 1.7 mm.

Colour. Body, mandible and legs light brown. Antenna light brown in basal part and dark brown in apical part. Wings hyaline. Pterostigma brown.

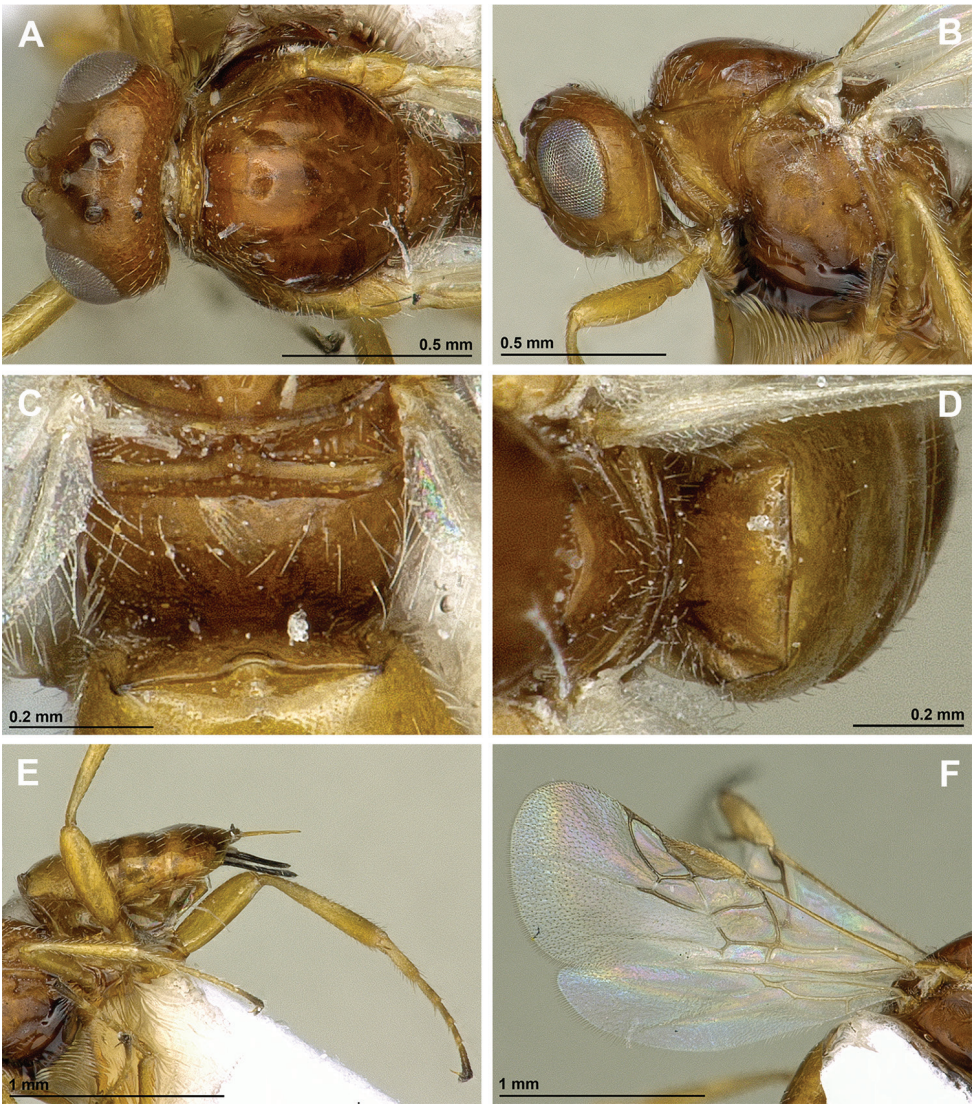

Figure 2. *Hoplocrotaphus hamooniae* sp. n. (female, holotype) **A** Head and mesoscutum, dorsal view **B** Head and mesosoma, lateral view **C** Propodeum, dorsal view **D** First metasomal tergite **E** Legs, metasoma and ovipositor, lateral view **F** Fore and hind wings.

Variation. All females have the same characters and ratios.

Male. Body 2.0 mm; fore wing 2.0 mm; hind wing 1.5 mm. Antenna 21-segmented and first flagellar segment twice as long as its maximum width. Eye in lateral view as wide as temple medially. Mesosoma in lateral view 1.4 times as long as high. First metasomal tergite 0.8 times as long as its apical width. Otherwise similar to female.

Distribution. Iran.

***Hoplocrotaphus mongolicus* Fischer, 1971**
Figures 3, 4

Hoplocrotaphus mongolicus Fischer, 1971: 69; Yu et al., 2016.

Material examined. 1 ♀ (holotype), Mongolia, Central aimak, 12 km S von Somon Bajanbaraat, 1380 m, 13.vii.1967, Exp. Dr. Z. Kaszab (Nr. 918) (HNHM).

Comparative diagnosis. This species is similar to *H. hamooniae* sp. n.; differences between both species are described under the latter species. Moreover, this species is similar to *H. mysteriosus* Fischer, 1971 but differs from it in having the temple in lower half with distinct prominence (Fig. 3B, E, F) (without prominence in *H. mysteriosus*: Fig. 5B, C, E, F), occipital carinae not strongly separated from hypostomal carina (widely separated from hypostomal carina in *H. mysteriosus*), first flagellar segment 3.1 times as long as its maximum width (3.7 times in *H. mysteriosus*), sixth flagellar segment 1.9 times as long as its maximum width (2.9 times in *H. mysteriosus*), POL 2.8 times OD (3.8 times in *H. mysteriosus*), OOL 1.9 times OD (3.5 times in *H. mysteriosus*), hind femur 3.3 times as long as its maximum width (4.0 times in *H. mysteriosus*), first metasomal tergite 1.3 times as long as its apical width (0.8 times in *H. mysteriosus*), marginal cell 3.1 times as long as its maximum width (4.2 times in *H. mysteriosus*), and vein 3-SR 1.3 times as long as vein 2-SR (0.8 times in *H. mysteriosus*).

Re-description. Female (holotype). *Head.* In dorsal view, 1.9 times as wide as median length, 1.3 times as wide as mesoscutum, smooth. Eye in lateral view 1.5 times as high as wide and 1.5 times as wide as temple medially. POL 2.8 times OD; OOL 1.9 times OD. Face 2.4 times as wide as high; inner margins of eyes subparallel. Clypeus 6.6 times as wide as high, slightly curved ventrally. Temple in lower half with distinct prominence. Occipital carina ventrally not widely separated from hypostomal carinae. Mandible weakly and evenly widened towards base. Antenna 15-segmented. Scape 1.5 times as long as pedicel. First flagellar segment 3.1 times as long as its apical width, 1.1 times as long as second segment; second to fourth segments 2.1 times; fifth to 12th 1.9 times, and 13th (apical) segment 2.1 times as long as their maximum width accordingly.

Mesosoma. In lateral view, 1.2 times as long as high. Mesoscutum 0.9 times as long as its maximum width. Posterior mesopleural furrow smooth.

Legs. Hind femur 3.3 times as long as its maximum width. Hind tibia about 7.5 times as long as its maximum subapical width, as long as hind tarsus. First segment of hind tarsus 1.6 times as long as second segment.

Wings. Length of fore wing 2.6 times its maximum width. Marginal cell 3.1 times as long as its maximum width. Vein 1-R1 0.3 times as long as pterostigma, 0.3 times as long as distance between apex of marginal cell and apex of wing. Veins r shorter than pterostigma broad. Vein 3-SR 1.3 times as long as vein 2-SR. Vein m-cu postfurcal. Hind wing 4.1 times as long as its maximum width.

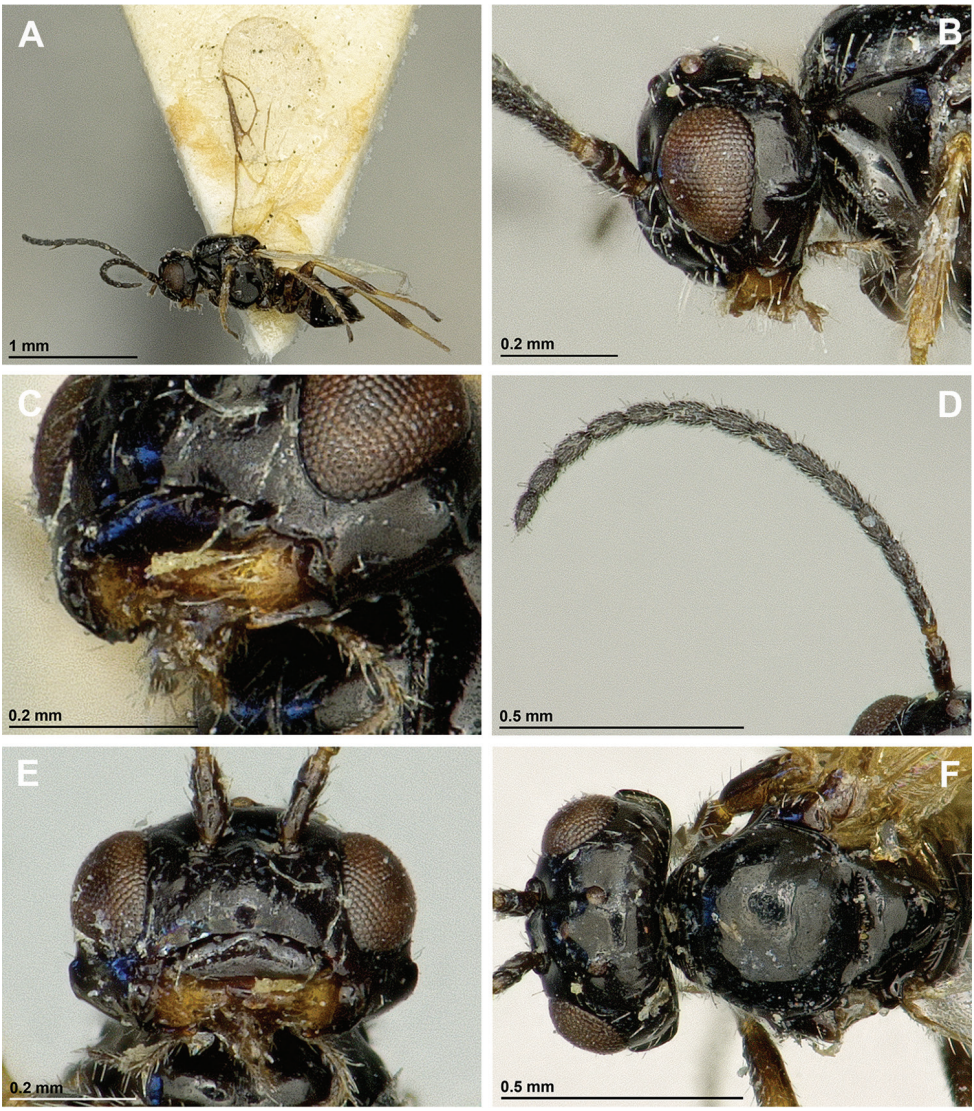

Figure 3. *Hoplocrotaphus mongolicus* Fischer, 1971 (female, holotype) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Head, front view **F** Head and mesoscutum, dorsal view.

Metasoma. First tergite weakly widened towards apex, 1.3 times as long as its apical width. Ovipositor not exerted, 0.5 times as long as first tergite, 0.1 times as long as hind femur.

Length. Body 1.6 mm; fore wing 2.0 mm; hind wing 1.3 mm.

Colour. Body, antenna, coxae and femora black. Mandible brown. Hind tibia light brown in basal part and darkened in apical. Wings hyaline. Pterostigma brown.

Male. Unknown. Distribution. Mongolia.

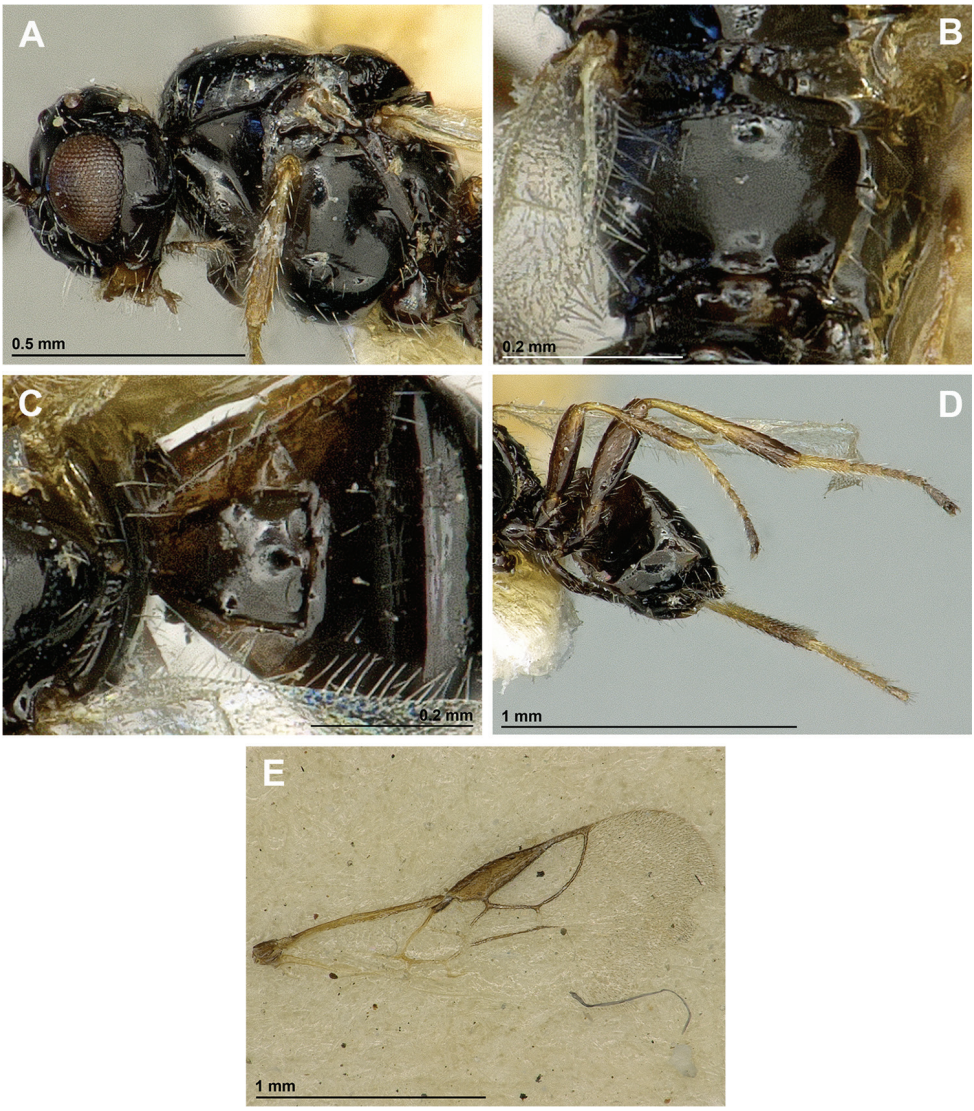

Figure 4. *Hoplocrotaphus mongolicus* Fischer, 1971 (female, holotype) **A** Head and mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Legs, metasoma and ovipositor, lateral view **E** Fore wing.

Hoplocrotaphus mysteriosus **Fischer, 1971**

Figures 5, 6

Hoplocrotaphus mysteriosus Fischer, 1971: 72; Papp, 1982: 243; Tobias and Jakimavicius, 1986: 99; Yu et al., 2016.

Material examined. 1 ♀ (holotype), Mongolia, Bajan-Ölgij aimak, 20 km NNW von der Stadt Ölgij, 2100 m, 2.vii.1968, Exp. Dr. Z. Kaszab (Nr. 1054) (HNHM).

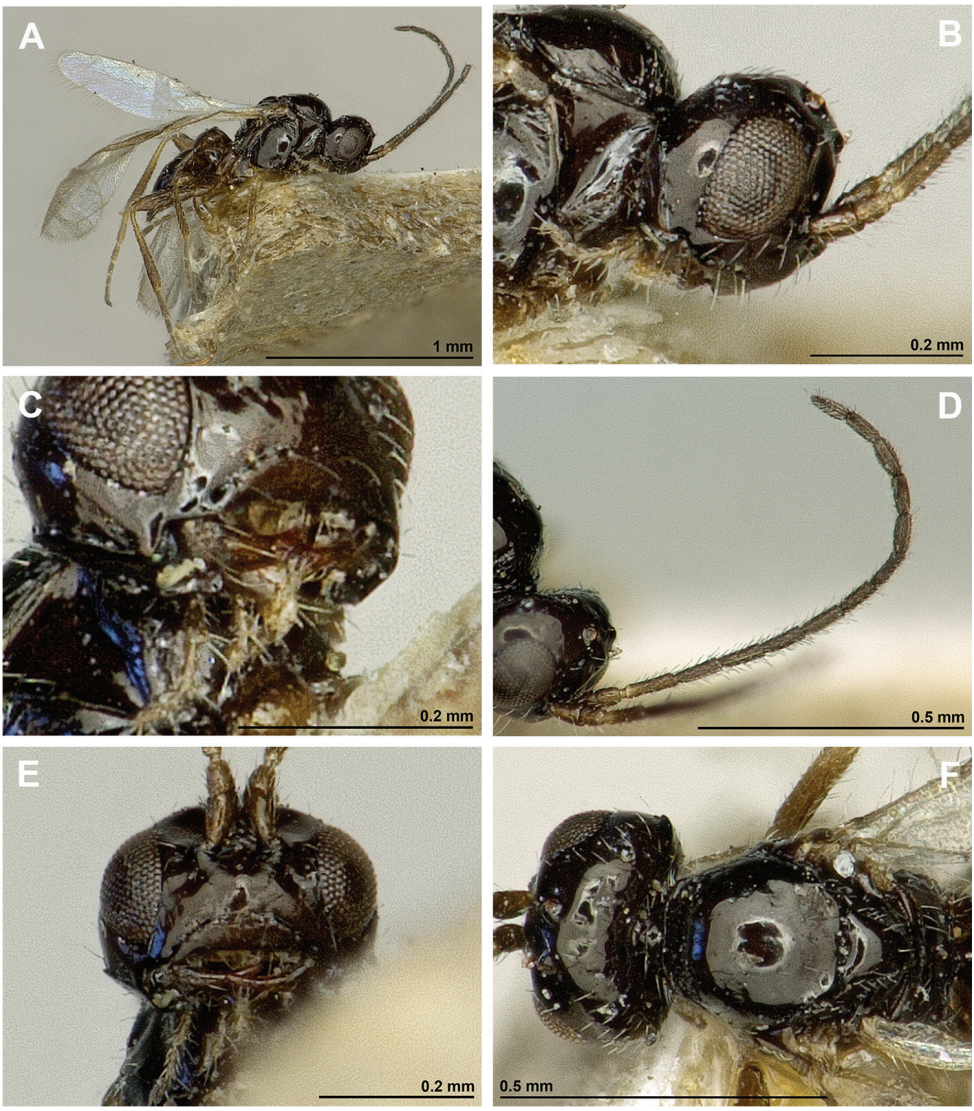

Figure 5. *Hoplocrotaphus mysteriosus* Fischer, 1971 (female, holotype) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Head, front view **F** Head and mesoscutum, dorsal view.

Comparative diagnosis. This species is similar to *H. mongolicus* Fischer; differences between both species are described under the latter species.

Re-description. Female (holotype).

Head. In dorsal view, 1.8 times as wide as median length, 1.3 times as wide as mesoscutum, smooth. Eye in lateral view 1.5 times as high as wide and 1.4 times as wide as temple medially. POL 3.8 times OD; OOL 3.5 times OD. Face 2.6 times as wide as high; inner margins of eyes subparallel. Clypeus 4.4 times as wide as high, slightly curved ventrally. Temple in lower half without prominence. Occipital carina ventrally

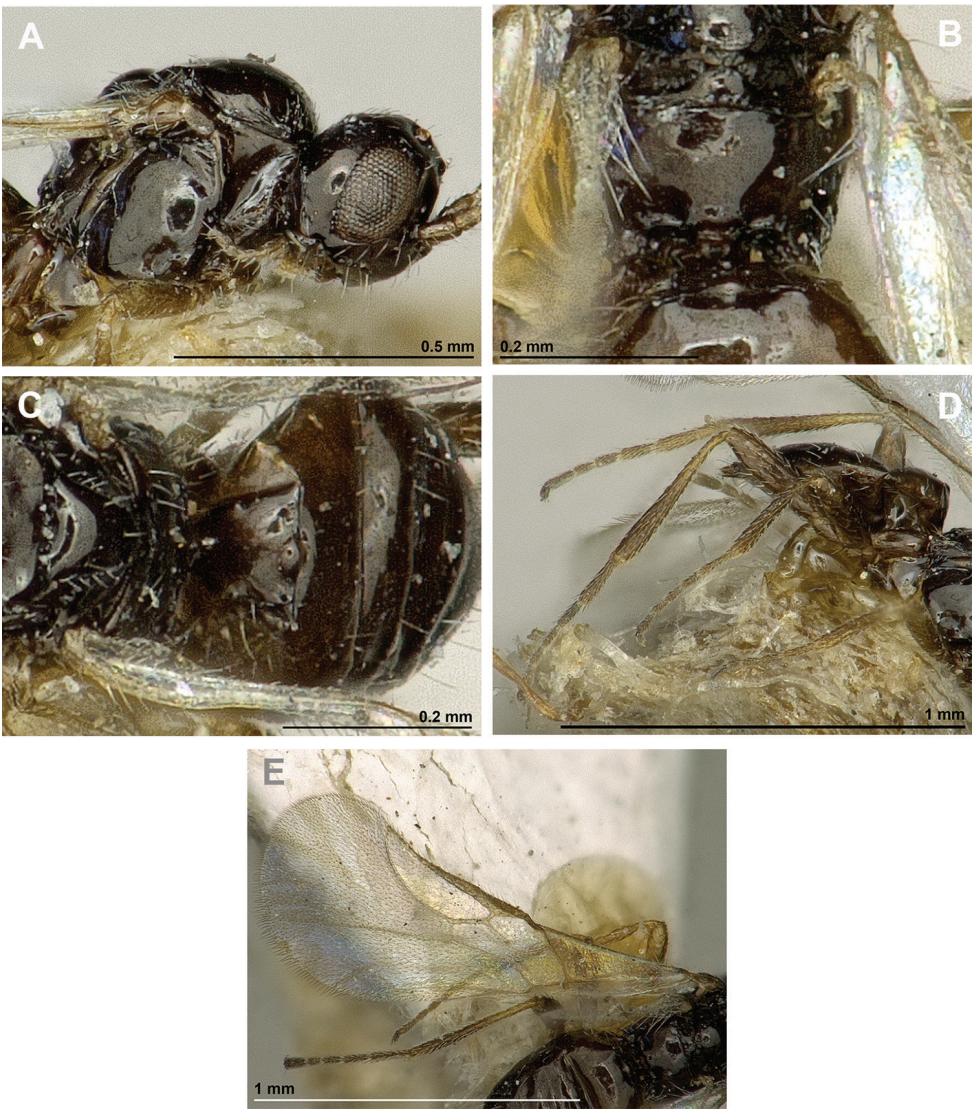

Figure 6. *Hoplocrotaphus mysteriosus* Fischer, 1971 (female, holotype) **A** Head and mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Legs, metasoma and ovipositor, lateral view **E** Fore wing.

rather widely separated from hypostomal carinae. Mandible weakly and evenly widened towards base. Antenna 14-segmented. Scape 1.5 times as long as pedicel. First flagellar segment 3.7 times as long as its apical width, 1.1 times as long as second segment; second and third segments 3.3–3.4 times; fourth and fifth 3.1 times; sixth to 11th 2.9 times, and 12th (apical) segment 3.1 times as long as their maximum width accordingly.

Mesosoma. In lateral view, 1.1 times as long as high. Mesoscutum about as long as its maximum width. Posterior mesopleural furrow smooth.

Legs. Hind femur 4.0 times as long as its maximum width. Hind tibia 8.2 times as long as its maximum subapical width, about as long as hind tarsus. First segment of hind tarsus 1.7 times as long as second segment.

Wings. Length of fore wing 3.0 times its maximum width. Marginal cell 4.2 times as long as its maximum width. Vein 1-R1 0.3 times as long as pterostigma, 0.5 times as long as distance between apex of marginal cell and apex of wing. Veins r shorter than pterostigma broad. Vein 3-SR 0.8 times as long as vein 2-SR. Vein m-cu distinctly postfurcal. Hind wing 4.2 times as long as its maximum width.

Metasoma. First tergite widened towards apex, 0.8 times as long as its apical width. Ovipositor not exerted, 0.4 times as long as first tergite, 0.1 times as long as hind femur. *Length.* Body 1.2 mm; fore wing 1.5 mm; hind wing 1.1 mm.

Colour. Body, antenna, mandible and legs dark brown. Wings hyaline. Pterostigma brown.

Male. Unknown.

Distribution. Mongolia, Romania.

Hoplocrotaphus pospelovi **Telenga, 1950**

Figures 7–9

Hoplocrotaphus pospelovi Telenga, 1950: 303; Tobias and Jakimavicius, 1986: 99; Yu et al., 2016.

Material examined. 1 male (lectotype, here designated), (head and antenna missing), Kazakhstan (not Uzbekistan, as in original description), "peski [sands] Koy-Temo, bl.[iz] [near] Terekshy, Priaral[skie] Karakumy [Priaral Kara-Kum], E. Luppova, 9.ix.[1]930", "*Hoplocrotaphus pospelovi* g. et sp. n., N. Telenga det." (ZISP); 1 male (?) (paralectotype), (mostly destroyed, only mesosoma and middle legs are presented on pin), Kazakhstan (not Uzbekistan, as in original description), golden circle, "peski [sands] Koylibay, M.[alye] Barsuki, Turg.[ay], Luppova, 30.vi.[1]931", "*Hoplocrotaphus pospelovi* g. et sp. n., N. Telenga det." (ZISP); 1 female, 2 males, Turkmenistan, "TSSR, Repetek, V. Tobias", 24 and 25.VI.1987 (ZISP).

Comparative diagnosis. This species is similar to *H. hamooniae* sp. n., but differs by having the mandible basally with distinct ventral lobe (without ventral lobe in *H. hamooniae*), first flagellar segment 3.3 times as long as its maximum width (2.4 times in *H. hamooniae*), sixth flagellar segment 2.6 times as long as its maximum width (2.0–2.1 times in *H. hamooniae*), marginal cell 2.0 times as long as its maximum width (3.3 times in *H. hamooniae*), OOL 2.8 times OD (1.7 times in *H. hamooniae*), and clypeus 4.6 times as wide as high (3.7 times in *H. hamooniae*).

Re-description. Male (lectotype and additional specimen).

Head. In dorsal view, 2.1 times as wide as median length, 1.3 times as wide as mesoscutum, smooth. Eye in lateral view 1.4 times as high as wide and 1.3 times as wide as temple medially. POL 2.8 times OD; OOL 2.8 times OD. Face 2.4 times as wide

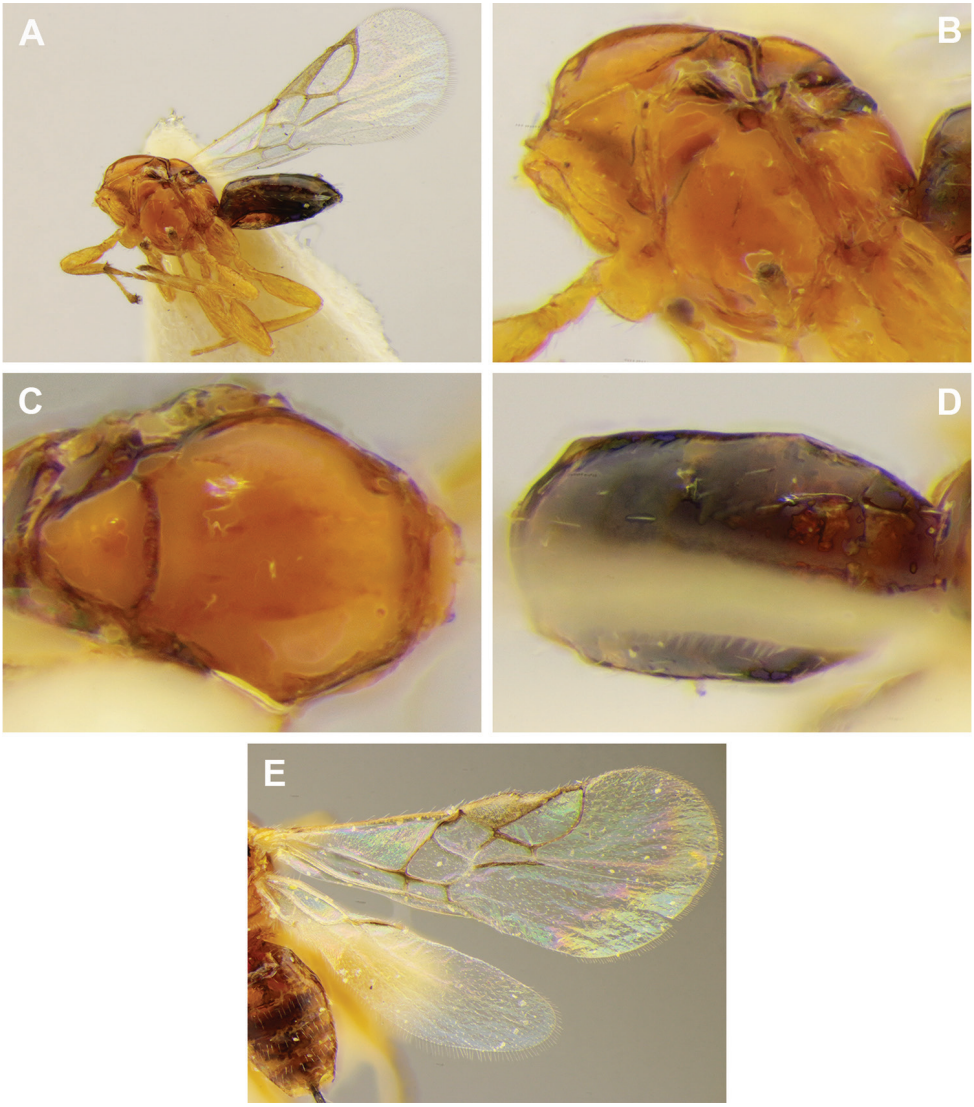

Figure 7. *Hoplocrotaphus pospelovi* Telenga, 1950 (**A–D** lectotype: male **E** specimen from Turkmenistan, female) **A** Habitus, lateral view **B** Mesosoma, lateral view **C** Mesoscutum, dorsal view **D** Metasoma, dorsal view **E** Fore and hind wings.

as high; inner margins of eyes subparallel. Clypeus 4.6 times as wide as high, slightly curved ventrally. Temple in lower half without prominence. Occipital carina ventrally widely separated from hypostomal carinae. Mandible basally with distinct ventral lobe. Antenna 17- segmented. Scape 1.5 times as long as pedicel. First flagellar segment 3.3 times as long as its apical width, 1.2 times as long as second segment; second segment 2.8 times; third to eighth segments 2.5–2.6 times; ninth to 14th 2.3 times, and 15th (apical) segment 3.3 times as long as their maximum width accordingly.

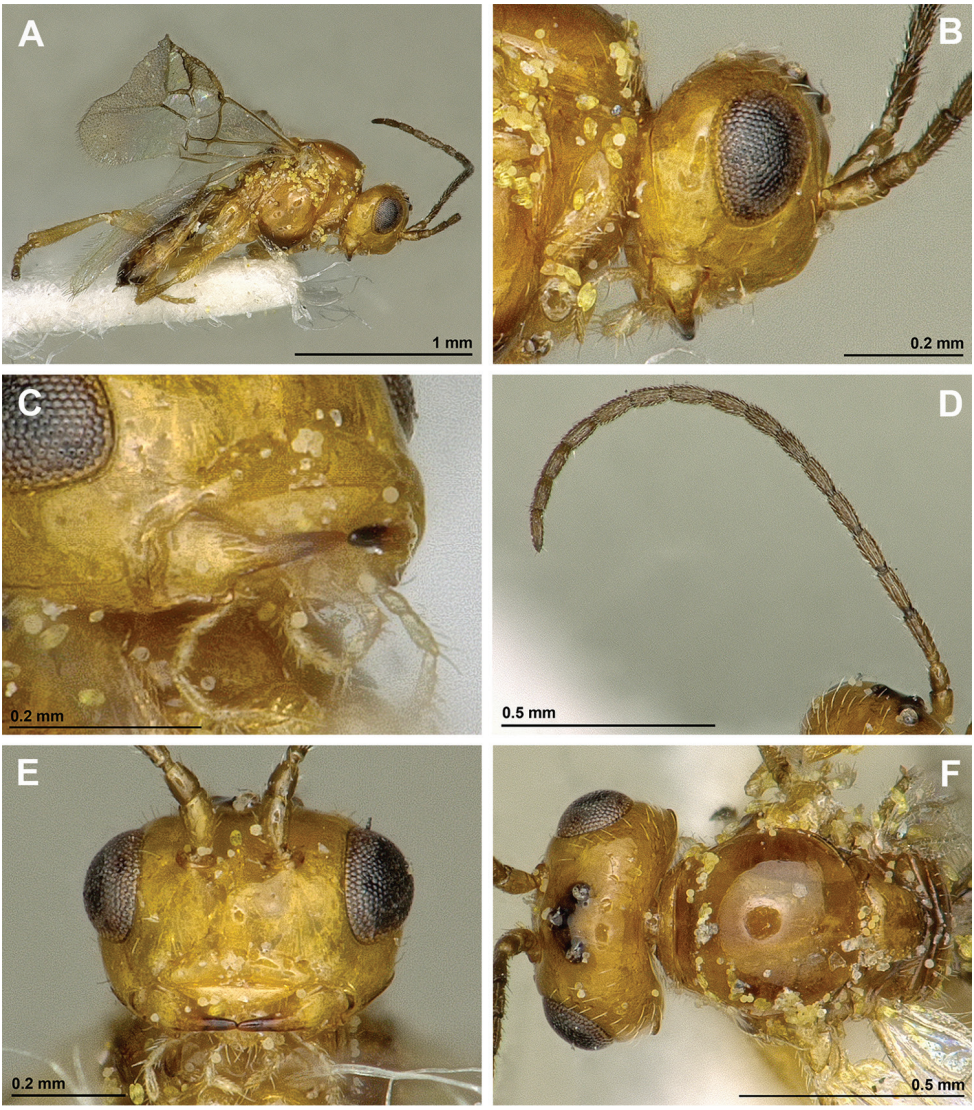

Figure 8. *Hoplocrotaphus pospelovi* Telenga, 1950 (male, specimen from Turkmenistan) **A** Habitus, lateral view **B** Head, lateral view **C** Mandible **D** Antenna **E** Head, front view **F** Head and mesoscutum, dorsal view.

Mesosoma. In lateral view, 1.3 times as long as high. Mesoscutum almost as long as its maximum width. Posterior mesopleural furrow smooth.

Legs. Hind femur 3.1 times as long as its maximum width. Hind tibia 6.5 times as long as its maximum subapical width, 1.1 times as long as hind tarsus. First segment of hind tarsus 1.5 times as long as second segment.

Wings. Length of fore wing 2.4 times its maximum width. Marginal cell 2.6 times as long as its maximum width. Vein 1-R1 0.25 times as long as pterostigma, 0.25 times as long as distance between apex of marginal cell and apex of wing. Veins r distinctly

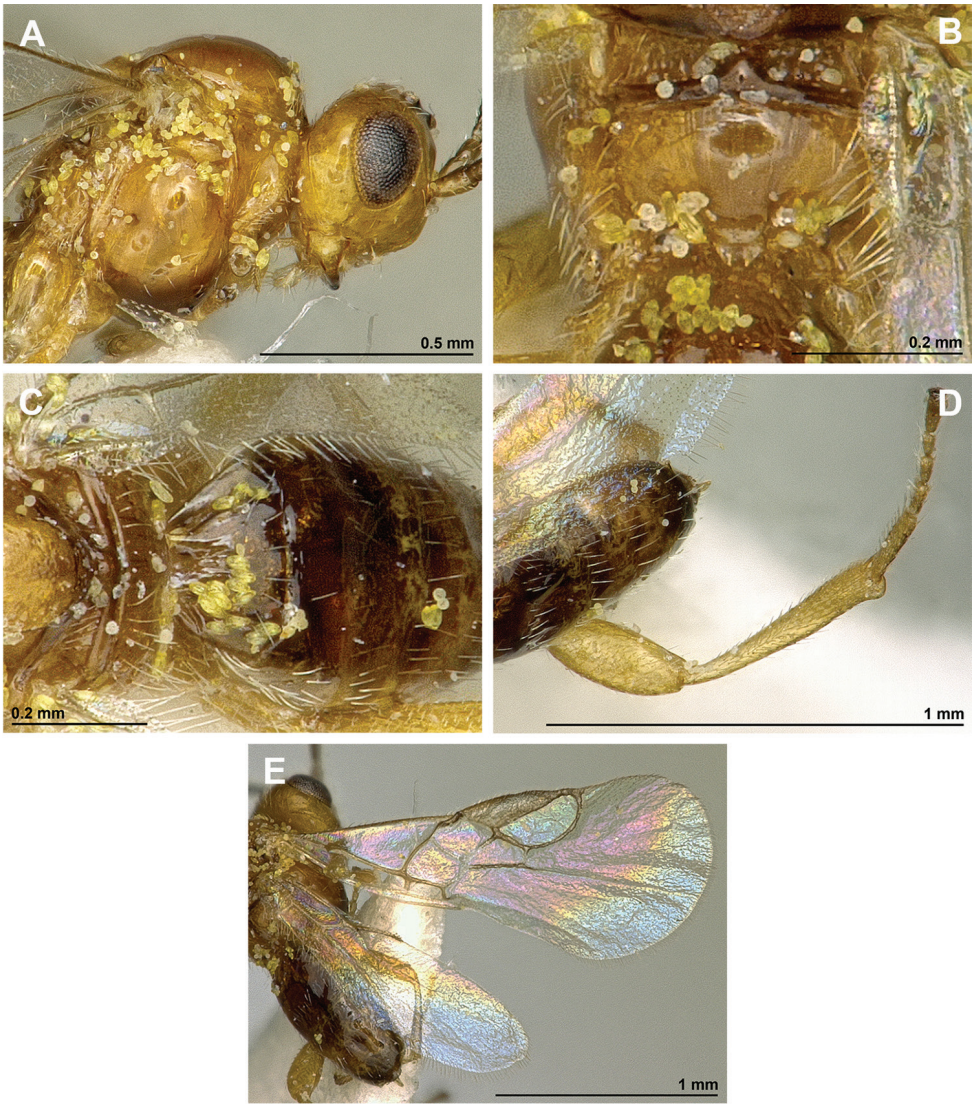

Figure 9. *Hoplocrotaphus pospelovi* Telenga, 1950 (male, specimen from Turkmenistan) **A** Head and mesosoma, lateral view **B** Propodeum, dorsal view **C** First metasomal tergite **D** Leg, lateral view **E** Fore and hind wings.

shorter than pterostigma broad. Vein 3-SR 0.9 times as long as vein 2-SR. Vein m-cu distinctly postfurcal. Hind wing 4.5 times as long as its maximum width.

Metasoma. First tergite widened towards apex, 0.9 times as long as its apical width.

Length. Body 1.3 mm; fore wing 1.5 mm; hind wing 1.2 mm.

Colour. Body mainly and legs light brown. Antenna brown. Metasoma dark brown. Wings hyaline. Pterostigma brown.

Variation. Body length 1.9 mm; fore wing 1.8 mm; hind wing 1.5 mm. *Head.* In dorsal view, 1.9 times as wide as median length, 1.4 times as wide as mesoscutum. Eye

in lateral view 1.4 times as high as wide and 1.25 times as wide as temple medially. POL 2.3 times OD; OOL 2.0 times OD. Face 1.6 times as wide as high. Clypeus 3.4 times as wide as highly. Scape 1.4 times as long as pedicel. First flagellar segment 2.7 times as long as its apical width, 1.1 times as long as second segment; second segment 2.6 times; following segments 2.4–2.5 times; and 15th (apical) segment 3.0 times as long as their maximum width accordingly. *Mesosoma.* In lateral view, 1.1 times as long as high. *Legs.* Hind femur 2.6–2.7 times as long as its maximum width. Hind tibia 5.5–5.7 times as long as its maximum subapical width. First segment of hind tarsus 1.8 times as long as second segment. *Wings.* Length of fore wing 2.3 times its maximum width. Marginal cell 3.1 times as long as its maximum width. Vein 1-R1 0.26–0.28 times as long as pterostigma, 0.24–0.26 times as long as distance between apex of marginal cell and apex of wing. Hind wing 3.9–4.0 times as long as its maximum width.

Metasoma. First tergite 0.7–0.8 times as long as its apical width. Antenna dark brown.

Female. *Head.* In dorsal view, 2.0 times as wide as median length. Eye in lateral view 1.3 times as high as wide and 1.4 times as wide as temple medially. POL 2.0 times OD; OOL 2.3 times OD. Inner margins of eyes weakly divergent below. Clypeus 3.0 times as wide as high. Antenna more than 6-segmented (apical segments missing). Scape 1.7 times as long as pedicel. First flagellar segment 3.2 times as long as its apical width, 1.2 times as long as second segment.

Mesosoma. In lateral view, 1.1 times as long as high. Mesoscutum 1.15 times as long as its maximum width.

Legs. Hind femur 3.0 times as long as its maximum width. Hind tibia 5.3 times as long as its maximum subapical width, almost as long as hind tarsus. First segment of hind tarsus 1.8 times as long as second segment.

Wings. Length of fore wing 2.4 times its maximum width. Marginal cell 2.6 times as long as its maximum width. Vein 1-R1 0.3 times as long as pterostigma, 0.2 times as long as distance between apex of marginal cell and apex of wing. Vein 3-SR as long as vein 2-SR. Hind wing 3.6 times as long as its maximum width.

Metasoma. First tergite 0.8 times as long as its apical width. Ovipositor distinctly exerted, 1.2 times as long as first tergite, 0.6 times as long as hind femur.

Length. Body 1.9 mm; fore wing 2.3 mm; hind wing 1.6 mm. Otherwise similar to male.

Distribution. Kazakhstan, Turkmenistan (new record).

Key to species of the genus *Hoplocrotaphus* Telenga

1 Mandible basally with rather distinct ventral lobe (Fig. 8C). Marginal cell 2.6–3.1 times as long as its maximum width (Figs 7E, 9E). – Antenna 17-segmented. Body length 1.3–2.1 mm. Body yellowish to orange. Kazakhstan, Turkmenistan..... ***H. pospelovi* Telenga (♀♂)**

– Mandible basally without ventral lobe (Figs 1D, 3C, 5C). Marginal cell 3.1–4.2 times as long as its maximum width (Figs 2F, 4E, 6E). **2**

2 Marginal cell of fore wing 4.2 times as long as its maximum width (Fig. 6E). Hind femur 4.0 times as long as its maximum width (Fig. 6D). First flagellar segment of ♀ 3.7 times as long as its maximum width (Fig. 5D). POL 3.8 times OD. OOL 3.5 times OD (Fig. 5F). – Antenna 14-segmented. Body length 1.2 mm. Body black to dark brown. Mongolia, Romania..... ***H. mysteriosus* Fischer (♀)**

– Marginal cell of fore wing 3.1–3.3 times as long as its maximum width (Figs 2F, 4E). Hind femur 3.3 times as long as its maximum width (Figs 2E, 4D). First flagellar segment of ♀ 2.4–3.1 times as long as its maximum width (Figs 1C, 3D). POL 2.3–2.8 times OD. OOL 1.7–1.9 times OD (Figs 2A, 3F). Antenna 15–21-segmented.....**3**

3 Temple in lower half with distinct subvertical prominence (Fig. 3B, C, E, F). Occipital carina ventrally not widely separated from hypostomal carinae (Fig. 3B, E). Body black to dark brown (Fig. 3A). First metasomal tergite 1.3 times as long as its apical width (Fig. 4C). Vein m-cu of fore wing distinctly postfurcal (Fig. 4E). Vein 3-SR of fore wing 1.3 times as long as vein 2-SR (Fig. 4E). Clypeus 6.6 times as wide as high (Fig. 3E). First flagellar segment of ♀ 3.1 times as long as its maximum width (Fig. 3D). Antenna 15-segmented. Body length 1.6 mm. Mongolia..... ***H. mongolicus* Fischer (♀)**

– Temple in lower half without distinct subvertical prominence (Figs 8B, E, F, 9A). Occipital carina ventrally not widely separated from hypostomal carinae (Figs 3B, C). Body light brown (Fig. 1A, B). First metasomal tergite 0.6–0.8 times as long as its apical width (Fig. 2D). Vein m-cu of fore wing interstitial (Fig. 2F). Vein 3-SR of fore wing 0.8 times as long as vein 2-SR (Fig. 2F). Clypeus 3.7 times as wide as high (Fig. 1D). First flagellar segment of ♀ 2.4 times as long as its maximum width (Fig. 1E). Antenna 20–21-segmented. Body length 2.0–2.1 mm. Iran..... ***H. hamooniae* sp. n. (♀♂)**

Discussion

The new species was found in association with *Tamarix stricta* Boiss. around Hamoon wetland during spring (April–May) and autumn (September–October). The absence during the hot summer period suggests two generations per year. These specimens were collected mainly early at night by light trapping at ground level, while no specimens were found in light traps mounted more than one meter above ground level during the whole year. The specimens share the pale body colour, but there is no morphological evidence of nocturnal activity (for example, enlarged compound eyes and ocelli: Tobias 1966), both are normal in size. It is likely that the parasitoids normally escape from the extremely hot weather during daytime by hiding among the *Tamarix* branches. The wing morphology has clues about flight ability and habitat preference (Quicke 2015). There is no evidence of the possible host of *H. hamooniae* sp. n. (as well as for other *Hoplocrotaphus* species) among the various mining dipterous larvae available on the wetland plants.

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RESEARCH ARTICLE

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Review of the *mandibularis* group of the genus *Dolichomitus* (Hymenoptera, Ichneumonidae, Pimplinae)

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Abstract

The *mandibularis* group of the genus *Dolichomitus* is reviewed. Three species are recognized, including a new species, *Dolichomitus flavicrus* **sp. n.** from Japan. The new species is closely related to *Dolichomitus khasianus* Gupta & Tikar, in having an entirely blackish underside of the metasoma, but can be separated from the latter by the smooth antero-median part of the first metasomal tergite between the latero-median carinae and a short longitudinal dark stripe on the posterior surface of the fore femur. A key to species of the *mandibularis* group is provided. Mitochondrial COI gene sequences were generated for *D. mandibularis* (Uchida) and *D. flavicrus* **sp. n.** to permit future comparisons.

Keywords

new species, Japan, description, parasitoid, *Pterocarya*, borer

Introduction

Dolichomitus Smith is a relatively large genus containing more than seventy species predominantly distributed in the Holarctic region but also extending to the Oriental and Neotropical regions (Gauld 1990, Yu et al. 2011). The *mandibularis* group, first recognized by Gupta and Tikar (1976), is one of the 9 species groups of the genus (Townes and Townes 1960, Gupta and Tikar 1976, Gauld 1991), characterized by the medially strongly bent mandibles with a shorter lower tooth. Two species of this group have

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been known, viz., *Dolichomitus khasianus* Gupta & Tikar from India and *Dolichomitus mandibularis* (Uchida) from Japan. Recently an additional species was discovered in Honshu, Japan and it turned out to be new to science through comparison with the types of known species.

Materials and methods

Both the holotypes of *Dolichomitus mandibularis* and *Dolichomitus khasianus* were borrowed from the Laboratory of Systematic Entomology, Hokkaido University, Japan (**SEHU**), and Zoologische Staatssammlung München, Germany (**ZSM**), respectively. The type specimens of the new species and other specimens examined are preserved in the collection of Osaka Museum of Natural History (**OMNH**) except for one paratype in the Natural History Museum, London (**BMNH**). External structures of specimens were observed under a steremicroscope (Nikon SMZ-800) and KEYENCE VHX-1000 digital microscope. Figures were prepared using the focus stacking function (combining several partially focused images) of the latter and the high resolution shot function of an Olympus E-M5 Mark II digital camera with 60 mm macro lens. See Matsumoto (2016) for DNA extraction, PCR and sequencing protocols. The INSD accession numbers for each sequence are mentioned in the specimens examined section. Terminology of adult morphology follows Gauld (1991).

Taxonomy

The *mandibularis* group of the genus *Dolichomitus*

The main recognition characters of the genus *Dolichomitus* are: tip of lower valve of ovipositor with a dorsal lobe that partially encloses tip of upper valve; dorsally complete occipital carina; T2 with basal oblique groove longitudinal rather than transverse; vein Rs+M of fore wing opposite vein cu-a; vein Cu1 of hind wing separated from M by less than 1.0× length of cu-a; upper tooth of mandible as long as lower tooth or longer (in *mandibularis* group and in some other species).

Among members of the genus *Dolichomitus*, the *mandibularis* group can easily be distinguished by the medially strongly bent mandibles (Fig. 1a).

Dolichomitus flavicrus Matsumoto, sp. n.

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Figs 1a–d, f, h, 2, 3

Description. Female. Head (Fig. 1a). Antennal flagellum with 40–41 segments; face densely covered with pubescence, between antennal socket and supraclypeal suture 0.5×

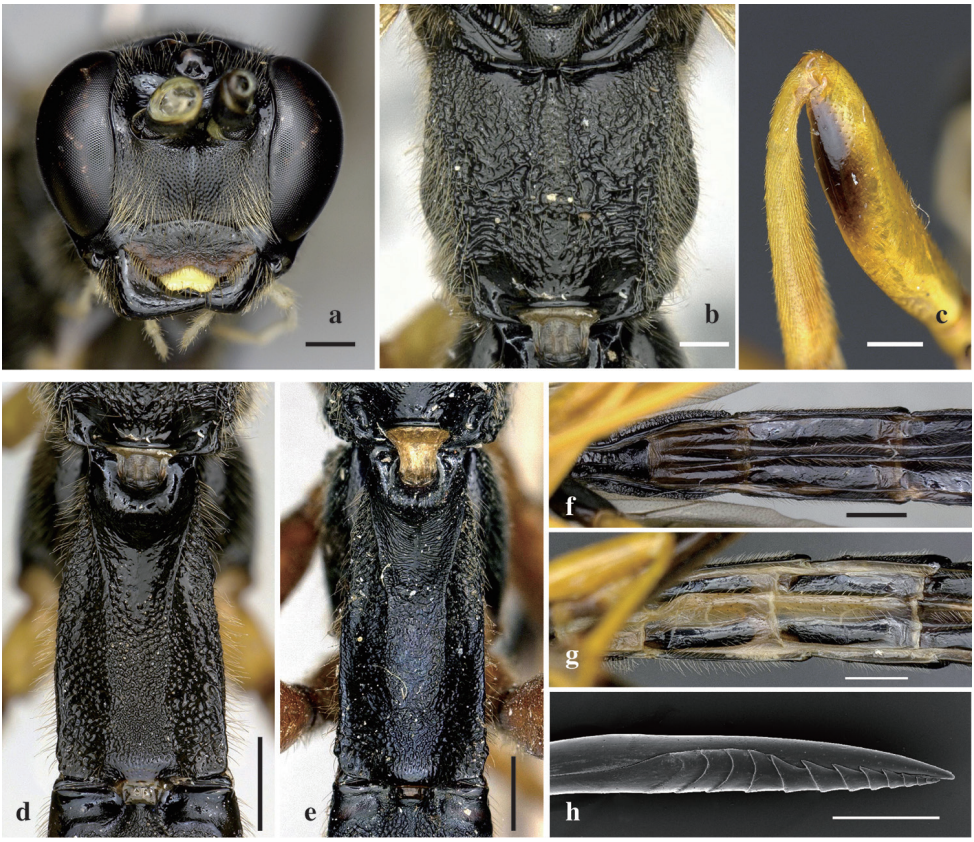

Figure 1. *Dolichomitus* species of the *mandibularis* group: **a–d, f, h** *D. flavicrus* sp n. (paratype) **e** *D. khasianus* (Holotype) **g** *D. mandibularis* **a** head in frontal aspect **b** propodeum in dorsal aspect **c** fore femur in posterior aspect **d, e** first metasomal tergite in dorsal aspect **f, g** first to third metasomal segments in ventral aspect **h** ovipositor tip in lateral aspect. Scale bars: 0.5mm (**a, b, c, h**); 1mm (**d, e, f, g**).

as long as its minimum width between eyes; clypeus flat, about 2.3× as wide as high, with apical margin bilobed, deeply incised medially; distance between eye and lateral ocellus 1.5× as long as maximum diameter of latter; mandible moderately tapered, at middle about 0.5× as wide as basal width; malar space about 0.3× basal width of mandible; vertex with inter-ocellar area weakly raised; outline of gena moderately rounded in dorsal view.

Mesosoma. Pronotum with anterior edge incised medially, medially thickened to form a posteriorly directed tooth, followed by median longitudinal groove reaching to posterior margin; epomia curved, lower end turning backwards; mesoscutum in front of scuto-scutellar groove 1.5–1.6× as long as wide in dorsal view, covered with moderately dense pubescence; mesopleuron moderately punctate and pubescent, with area below episternal scrobe moderately depressed, mesopleural suture distinctly foveolate, below episternal scrobe, foveae indistinct above episternal scrobe; scutellum moderately convex; metapleuron moderately convex medially, entirely reticulate-ru-

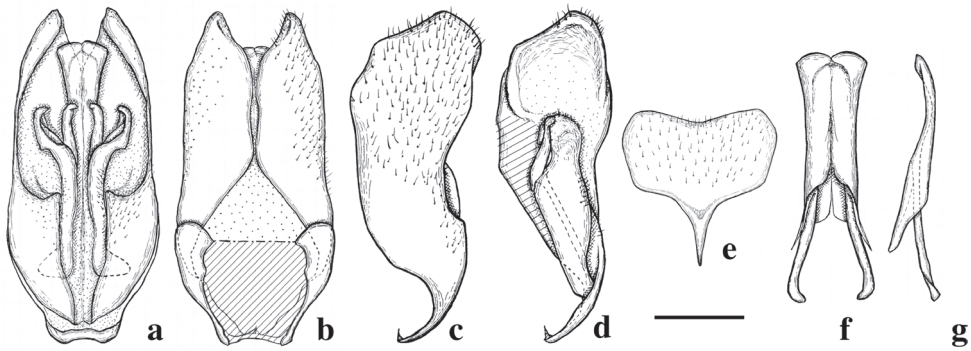

Figure 2. Male genitalia of *D. flavicrus* sp. n. (paratype): **a** ventral aspect **b** dorsal aspect **c** paramere, lateral aspect **d** paramere, inner aspect **e** subgenital plate, ventral aspect **f** aedeagus, ventral aspect **g** aedeagus, lateral aspect. Scale bar: 1 mm.

gose; propodeum (Fig. 1b) entirely reticulate-rugose, moderately densely covered with pubescence, with lateromedian longitudinal carinae present from base to middle, almost replaced by wrinkles; lateral longitudinal carina indistinct anteriorly, replaced by rugosity; submetapleural carina distinct, posteriorly fused with fine ventral transverse wrinkles in front of each hind coxal cavity.

Wings (Fig. 3a). Fore wing with vein Rs+M opposite cu-a; 2rs-m as long as 3rs-m, slightly shorter than vein M between 2rs-m and 2m-cu; vein M between 3rs-m and 2m-cu about 0.2× length of M between 2rs-m and 2m-cu, vein Cu1a separated from 1m-cu by about 1.2× length of Cu1b; vein cu-a weakly inclivous. Hind wing with vein M+Cu almost straight; distal abscissa of Cu1 present, reaching wing margin; vein Cu1 separated from M by 0.5× length of cu-a; vein cu-a reclivous to vein 1A.

Legs. Fore femur moderately inflated, 4.3–4.4× as long as wide; hind femur moderately stout, about 4× as long as its maximum width; hind tibia about 10.5× as long as its apical width; first tarsal segment of hind leg slightly longer than second and third segments combined; fifth segment about as long as second.

Metasoma. First metasomal tergite (Fig. 1d) with median longitudinal carinae distinct, moderately convergent posteriorly in dorsal view, extending to 0.5 of T1; median part between median longitudinal carinae strongly raised posteriorly, with median basal depression nearly smooth, densely puncto-reticulate posteriorly, lateral surface rugose; posterior half of lateral longitudinal carina distinct; spiracle situated at basal 0.35 of T1, slightly below level of lateral carina, encircled by deep oblong groove; T2 with antero-lateral corners strongly impressed in front of pair of antero-lateral oblique grooves; central area of T2 strongly raised, with punctures very dense on dorsal surface and rather sparse laterally. First metasomal tergite 2.0× as long as its apical width; T2 about 1.1× as long as T1 and about 1.5× as long as its apical width. Ovipositor very long, about 70 mm, projecting beyond apex of metasoma by 10.0× length of hind tibia; ovipositor with expanded area of lower valve bearing 5 grooves,

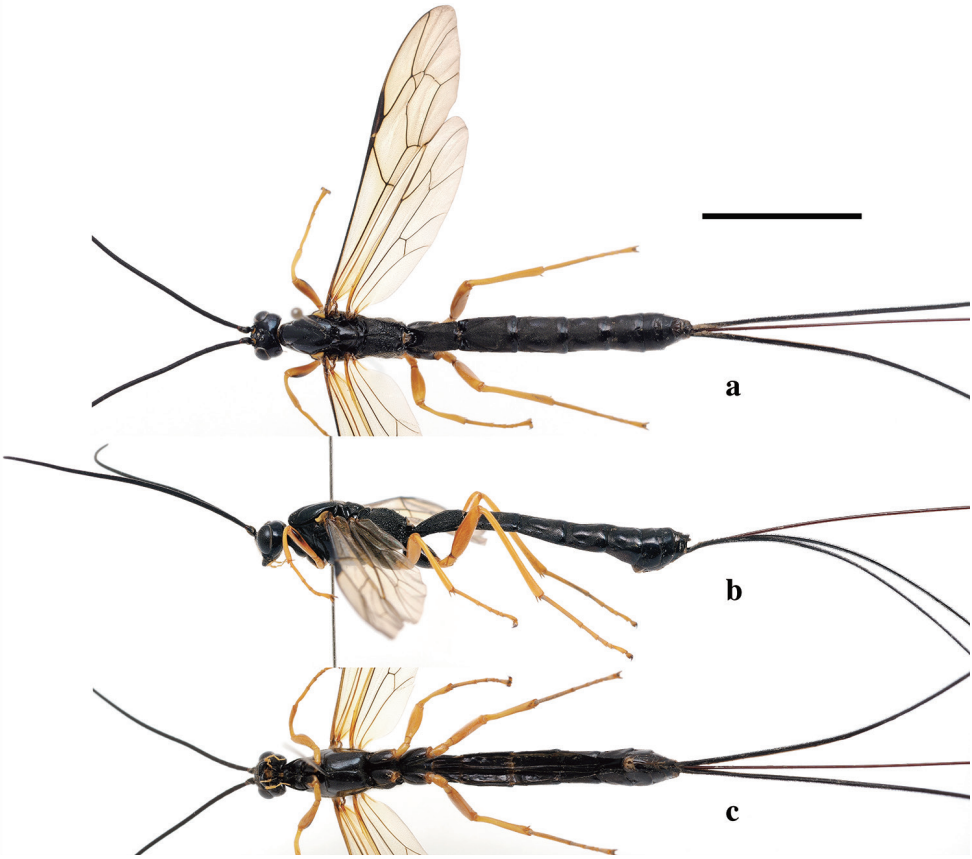

Figure 3. Holotype female of *D. flavicrus* sp. n.: **a** dorsal aspect **b** lateral aspect **c** ventral aspect. Scale bar: 10 mm.

the most proximal 4 of which are reclivous, followed by apical 7 teeth (Fig. 1h); ovipositor sheath bearing short setae which are about 1.1× as long as width of sheath.

Coloration. Head, mesosoma and metasoma including mesosternum and membranous area between sclerites black (Figs 1f, 3c); lower half of clypeus tinged with reddish brown (Fig. 1a); labrum, maxillary and labial palpi yellow. Tegula and parategula yellow. Wings weakly tinged with yellowish brown, slightly darkened along distal margin. Legs largely vivid yellow, except for black coxae, short longitudinal dark stripe on posterior surface of fore femur (Fig. 1c) and dark brown tip of tarsal claw.

Male. Very similar to female in morphology and colouration. Flagellum with 40 segments. Genitalia as in Fig. 2; subgenital plate (Fig. 2e) transverse, moderately covered with short pubescence, weakly incised at the middle, posteriorly; paramere (Fig. 2c, d) moderately long, angular, with ventral margin concave, apical half of outer side bearing rather dense short pubescence; apex of distivolsella flat (Fig. 2d); gonolacinia slightly turned inwards (Fig. 2a); aedeagus (Fig. 2f, g) stout and flat, with lateral

sides almost parallel, slightly divergent toward apex; tip of aedeagus weakly incised at middle, laterally squarish.

Length. Fore wing 20- 22 mm in ♀ (21 mm in holotype), 18 mm in ♂.

Type series. ***Holotype.*** ♀ (Fig. 3), pinned, 22. V. 2016, Akazai-keikoku (35.2149°N, 134.4936°E, (WGS 84), 510m a.s.l.), Shisou-shi, Hyogo Pref., Japan (Rikio Matsumoto), OMNH TI-522, DNA sample: OMNH_Pol-420, INSD accession number LC337798.

Paratypes. 2♀, same data as holotype; 1♂3♀, 11.VI.2001, same locality as holotype (1♀ in BMNH).

Distribution. Japan (Honshu).

Remarks. This species is closely related to *D. khasianus,* from which it can be separated by a short and longitudinal dark stripe on the posterior surface of the fore femur, less developed epomia and lack of fine transverse striations on the antero-median part of the first metasomal tergite between the latero-median carinae.

All known specimens were collected while flying around nearly dead *Pterocarya rhoifolia* Sieb. et Zucc trees (Juglandaceae). In several cases, females were observed investigating the trunk of the tree with their antennae and thrusting their ovipositors into it. A male was also observed flying around the trunk.

Etymology. The specific name refers to the golden yellow legs contrasting with the black mesosoma and metasoma.

Dolichomitus khasianus **Gupta & Tikar**

Figs 1e, 4

Dolichomitus khasianus Gupta & Tikar, 1976: 64.

Remarks. This species is closely related to *Dolichomitus flavicrus* sp. n. Fore and mid coxae black, femora, tibiae and tarsi of mid and hind legs entirely concolorous yellow to reddish yellow, underside of metasoma including mesosternum and membranous area between sclerites entirely blackish in these species. However this species can be distinguished from the latter by the lack of a dark stripe on the posterior surface of the fore femur and by fine and dense transverse striations on the antero-median part of the first metasomal tergite (Fig. 1e).

This species was described based on a single female from India. Sheng & Sun (2010) recorded *D. khasianus* from Yunnan in China.

Length. Fore wing 25 mm, ovipositor sheath 95 mm.

Male. Unknown.

Specimens examined. Holotype ♀ of *Dolichomitus khasianus* Gupta & Tikar (Fig. 4), "Khasia Hills, Assam, Athimus K.", India (ZSM).

Distribution. India, China.

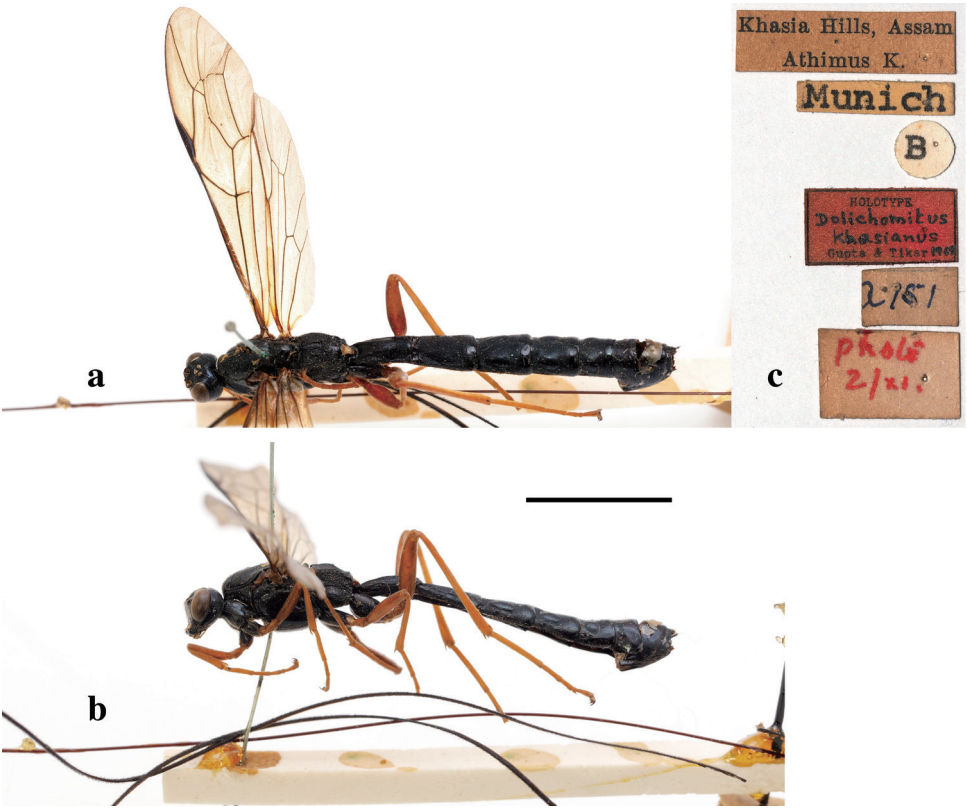

Figure 4. Holotype female of *D. khasianus*: **a** dorso-lateral aspect **b** lateral aspect **c** labels. Scale bar: 10 mm.

Dolichomitus mandibularis **(Uchida)**
Figs 1g, 5

Ephialtes mandibularis Uchida, 1932: 160.
Dolichomitus mandibularis: Townes, Momoi & Townes, 1965: 19.

Remarks. Relatively small species among members of the *mandibularis* group, with fore wing length 15mm or less. This species differs from *D. khasianus* and *D. flavicrus* sp. n. by the underside of the metasoma being not entirely blackish (Fig. 1g), with whitish membranous areas adjacent to sternites, and by its reddish fore and mid coxae (Fig. 5) and brown hind femur which is obviously darker than fore and mid femora (in the latter two species almost entirely yellow to reddish yellow).

Length. Fore wing 11–15mm in ♀, 11–13 mm in ♂.

Specimens examined. Holotype ♀ of *Ephialtes mandibularis* Uchida (Fig. 5), 1.VII.1929, Minoo, Osaka, (C.Teranishi) (SEHU); 6♂2♀, 2.V.2016, Byakugouji-cho,

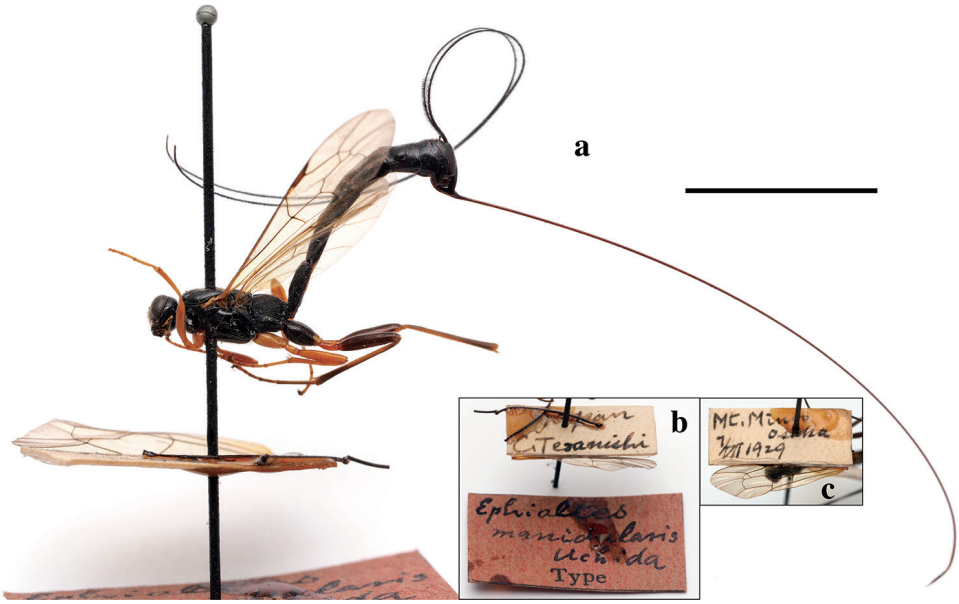

Figure 5. Holotype female of *D. mandibularis*: **a** lateral aspect **b** labels **c** underside of data label. Scale bar: 10 mm.

Nara-shi, Nara Pref. (R.M.), (1♂: DNA sample: OMNH_Pol-413, INSD accession number LC337797); 2♂, 7.V.2016, same locality, (R.M.); 2♀, 16.V.2016, same locality, (R.M.) (1♀ DNA sample: OMNH_Pol-384, INSD accession number LC337796); 1♀, 18.VI.2006, Mikusayama, Nose-shi, Osaka Pref., (R.M.); 1♀, 19.V.1941, Tsuyutani, Aoya-cho [Tottori-shi], Tottori Pref., (H. Aoki) ; 1♀, 17.VI.1953, Tottori Pref. (H. Aoki).

Distribution. Japan (Hokkaido, Honshu); China (Sheng and Sun 2002).

Remarks. All male specimens were collected while flying along a trunk of an unidentified dead deciduous tree.

Key to species of the *mandiburalis* group of *Dolichomitus*

1 Mandible strongly bent at right angle in the middle (Fig.1a) .... ***mandibularis* group**...**2**

– Mandible weakly and evenly bent ..... **other species groups**

2 Underside of metasoma blackish all over including membranous areas adjacent to sternites (Fig. 1f). Fore and mid coxae black (Figs 3b, c, 4b), hind femur yellow to reddish yellow, concolorous with fore and mid femora (Figs 3, 4). Larger species with fore wing 20 mm or more..... **3**

– Underside of metasoma not entirely blackish, with membranous areas adjacent to sternites whitish (Fig. 1g). Fore and mid coxae reddish yellow (Fig.

5), hind femur brown, obviously darker than fore and mid femora (Fig. 5). Smaller species with fore wing about 15 mm ..... ***mandibularis***

3 Legs entirely reddish yellow except coxae (Fig. 4). Fore femur without dark stripe on posterior surface. Epomia developed. First metasomal tergite (Fig. 1e) with fine transverse striations on antero-median part between latero-median carinae, medially rugulose ..... ***khasianus***

– Legs entirely bright yellow except coxae (Figs 1c, 3). Fore femur with short longitudinal dark stripe on posterior surface (Fig. 1c). Epomia less developed. First metasomal tergite (Fig. 1d) without fine transverse striations on antero-median part, medially areolate-punctate..... ***flavicrus* sp. n.**

Discussion

Because of their large bodies and long ovipositors, the genus *Dolichomitus* is one of the most conspicuous and well-known genera in the family Ichneumonidae. A considerable number of taxonomic and faunal studies have been published for several biogeographical regions (Townes and Townes 1960, Gupta and Tikar 1976, Gauld 1991, Sheng and Sun 2002, 2010, Zwakhals 2010, Choi et al. 2016) and plenty of distributional records are available. However, the *mandibularis* group is known only from the Himalayas, South-western China and Japan, and not recorded in other regions. This distribution suggests that the *mandibularis* group is one of the representatives of a Sino-Japanese element of insects and plants (Shirozu 1947).

The known hosts of the genus *Dolichomitus* are coleopteran borers of dead wood, mainly belonging to Cerambycidae, and species of Curculionidae and Melandryidae are also recorded as hosts (Townes and Townes 1960, Fitton et al. 1988, Gauld 1991). No host record is available for members of the *mandibularis* group. However, the observed oviposition behaviour of females of *Dolichomitus flavicrus* sp. n., thrusting their ovipositors into dead *Pterocarya rhoifolia* trees, suggests that the host of this species is a borer of this tree. A cerambycid, *Chloridolum* (*Chloridolum*) *thaliodes* Bates is one of the most abundant species infesting dead or nearly dead *Pterocarya rhoifolia* at the collecting site. No other borers with enough biomass as a host for the larval development of such a large parasitoid as *D. flavicrus* was found there, so *C. thaliodes* is the most plausible candidate for the host of *D. flavicrus*, although confirmation is needed. In such a case, DNA barcode sequences of *D. flavicrus* would be helpful in identification of larvae parasitizing the host.

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