

Systematics, biology and distribution of Microdontomerus iridis (Picard, 1930), comb. n. (Hymenoptera, Torymidae, Toryminae, Microdontomerini), a parasitoid of Mantodea oothecae

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Academic editor: H. Baur | Received 9 December 2015 | Accepted 13 February 2016 | Published 1 March 2016 http://zoobank.org/6CE5E5B8-23C3-4292-924C-4419000F03ED

Citation: Janšta P, Delvare G, Krogmann L, Schütte K, Peters RS (2016) Systematics, biology and distribution of *Microdontomerus iridis* (Picard, 1930), comb. n. (Hymenoptera, Torymidae, Toryminae, Microdontomerini), a parasitoid of Mantodea oothecae. Journal of Hymenoptera Research 48: 1–18. doi: 10.3897/JHR.48.7470

Abstract

Here, we report on a unique parasitoid wasp species of Toryminae reared from oothecae of praying mantids in the Mediterranean region. Based on the first available large specimen series, we transfer the species to *Microdontomerus iridis* **comb. n.** (from *Torymus*), describe the so far unknown male, designate a neotype, expand the known geographical distribution by adding new records from Greece, Spain and Turkey, and provide the first images of live specimens of the species as well as information on its larval biology. We also transfer *Microdontomerus carayoni* comb. n. from *Idiomacromerus*.

Keywords

Chalcidoidea, Mediterranean area, ectoparasitoid, Iris oratoria, larval biology

Introduction

Torymus iridis (Picard, 1930) is an exceptional species in the species-rich and biologically diverse subfamily Toryminae, as it is one of very few species with a reliable host record of Mantodea oothecae outside the strictly Mantodea oothecae-associated Podagrionini.

However, data on this species are very scarce. The only two published records are the original description by Picard (1930) from oothecae of *Iris oratoria* (Linnaeus, 1758) and an additional record from the same host species by Bernard (1936). Both records were restricted to France. The male remained unknown.

We reared a non-podagrionine species from *I. oratoria* oothecae collected in France, Greece, Spain and Turkey, and tentatively identified it as *Torymus iridis*. The availability of this larger series, for the first time also including males, led us to revise the taxonomic status of this biologically exceptional species.

In this study, we transfer the species to the correct genus and tribe, provide a description of the male, designate a neotype due to all historic material including the type specimens apparently having been lost, update and expand the known geographical distribution, and provide the first photographs of live specimens of the species as well as additional biological data.

Material and methods

Oothecae of *Iris oratoria* were collected from several locations in France, Greece, Spain and Turkey. Oothecae were collected in open Mediterranean steppe habitats under stones (Greece, Spain, and Turkey), glued to the substrate or to the stones, or very near the coast on outer walls or stakes (France).

The oothecae were subsequently stored in boxes or Petri dishes at room temperature. Emerging specimens were card mounted or stored in 96% alcohol at -20 °C. In total, we reared 23 females and 7 males of the wasp species from six oothecae of *Iris oratoria*. Additional oothecae of *Iris oratoria* were collected in Spain, some of which showed emergence holes similar to those formed by emerging wasps reared in the lab. These were dissected to check for parasitoid remains.

Pictures of live and mounted specimens were taken with a Keyence VHX-500F digital microscope. Other mounted specimens, including the neotype, were photographed with a JVC KY-75U 3CCD digital camera attached to an EntoVision binocular microscope, and the serial images obtained combined with Cartograph 5.6.0 (Microvision, Evry, France) software which allows precise measurements. Additional specimens were photographed with a Leica DXM 1200 digital camera attached to a Leica MZ 16 APO microscope and processed using Auto-Montage (Syncroscopy) software. Photographs were digitally optimized (artefacts removal, background standardization) using Photoshop[®] V. All figure plates were built using CorelDRAW[®].

Characters used for measurements of all specimens, their definition and abbreviation are listed in App. 1. They mostly follow Graham (1969), Gibson et al. (1997), Graham and Gijswijt (1998), Krogmann and Vilhelmsen (2006) and Baur (2015) or are newly defined. Some additional abbreviations which are not mentioned in Appendix 1 are: F1–F6 = funicle segments 1–6; Gt_1-Gt_5 = gastral terga 1–5; MPS = multiporous plate sensilla; OI (ovipositor index) = ratio of ovipositor length to length of metatibia. Terms for surface sculpture follow Harris (1979).

The measurements (in μ m) of characters of individuals of both sexes are compiled in Suppl. material 1. An overview of the basic descriptive statistics for each body measurement and their ratios are given in App. 2 and 3. All measurements were made with special reference to the correct orientation: eye length was measured in dorsal view, oral fossa breadth was measured in ventral view; all mesosomal and gastral tergites were measured in dorsal view along the median line except length of pronotum which was measured from lateral view; ovipositor length was measured as the part of the ovipositor sheaths that extends beyond the tip of the last gastral tergite.

SEM images of uncoated specimens were prepared at the Department of Palaeontology of the National Museum in Prague using a Hitachi S-3700N scanning electron microscope.

Collection acronyms used are CUPC = Charles University in Prague, Faculty of Science, Department of Zoology, Prague, Czech Republic; GDPC = Gérard Delvare personal collection, Montpellier, France; MNHN = Muséum National d'Histoire Naturelle, Paris, France; SMNS = State Museum of Natural History Stuttgart, Germany; ZMH = Zoological Museum Hamburg, Germany; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Results

Taxonomy

Microdontomerus iridis (Picard, 1930), comb. n.

Figs 1-25

Callimome iridis Picard, 1930: 89–90, ♀ (original description from France [Provence], syntypes in MNHN); Bernard 1936: 70 (host record of male and female), Graham and Gijswijt 1998: 161 (catalog, species inquirenda) *Torymus iridis*: Grissell 1995: 282 (generic transfer, distribution)

Material examined. Neotype female (in MNHN), FRANCE: Hérault, Palavas-les-Flots, between city and Maguelone Cathedral, 1 m a. s. l., 43.515167°N, 3.901833°E, February 1979, ex egg-case of *Iris oratoria* on stake, Foucart A. leg.

Non-type specimens: FRANCE, same data as neotype, 4 males (in GDPC); Aniane, city, 66 m a.s.l., 43.686528°N, 3.584361°E, 23.vii.1986, ex egg-case of *I. oratoria* on wall, Delvare G. leg., 1 female (in GDPC). GREECE, Kerkini Laka National Park, Ker-



Figures 1–4. *Microdontomerus iridis*, female neotype (scale bar 0.15 mm, unless indicated otherwise). **I** Habitus, lateral (scale bar 1 mm) **2** Head, dorsal **3** Mesosoma (partially), dorsal **4** Mesoscutellum (partially), metascutellum and propodeum, dorsal.

kini Mountains foothills, 41.277868°N, 23.214595°E, 254 m a.s.l., 4.v.2010, ex eggcase of *I. oratoria*, Fusu L. & Popovici O. leg., 9 females, 5 males (in GDPC); SPAIN, Extremadura, rio Magasca, Nordhang, near Trujillo, 5.viii.2009, 10 females, 1 male, em. i. 2010 (1 female), iii.2010 (1 female), v.2010 (4 females), 30.vi.2010 (2 females), 15.vii.2010 (1 male), vii.2010 (2 females) (in SMNS [2 females], ZFMK [2 females], ZMH [6 females, 1 male]); TURKEY, Izmir prov., Cukuralan, GPS 39.17437°N, 026.92825°E, 460m a.s.l., 21.iv.2011, em. 18.v.2011, 8 females, 3 males (in CUPC).

Condition of the neotype. Specimen complete, glued on rectangular card, right hind wing removed and glued on card.



Figures 5–10. *Microdontomerus iridis*, female (scale bar 0.2 mm). **5** Head, frontal, arrow indicates depression in cuticle sculpture (specimen from Greece) **6** Head, posterior (specimen from Turkey) **7** Antenna, lateral (specimen from Turkey) **8** Mesosoma, lateral (specimen from Greece) **9** Hind leg, lateral (specimen from Turkey) **10** Metasoma, dorsal (specimen from Greece).

Comments. The species was described from four females, which were housed in the Abeille de Perrin collection (in MNHN). Locating these specimens remained unsuccessful. The French entomologist Abeille de Perrin lived and worked in Marseille. Therefore, it is possible that the ootheca of *I. oratoria* from which the syntype specimens emerged was collected in the department Bouches-du-Rhône.

Diagnosis. Head 1.09–1.18× as broad as high and 1.87–2.04× as broad as long. Anterior margin of clypeus straight and recessed relative to corners of oral fossa.

Scrobes bare and less sculptured relative to the rest of face and interantennal area. Toruli inserted above ventral level of eye. Face between lateral level of eye and toruli with small depression contrasting with nearby surface sculpture. OOL about as long as LOD. Antenna with scape not reaching anterior ocellus; flagellum with two anelli and six funicular segments, all funicular segments transverse. Posterior part of midlobe of mesoscutum and entire mesoscutellum flattened dorsally; mesoscutellum less sculptured in contrast to pronotum and mesoscutum. Fore wing with speculum reaching end of marginal vein; costal cell dorsally with one row of setae along anterior margin, cubital cell without setae and basal cell at most with few setae along anterior margin; basal and cubital setal line complete; marginal vein $1.40-2.00\times$ as long as postmarginal vein and $2.55-3.78\times$ as long as stigmal vein. All tarsi slightly longer than tibiae, metafemur simple, without any tooth. Metasoma with hypopygium reaching almost end of gaster; Gt₁ incised medially, Gt₂–Gt₃ distinctly emarginate medially, Gt₄–Gt₅ slightly emarginate. Ovipositor $0.65-0.79\times$ as long as body; OI 2.50-2.90.

Description: FEMALE neotype. Body length excluding ovipositor 2.14 mm; length of ovipositor 1.51 mm. Head, mesosoma, meso- and metacoxa and metasoma metallic bronze green with coppery reflections, especially on mesonotum (Fig. 1). Lower part of scape, tegula, pro- and mesofemur and pro-, meso- and metatibia pale yellow. Procoxa brown in proximal part, pale yellow in distal part. Metafemur pale yellow with brownish spot in the middle; pro-, meso- and metatarsus pale yellow proximally and brownish distally. Distal part of scape, flagellum and ovipositor brown. Pedicel brown with metallic reflection. Fore wing slightly infumate, wing venation pale brown, setae brown.

Head. Head 1.10× as broad as high; 1.99× as broad as long (Fig. 2); 1.12× as broad as mesonotum at its widest part in dorsal view. Temple short, strongly converging, one quarter as long as eye. Eyes separated by 1.10× their own height, eye 1.81× as high as long. Head slightly reticulate with thin, short, pale setae on face, vertex and temple which are about as long as two meshes of the reticulation; scrobe more finely reticulate, without setae. Face between lateral level of eye and torulus with small depression in cuticle sculpture (Fig. 5). Clypeus with anterior margin nearly straight and recessed relative to corners of oral fossa; ventral part of clypeus smooth (Fig. 5). Malar space two thirds as long as breadth of oral fossa and $0.49 \times$ as long as eye height. Occipital carina absent (Fig. 6). Antenna with scape 3.90x and pedicel 1.46x as long as broad, the former not reaching ventral margin of anterior ocellus; torulus inserted hardly above ventral level of eye. Combined length of pedicel and flagellum 1.20× as long as breadth of head. Flagellum with two anelli, the first narrower, the second as broad as pedicel; remaining flagellomeres barely to distinctly transverse, with F1 the smallest, 0.73× as long as broad, hardly wider than pedicel, and bearing only few MPS; F2–F6 of about same dimensions, 0.79–0.85× as long as broad (Fig. 7). POL 2.94× OOL, OOL 0.98× LOD.

Mesosoma. Mesosoma 1.74x as long as broad. Pronotum 0.78× as broad as mesoscutum. Pronotum and mesoscutum fairly faintly and irregularly reticulate, especially on posterior part of mesoscutum, and covered with thin, short, pale setae (Fig. 3). Posterior part of midlobe of mesoscutum and entire mesoscutellum flattened dorsally (Fig. 8). Notaulus narrow, weakly impressed and obliterated by sculpture. Mesoscutellum $1.06\times$ as long as broad, without frenal area. Mesoscutellum and axilla more sparsely covered with setae and less sculptured than posterior part of midlobe of mesoscutum, partly coriaceous. Propodeum delicately reticulate, with incomplete and barely visible median carina (Fig. 4). Hind leg with coxa alutaceous, covered by setae dorsally and ventrally, $2.53\times$ as long as broad; metafemur $3.59\times$ as long as broad, without any tooth; metatibia $6.76\times$ as long as broad; metatarsus long, $1.04\times$ as long as metatibia (Fig. 9). Fore wing $2.35\times$ as long as wide, slightly infumate along wing venation, with dense brown setae on disc; speculum reaching end of marginal vein; costal cell dorsally with one row of setae along anterior margin, with one row of setae ventrally on basal half and 3-4 rows at end of cell, basal and cubital cell bare; basal and cubital setal line complete; marginal vein $1.82\times$ as long as postmarginal vein and $3.87\times$ as long as stigmal vein; venation pale brown (Fig. 1).

Metasoma. Metasoma 1.24× as long as mesosoma (but somewhat collapsed). Petiole very short, strongly transverse. Gaster with very shallow alutaceous sculpture; Gt_1 incised medially, Gt_2 – Gt_3 distinctly emarginate medially, Gt_4 – Gt_5 slightly emarginate medially (Fig. 10); tip of hypopygium almost reaching apex of gaster (Fig. 1). OI 2.76.

Variation. In a number of specimens the head, mesosoma, meso- and metacoxa and metasoma are metallic coppery green with purple reflections. Scape varies from brown in distal part to entirely brown. Tegula varies from pale yellow to pale brown in distal part or even entirely brown. In some darker specimens the procoxa is pale brown to brown in proximal part or entirely brown, sometimes with metallic coppery green reflections; pro- and mesofemur sometimes pale brown in the middle; metafemur entirely brown with metallic reflections and all tarsi except pretarsus brownish. The mesosoma of the French specimens is more slender than that of the females from Greece. Mesoscutellum and axilla slightly less sculptured than posterior part of midlobe of mesoscutum, almost alutaceous, sometimes only less reticulate. Basel cell of fore wing without setae, in some specimens with up to 10 setae in one row along anterior margin. Body length excluding ovipositor varies between 1.65 and 2.50 mm; length of ovipositor varies between 1.07 and 1.68 mm. Ranges and median of measurements and body ratios are given in App. 2 and 3 (for raw data, see Suppl. material 1).

MALE. Length of body 1.90–2.40 mm. Mostly similar to females (Figs 11, 13, 14, 15, 16) except following: one specimen (Spain) metasoma with yellow subbasal ring extending from distal part of Gt_1 to proximal part of Gt_2 (Fig. 12). Temple long and less converging, 0.32–0.60× length of eye, hence head less transverse, 1.77–1.96× as broad as long. Head with vertex more vaulted. Eye smaller, 1.43–1.6x as high as long, separated by 1.16–1.20× their own height. Oral fossa wider, malar space 0.49–0.51× breadth of oral fossa. Funicular segments somewhat less transverse than in the female. F1 and F2 two third as long as broad, F6 and clava respectively 0.61× and 1.87× as long as broad (Fig. 17). Pro- and metafemur distinctly swollen (Figs 18, 19), 2.14–2.35× respectively 2.57–2.71× as long as broad, the latter distinctly serrate posteriorly. Pro-



Figures 11–19. *Microdontomerus iridis*, male (scale bar 0.2 mm, unless indicated otherwise). 11 Habitus, lateral (specimen from Turkey, scale bar 0.5 mm) 12 Habitus, lateral (specimen from Spain, scale bar 0.5 mm) 13 Head, frontal, arrow indicates depression in cuticle sculpture (specimen from Greece) 14 Head, frontolateral, arrow indicates depression in cuticle sculpture (specimen from Turkey) 15 Head, posterior (specimen from Turkey) 16 Mesosoma, dorsolateral (specimen from Turkey) 17 Antenna, lateral (specimen from Turkey) 18 Fore leg, lateral (specimen from Greece) 19 Hind leg, lateral (specimen from Greece).

podeum sloping at only about 30° relative to surface of mesoscutellum. Other measurements as follows: POL 2.30–2.60× OOL; OOL 1.00–1.30× LOD. The variation in relative length of flagellomeres is as follows: F1 0.40–0.82×, F2–F5 0.64–0.85×, F6 0.67–0.77× and clava 1.87–2.62× as long as broad. Mesosoma and mesoscutellum 1.80–2.00× respectively 1.07–1.21× as broad as long; pronotum 0.75–0.88× as long as mesoscutellum; metatibia 5.70–6.50× as long as broad; metatarsus 1.06–1.08× as long as metatibia; fore wing 2.16–2.3× as long as wide, marginal vein 1.48–2.07× and



Figures 20–25. 20 *Microdontomerus iridis*, lateral, male pupa on host egg (specimen from Spain) 21 *M. iridis*, lateral, male pupa removed from host egg (specimen from Spain) 22 *M. iridis*, female on host oo-theca (specimen from Spain) 23 *M. iridis*, male on host ootheca (specimen from Spain) 24 Rio Magasca, Spain, habitat of *M. iridis* 25 *Iris oratoria* (upper) and *Ameles* sp. (lower) oothecae from Spain, rio Magasca.

 $2.73-3.44\times$ as long as postmarginal vein respectively stigmal vein; metasoma 0.80- $1.20\times$ as long as mesosoma but depending on degree of collapsing.

Taxonomic remarks

Taxonomic placement

Microdontomerus iridis (Picard, 1930) was erroneously placed in *Callimome*, now considered a synonym of *Torymus* (see Grissell 1995), and classified in the tribe Torymini.

However, it lacks the defining synapomorphy of Torymini, i.e., the sinuous suture between mesepimeron and metapleuron, with the anterior margin of the metapleuron projecting forward.

In the key to genera of Toryminae by Grissell (1995), *M. iridis* falls into couplet 49 (genera *Idiomacromerus* and *Microdontomerus*). However, Grissell (1995) found it difficult to distinguish some species of *Idiomacromerus* from *Microdontomerus* and vice versa. The only character used for recognition of these two genera was the number of anelli. Later, Grissell (2005) found more reliable characters and separated these two genera based on the presence or absence of the occipital carina. *Microdontomerus iridis* has no occipital carina (Figs 6, 15) which defines the genus *Microdontomerus* (Grissell 1995, 2005). The classification in *Microdontomerus* is also supported by the study of Janšta et al. (unpublished) that uses molecular data to infer the phylogeny of Torymidae. In this study, *M. iridis* is placed within a monophyletic clade together with other species of *Microdontomerus*.

Recognition of the species

Only five species of Microdontomerus are known from the Old World: four Palaearctic (M. albipes (Giraud, 1870), M. annulatus (Spinola, 1808), M. iridis (Picard, 1930), M. ovivorus (Steffan, 1967)), and one Afrotropical (M. senegalensis (Risbec, 1951)) (Noyes 2015). This genus is much more diverse in the Nearctic (Grissell 2005), with 19 species described. Microdontomerus iridis differs from the Old World species by the presence of two anelli. However, the list in Noyes (2015) is mostly based, for the Old World species, on the catalogue by Grissell (1995) in which the division between *Microdonto*merus and Idiomacromerus is demarcated by the number of anelli. Both the distinction and the accordant list are out of date. An examination of collections at hand showed that several species, which would be classified as *Microdontomerus* according to the presence or absence of an occipital carina (Grissell 2005), are currently included in Idiomacromerus. This is the case for Microdontomerus carayoni comb. n. (based on the examination of the holotype, in MNHN) and at least four undescribed species, all distributed in the Mediterranean area or Central Asia. They all have extensive pale colouring - mostly yellow - at least on the metasoma, sometimes on the whole body, while *M. iridis* only has very reduced yellow spots on Gt₂₋₅, usually visible on specimens in alcohol; in dried specimens the metasoma collapses and tergites overlap each other, masking the yellow spots. Microdontomerus iridis indeed differs from the majority of species presently classified in *Idiomacromerus* by the absence of the occipital carina. The specific host is another key feature for the recognition of the species. No other non-podagrionine and non-palachiine Torymidae has been recorded from mantid egg-cases, except Microdontomerus senegalensis (Risbec, 1951) (reared from Tarachodes saussurei, maybe as hyperparasitoid of podagrionines), which differs from *M. iridis* by having only a single anellus and seven funicular segments according to the original description and illustration (Risbec 1951: fig. 154e, p. 319).

Assignment to Callimome iridis

A neotype is designated because we were unable to locate or trace the type specimen or any material referred to by Bernard (1936) in the collection of the Paris museum (MNHN). Apparently, all material used for the description and other publications so far, is lost, and a neotype designation was necessary to fix the taxonomic status of the species. The assignment of the recently reared torymids that we examined in this study to *C. iridis* is based on the fact that *C. iridis* is the only known non-podagrionine Toryminae species from *I. oratoria*, the host from which all specimens examined by us were reared. In fact, surveys of parasitoids of Mantodea in the Palaearctic (unpublished) showed that the parasitoids of *I. oratoria* are host-specific and, except rarely for *Podagrion* spp., do not host-shift to other mantid species. Furthermore, the recently reared specimens completely agree with the original description of *C. iridis*, especially in the colour of the body and appendices, the sculpture of the mesosoma, and the relative length of the exserted part of the ovipositor.

Biology. All specimens were reared from oothecae of *Iris oratoria* (Mantodea). Dissection of additional oothecae with emergence holes (same locality data as the examined *M. iridis* from Spain; oothecae deposited at ZMH) showed that *M. iridis* is an egg ectoparasitoid, feeding on one host egg per specimen (Figs 20, 21). Figs 22 and 23 show a female and a male specimen respectively on its host ootheca.

Distribution. According to published records (Picard 1930), *M. iridis* is restricted to southern France. We significantly expand the known distribution by adding new records from Greece, Spain and Turkey. Based on all parasitoid records and the known host distribution (Battiston et al. 2010) we assume that *M. iridis* is distributed over the entire Mediterranean region. Figures 24 and 25 show the Spanish collection site of *M. iridis* and the host ootheca glued on stone.

Discussion

The most striking feature of *M. iridis*, for which we present all necessary taxonomic actions as well as new data on its life history, is the apparently very specific association with an unusual host, the egg cases of *Iris oratoria*. Although *Microdontomerus* is not a species-rich group with little morphological variation between species, the host range within the genus *Microdontomerus* is very broad. Larvae of *Microdontomerus* species are known as parasitoids of various life stages of Lepidoptera (including eggs), larvae of solitary bees and larvae of Cynipidae (both Hymenoptera) and Tephritidae (Diptera), eggs of beetles (Buprestidae) and Mantodea eggs (two species). Some species are hyperparasitoids of Ichneumonidae, Braconidae (Hymenoptera) and Tachinidae (Diptera) larvae in caterpillars (Lepidoptera) and larvae of Buprestidae, Cerambycidae and Curculionidae (Coleoptera) (Grissell 2005). In fact, the genus is a striking example of the evolution of very different host associations in closely related species that can be found in many groups of Toryminae (see Noyes 2015). However, while we were able

to provide some data for *M. iridis*, in general, little biological information is available for most species of *Microdontomerus*. Verification of host records is required and many biological features still need to be understood before we will fully appreciate the evolution of host associations in *Microdontomerus* and related groups.

Acknowledgements

We are indebted to Antoine Foucart (from Cirad, Montpellier, France), Ovidiu A. Popovici and Lucian Fusu (both from Alexandru Ioan Cuza University, Iasi, Romania) for collecting egg-cases and providing us the material. We are also grateful to Claire Villemant and Agnièle Touret-Alby (from MNHN, Paris, France) for facilitating access of the MNHN collections, and to Trevor Burt for linguistic help. We thank Hannes Baur, Stefan Schmidt and one anonymous reviewer for valuable comments on the manuscript. Examination of specimens using the Hitashi S-3700N scanning electron microscope was possible due to the Barrande I project, partially supported by the European Union.

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Appendix I

Abbreviation, name and definition of the 62 measurements used in this study (See Material and methods for further information).

Abbreviation	Character name	Character definition
ant.l	Pedicel + flagellum length	Combined length of pedicel plus flagellum, outer aspect (Graham 1969)
aod.d	AOD	Anterior (=median) ocellus diameter
as2.l	Apical spur of mesotibia length	Length of apical spur of mesotibia
as3.l	Apical spur of metatibia length	Length of the longest apical spur of metatibia
bod.l	Body length	Sum of lengths of head, mesosoma and metasoma
cc1.l	Costal cell of fore wing length	Length of costal cell of fore wing, measured from end of humeral plate to the point at which the submarginal vein touches the leading edge of the wing
clv.b	Clava breadth	Greatest breadth of clava, outer aspect (Baur 2015)
clv.l	Clava length	Greatest length of clava, outer aspect (Baur 2015)
eye.h	Eye height	Greatest length of eye height, lateral view (Baur 2015)
eye.l	Eye length	Length of eye, dorsal view (Graham 1969)
fl3.b	First funicular segment breadth	Greatest breadth of first funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fl3.1	First funicular segment length	Greatest length of first funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fl4.b	Second funicular segment breadth	Greatest breadth of second funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fl4.1	Second funicular segment length	Greatest length of second funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fl8.b	Sixth funicular segment breadth	Greatest breadth of sixth funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fl8.1	Sixth funicular segment length	Greatest length of sixth funicular segment (= third flagellar segment), outer aspect (Baur 2015)
fm1.b	Profemur breadth	Greatest breadth of profemur, outer aspect
fm1.l	Profemur length	Length of profemur, from distal end of trochanter to tip of profemur, measured along midline, outer aspect
fm2.b	Mesofemur breadth	Greatest breadth of mesofemur, outer aspect
fm2.l	Mesofemur length	Length of mesofemur, from distal end of trochanter to tip of mesofemur, measured along midline, outer aspect
fm3.b	Metafemur breadth	Greatest breadth of metafemur, outer aspect (Baur 2015)
fm3.l	Metafemur length	Length of metafemur, from distal end of trochanter to tip of metafemur, measured along midline, outer aspect (Baur 2015)
frv.b	Frontovertex breadth	Minimal distance between compound eyes at level level of median ocellus

Abbreviation	Character name	Character definition
fwi.b	Fore wing breadth	Greatest breadth of fore wing, measured at about right angle to marginal and postmarginal veins (Baur 2015)
fwi.l	Fore wing length	Greatest length of fore wing, measured from end of humeral plate to tip of wing (Baur 2015)
hea.b	Head breadth	Greatest breadth of head, dorsal view (Baur 2015)
hea.h	Head height	Distance between anterior margin of clypeus and anterior edge of anterior ocellus, frontal view (Baur 2015)
hea.l	Head length	Length of head, dorsal view (Graham 1969)
hwi.b	Hind wing breadth	Greatest breadth of fore wing, measured at about right angle to marginal and postmarginal veins
hwi.l	Hind wing length	Greatest length of hind wing, measured from end of humeral plate to tip of wing
hwv.l	Hind wing venation length	Combined length of submarginal and marginal vein of hind wing, measured as direct distance from end of humeral plate to the apical end of marginal vein
lof.h	Lower face height	Distance between anterior margin of clypeus and lower margin of torulus (Baur 2015)
mav.l	Marginal vein length	Length of marginal vein, distance between the point at which the submarginal vein touches the leading edge of the wing and the point at which stigmal vein and postmarginal vein unite (Graham 1969)
msc.b	Mesoscutum breadth	Greatest breadth of mesoscutum just in front of level of tegula, dorsal view (Baur 2015)
msc.l	Mesoscutum length	Length of mesoscutum along median line from posterior edge of pronotum to posterior edge of mesoscutum, dorsal view (Baur 2015)
msp.l	Malar space	Distance between the point where malar sulcus enters mouth margin and malar sulcus enters lower edge of eye, lateral view (Graham 1969)
mss.l	Mesosoma length	Length of mesosoma along median line from anterior edge of pronotum collar to posterior edge of nucha, dorsal view (Baur 2015)
mts.l	Metasoma length	Length of metasoma, measured from anterior margin of petiole to the tip of the last gastral tergite, dorsal view
of.b	Oral fossa breadth	Intermalar distance, ventral view (Graham 1969)
ool.l	OOL	Shortest distance between posterior ocellus and eye margin, dorsal view (Graham 1969)
ovi.l	Ovipositor length	Length of ovipositor, measured as the part of the ovipositor sheaths that extend beyond the tip of the last gastral tergite
pdl.b	Pedicel breadth	Greatest breadth of pedicel, outer aspect (Baur 2015)
pdl.l	Pedicel length	Length of pedicel, outer aspect (Baur 2015)
pmv.l	Postmarginal vein length	Length of postmarginal vein (Graham 1969), distance between the point at which the stigmal vein and postmarginal vein unite, apically to where the vein appears to end (Baur 2015)
pnt.l	Pronotum length	Distance between anterior edge of neck to posterior edge of collar, lateral view
pod.d	POD	Posterior (=lateral) ocellus diameter
pol.l	POL	Shortest distance between posterior ocelli, dorsal view (Graham 1969)
scp.b	Scape breadth	Greatest breadth of scape, outer aspect (Baur 2015)
scp.l	Scape length	Length of scape exclusive of radicle, outer aspect (Graham 1969)
sct.b	Mesoscutellum breadth	Greatest breadth of mesoscutellum (=scutellum), dorsal view
sct.l	Mesoscutellum length	Length of mesoscutellum (=scutellum) along median line from posterior edge of mesoscutum to posterior edge of mesoscutellum, dorsal view (Baur 2015)

Abbreviation	Character name	Character definition		
stv.l	Stigmal vein length	Length of stigmal vein, distance between the point at which stigmal vein and postmarginal vein unite apically, and the distal end of the stigma (Graham 1969)		
ta1.l	Protarsus length	Length of protarsus, including pretarsus		
ta2.l	Mesotarsus length	Length of mesotarsus, including pretarsus		
ta3.l	Metatarsus length	Length of metatarsus, including pretarsus (Baur 2015)		
tb1.l	Protibia length	Length of protibia, measured along midline, outer aspect		
tb2.b	Mesotibia breadth	Apical breadth of mesotibia, outer aspect		
tb2.l	Mesotibia length	Length of mesotibia, measured along midline, outer aspect		
tb3.b	Metatibia breadth	Apical breadth of metatibia, outer aspect (Baur 2015)		
tb3.l	Metatibia length	Length of metatibia, measured along midline, outer aspect (Baur 2015)		
tmp.l	Temple length	Length of temple, dorsal view (Graham 1969)		
tod.b	Torulo-ocular distance	Breadth of distance between outer margin of torulus and inner margin of eye, measured along an imaginary line connecting the ventral margins of the antennal toruli, frontal view		

Appendix 2

Overview of 62 measurements (in μ m) of *Microdontomerus iridis* showing minimum, maximum and median values for each character (See Appendix 1 for character name and definition).

		Female			Male	
Measurement	Min	Max	Median	Min	Max	Median
hea.b	459	614	570	530	617	600
hea.l	236	311	290	270	344	330
hea.h	392	530	500	473	584	554
frv.b	257	338	324	331	392	338
eye.l	170	220	200	180	315	233
tmp.l	35	70	60	75	110	105
pol.l	61	170	160	140	180	178
ool.l	42	65	58	60	75	70
pod.d	40	60	50	50	69	60
aod.d	47	62	56	82	82	82
eye.h	250	338	300	260	325	300
msp.l	95	155	130	130	159	150
of.b	182	260	230	260	320	297
tod.b	115	115	115	904	1041	952
lof.h	117	117	117	158	158	158
scp.l	180	200	190	200	224	210
scp.b	47	60	60	60	70	60
pdl.l	60	80	80	75	85	80
pdl.b	45	69	50	50	58	50
ant.l	425	653	633	677	677	677
fl3.1	47	60	55	20	50	45
fl3.b	60	80	73	50	76	60
fl4.1	50	65	56	45	56	55

	Female		Male			
Measurement	Min	Max	Median	Min	Max	Median
fl4.b	66	90	78	60	84	65
fl8.1	50	70	60	50	58	55
fl8.b	75	100	85	65	95	75
clv.l	150	190	179	140	178	170
clv.b	70	100	85	60	80	75
mss.l	617	950	870	797	1030	945
msc.b	411	567	520	473	594	512
pnt.l	149	257	223	243	297	257
msc.l	253	392	361	338	405	378
sct.l	243	338	320	311	340	320
sct.b	233	320	308	280	322	290
fm1.l	288	397	384	400	508	470
fm1.b	82	128	116	170	224	210
tb1.l	288	341	320	452	452	452
ta1.l	346	346	346	406	406	406
fm2.l	397	410	404	480	480	480
fm2.b	96	98	97	151	151	151
tb2.l	288	443	431	541	541	541
tb2.b	64	64	64	89	89	89
as2.1	78	78	78	103	103	103
ta2.l	370	494	420	?	?	?
fm3.l	384	570	505	460	572	540
fm3.b	96	160	150	170	216	210
tb3.l	432	675	610	530	657	630
tb3.b	80	105	90	90	110	100
as3.l	81	81	81	81	81	81
ta3.l	466	720	625	560	700	680
fwi.l	1315	1760	1620	1380	1808	1600
fwi.b	548	830	720	600	822	730
cc1.l	466	636	603	712	712	712
mav.l	270	340	310	270	320	310
stv.l	78	110	100	78	110	100
pmv.l	160	230	180	140	210	170
hwi.l	932	1233	1192	1329	1329	1329
hwi.b	247	307	288	301	301	301
hwv.l	521	736	699	795	795	795
mts.l	849	1300	1075	780	1200	959
ovi.l	1069	1720	1600	?	?	?
bod.l	1644	2500	2155	1900	2400	2200

Appendix 3

	Female		Male			
Ratio of measurements	Min	Max	Median	Min	Max	Median
hea.b / hea.l	1.87	2.04	1.96	1.73	1.96	1.79
hea.b / hea.h	1.09	1.18	1.13	1.03	1.16	1.09
frv.b / eye.h	0.96	1.1	1.01	1.13	1.2	1.19
pol.l / ool.l	2.5	3.1	2.74	2.27	2.6	2.43
ool.l / pod.d	0.91	1.3	1.1	1	1.27	1.2
msp.l / eye.h	0.38	0.49	0.44	0.48	0.51	0.5
msp.l / of.b	0.52	0.76	0.57	0.47	0.54	0.5
ant.l / hea.h	0.93	1.2	1.14	1.1	1.1	1.1
scp.l / scp.b	3	4.15	3.25	3	3.73	3.5
pdl.l / pdl.b	1.13	1.6	1.45	1.38	1.7	1.55
fl3.1 / fl3.b	0.63	0.92	0.75	0.4	0.82	0.69
fl4.1 / fl4.b	0.63	0.87	0.7	0.64	0.85	0.77
fl8.1 / fl8.b	0.56	0.87	0.7	0.61	0.77	0.69
clv.l / clv.b	1.67	2.6	2.12	1.87	2.97	2.27
mss.l / msc.b	1.41	1.86	1.69	1.34	2	1.89
msc.l / msc.b	0.62	0.74	0.67	0.59	0.82	0.75
pnt.l / sct.l	0.6	0.79	0.69	0.75	0.88	0.81
sct.l / sct.b	0.98	1.14	1.03	1.01	1.21	1.1
fm1.l / fm1.b	3.1	3.5	3.29	2.14	2.35	2.29
ta1.l / tb1.l	1.01	1.08	1.05	0.9	0.9	0.9
ta2.l / tb2.l	0.97	1.29	1.12	?	?	?
fm3.1 / fm3.b	3.27	4	3.55	2.57	2.71	2.62
ta3.l / tb3.l	1.02	1.11	1.05	0.98	1.08	1.08
fwi.l / fwi.b	2.05	2.5	2.29	2.16	2.3	2.22
cc1.l / fwi.l	0.35	0.37	0.37	0.39	0.39	0.39
mav.l / stv.l	2.55	3.87	3.1	2.73	4.03	3.1
mav.l / pmv.l	1.4	2	1.7	1.48	2.07	1.88
hwi.l / hwi.b	3.78	4.14	4.02	4.41	4.41	4.41
mts.l / mss.l	1.16	1.53	1.24	0.8	1.2	1.05
ovi.l / tb3.l	2.44	2.86	2.63	?	?	?
ovi.l / bod.l	0.65	0.79	0.72	?	?	?

Overview of ratios of various measurements of *Microdontomerus iridis* showing minimum, maximum and median values (See Appendix 1 for character name and definition).

Supplementary material I

Measurements of female and male characters of *Microdontomerus iridis* used in this study

Authors: Petr Janšta, Gerard Delvare, Lars Krogmann, Kai Schütte, Ralph S. Peters Data type: measurement

- Explanation note: Measurements (in μm) of female and male characters of *Microdontomerus iridis* used in this study (See Material and methods for collection acronyms; see Appendix 1 for character name and definition).
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RESEARCH ARTICLE



Taxonomy of the Indo-Malayan presocial potter wasp genus *Calligaster* de Saussure (Hymenoptera, Vespidae, Eumeninae)

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Academic editor: <i>M. Ohl</i>	Received 2 November 2015	Accepted 14 December 2015	Published 1 March 2016
	http://zoohank.org/5C371RB3-3	FBE-4FF2-877E-A60F1A603F11	

Citation: Nugroho H, Ubaidillah R, Kojima J (2016) Taxonomy of the Indo-Malayan presocial potter wasp genus *Calligaster* de Saussure (Hymenoptera, Vespidae, Eumeninae). Journal of Hymenoptera Research 48: 19–32. doi:

10.3897/JHR.48.7045

Abstract

The taxonomic history and current taxonomic status of the presocial potter wasp genus *Calligaster* de Saussure, 1852, at generic and species levels are reviewed. The hitherto-unknown female of *Calligaster viridipennis* Giordani Soika, 1960, is described based on specimens newly collected in Central and Southeast Sulawesi. A key to species is also provided.

Keywords

Vespidae, Eumeninae, Calligaster, presocial potter wasps, taxonomy, Indo-Malayan

Introduction

Since Williams (1919) described detailed natural history of *Calligaster williamsi* Bequaert, 1940, under the name of *Zethus (Calligaster) cyanopterus* de Saussure, 1852, *Calligaster* wasps have been considered to practice fully progressive provisioning, and thus to be ones of several subsocial or presocial potter wasps (Cowan 1991). The nesting behavior of *Calligaster* wasps is unique in the Oriental potter wasps in that, as the wasps of the Neotropical subgenus *Zethoides* of the genus *Zethus* Fabricius, they make a nest with plant material (leaves cut into small pieces) and that they nest communally with sisters. All these behavioral characters of *Calligaster* allow us to consider the genus key to our better understanding of evolution of social and nesting behavior in the Vespidae (Cowan 1991).

Nevertheless, the phylogenetic position of *Calligaster* in the Eumeninae or even in the Vespidae has not yet been fully studied. Calligaster, in which six valid species are currently recognized, is in general considered as a genus comprising the potter wasp tribe Zethini, together with the following genera: Argentozethus Stange, 1979 (Neotropical in distribution), Australozethus Giordani Soika, 1969 (Australian), Ctenochilus de Saussure, 1856 (Neotropical), Deuterodiscoelius Dalla Torre, 1904 (Australian), Discoelius Latreille, 1809 (Palearctic), Elimus de Saussure, 1852 (Papua-Australian), Ischnocoelia Perkins, 1908 (Australian), Macrocalymma Perkins, 1908 (Australian), Pachycoelius Giordani Soika, 1969 (Australian), Paramischocyttarus Magretti, 1884 (Afrotropical, Palearctic), Protodiscoelius Dalla Torre, 1904 (Neotropical), Raphiglossa Saunders, 1850 (Afrotropical, Palearctic) and Zethus Fabricius, 1804 (worldwide other than Palearctic) (Richards 1962, Bohart and Stange 1965, Giordani Soika 1969, Stange 1979, Pickett and Carpenter 2010, Hermes et al. 2013). Calligaster is Indo-Malayan endemic, occurring from the eastern part of the Indian subcontinent in the west to Sulawesi Island of Indonesia and the Philippines in the east. The genus was not included in Hermes et al.'s (2013) detailed phylogenetic analyses using morphological characters in the Eumeninae.

Furthermore, despite such interesting aspects of *Calligaster* from the viewpoints of evolution of social and nesting behavior, phylogeny and biogeography, its taxonomy at generic as well as species levels is not yet revised even though such a taxonomic revision would provide us with robust bases for these studies. In the present paper, the history of taxonomy and current taxonomic status of *Calligaster* at generic and species levels are reviewed, together with a description of the hitherto-unknown female of *C. viridipennis* Giordani Soika, 1960, and a key to species.

Material and methods

The present study is based on specimens deposited in the collections of the Museum Zoologicum Bogoriense (MZB), Cibinong, Indonesia; Natural History Collection at Ibaraki University (IUNH), Mito, Japan; National Museum of Nature and Science (NMST), Tsukuba, Japan and the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam.

Each species account is accompanied by the original citation; sex(es) and locality(ies), if mentioned, are given together with the repository(ies) of name-bearing type specimen(s) in parentheses. Distributional data are summarized under "Distribution". The acronyms

of the type repositories are as follows: BMNH, The Natural History Museum, London; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A; MSNG, Museo Civico di Storia Naturale di Genova Giacomo Doria, Genova; RMNH, Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands; USC, University of San Carlos, Cebu City, Philippines; ZMB, Zoologisches Museum der Humboldt Universität, Berlin.

Morphological characters and marking patterns were observed on pinned-anddried specimens under a stereoscopic dissecting microscope. Male genitalia of some species were dissected, cleared in lactic acid, and observed in glycerin under a stereoscopic dissecting microscope. Line drawings were made by using the drawing tube attached to the microscope. Terminology on morphological characters mainly follows Bohart and Stange (1965), Carpenter and Cumming (1985), that on surface sculpturing follows Harris (1979), and on male genitalia mainly follows Bitsch (2012).

Taxonomy

Genus Calligaster de Saussure

Calligaster de Saussure, 1852: 22. Type species: *Calligaster cyanoptera* de Saussure, 1852, by subsequent designation of Ashmead (1902: 205).

Diagnosis. The genus *Calligaster* can be differentiated from any other eumenine genera by the combination of the following characters: labial and maxillary palpus with three and six palpomeres respectively; mid tibia with two spurs; mesepisternum with horizontal suture absent; propodeum with propodeal orifice rounded dorsally, apical valvula short and rounded, and submarginal carina not projecting as pointed lobe above valvula; metasomal segment I petiolate; tergum I in dorsal view abruptly widened laterally shortly after basal slit, then nearly parallel-sided apically, with longitudinal striae; metasomal sternum II with basal fossa; male characters: terminal antennal flagellomere simple; distal lobe of gonocoxite sub-truncated; gonostyle subapically with a tuft of short and thin hairs; basivolsella long and narrow, slightly enlarged at the base, with an obliquely truncated apex.

Remarks. *Calligaster* was proposed by de Saussure (1852: 23, Pl. IX fig. 6) as a genus to accomodate his two species from "Java": *Calligaster cyanoptera* de Saussure, 1852 and *C. hero* de Saussure, 1852. Later, he (de Saussure 1855: 115) synonymized *C. hero* under *Zethus gigas* Spinola, 1841, which is a South American *Zethus* species and is now treated as a synonym of *Zethus coeruleopennis* (Fabricius, 1798) (Bohart and Stange 1965). Although de Saussure (1855) did not refer to the type locality of *C. hero* given in de Saussure (1852) (= "Java"), it may have been certainly based on an erroneous labeling. Ashmead (1902) designated *C. cyanoptera* de Saussure as the type species of *Calligaster* de Saussure, 1852.

The taxonomic status of *Calligaster* had not been stabilized until Bequaert (1928) reinstalled its generic status; that is, de Saussure (1855) treated it as a division in the genus *Zethus*; Gribodo (1892), possibly having followed de Saussure (1855), treated *Calligaster* as a subgenus in the genus *Zethus* when he described *Zethus javanus* (=*C. cyanopterus*); Dalla Torre (1904) treated *Calligaster* as a genus; and Cameron (1904, 1909) described two species of *Zethus*, which Bequaert (1928) transferred to the genus *Calligaster*. But, establishment of the concept of *Calligaster* currently accepted by most of the vespid taxonomists was of Giordani Soika (1960).

Key to species of Calligaster

As no specimens were available to us, the characters for *C. etchellsii* and *C. zetteli* were extracted from Cameron (1909) and Bequaert (1928), and Gusenleitner (2006), respectively. Neither information of the male characters of *C. zetelli* nor of the female of *C. etchellsi* is available to us. In *Calligaster*, we have observed distinct morphological differences between sexes in the head characters, while characters of the mesosoma and metasoma (except for the number of metasomal segments and genital organs) are nearly the same between the sexes. In the following key, sex is specified only for the head characters.

1	Metasomal tergum I other than basal petiolate part in lateral view hardly
	convex dorsally (Fig. 4)
_	Metasomal tergum I other than basal petiolate part in lateral view more or
	less distinctly convex dorsally (Figs 1, 3, 5)
2	Female clypeus with dense and coarse punctures. Propodeum with dorsal face
	smooth and barely punctured. Metasomal tergum II basally barely punctured,
	apically with sparse minute punctures. Female mandible entirely black
_	Female clypeus with sparse minute punctures. Propodeum with dorsal face
	coarsely punctured. Metasomal tergum II entirely with sparse minute punc-
	tures. Female mandible with vellow basal spot
	<i>C. zetelli</i> Gusenleitner [male unknown]
3	Male clypeus in frontal view about 1.5 times as wide as high. Body black
0	entirely or with bright yellow markings
_	Male clypeus in frontal view about 2 times as wide as high; ventral margin
	shallowly emarginate medially. Body with pale-yellow markings
	<i>C. etchellsii</i> (Cameron) [female unknown]
4	Metasomal tergum I in lateral view without distinct subanical depression
1	(Fig. 1): in dorsal view strongly convex along lateral margin (Fig. 6). Wings
	fugeus with granich number inideannes. C minidir quarter Condeni Seiles
	iuscous, with greenish-purple indescenceC. virunpennis Giordani Soika
-	Metasomal tergum I in lateral view distinctly constricted subapically (Figs
	3, 5); in dorsal view nearly parallel-sided, with slight subapical constriction
	(Figs 7, 9). Wings fuscous, with blue-green and purple iridescence5

Calligaster cyanoptera de Saussure, 1852

Figs 3, 7, 10, 14, 17, 19–22

- Calligaster cyanoptera de Saussure, 1852: 23, pl. IX figs. 7, 7a, ♀, "Java", syntypes (?RMNH).
- *Zethus cyanopterus*; de Saussure 1855: 115 (here called *Zethus cyanopterus* Lep. [!]), 123 (in division *Calligaster*; ♂).
- Zethus (Calligaster) cyanoptera; Gribodo 1892 (1891): 260.
- Zethus (Calligaster) javanus Gribodo, 1892 (1891): 261, ♂ (in subgenus Calligaster),
 "Kaliparè (Giava orientale)", holotype [by monotypy] (MSNG). Synonymized under Calligaster cyanoptera de Saussure, 1852 by van der Vecht (1937: 262).
- Calligaster javana; Dalla Torre 1904: 17 (cat.).
- "Zethus erythrostomus Cameron" Meade-Waldo, 1914: 404, "Java", holotype [by monotypy] (BMNH), as a synonym of *Calligaster cyanopterus* de Saussure. Available under Article 11.6.1 of the International Code of Zoological Nomenclature.

Diagnosis. *Calligaster cyanoptera* is distinguished from its congeners by the combination of the following characters: metasomal tergum I in lateral view moderately convex dorsally, with distinct preapical depression (Fig. 3), in dorsal view nearly parallel-sided, relatively slender, about 2.5 times as long as its maximum width (Fig. 7); female clypeus in frontal view about 1.5 times as wide as high, with ventral margin more or less truncated rather than broadly rounded (Fig. 10); male clypeus in frontal view about 1.5 times as wide as high, with semi-elliptic emargination at ventral margin (Fig. 14); tergum I hardly punctured, so that dorsal striae are more or less conspicuous (Fig. 7).

Material examined. JAVA: 13° (MZB), Tjikadjang, Bandjarwangi, alt. 8–900 m, 7–10.iv.1939, M.A. Lieftinck; 13° (MZB), Priangan, Gn. [= "Mt."] Limboeng, alt. 1000 m, 28.vii.1934, M.A. Lieftinck; 19° (MZB), Priangan, Gn. Limboeng, 1000 m, 28.vii.1934, M.A. Lieftinck; 23° (MZB), Djampang, Gn. Tjimerang, xii.1932, M. E. Walsh; 19° (MZB), Djasinga, 4.xii.1938, M. A. Lieftinck; 13° (MZB), Djampang Tengah, G. Tjisoeroe, alt. 600–800 m, 1933, M. E. Walsh; 13° (MZB), G. Gedeh, Tjiboenar, 14.xi.1929, F.C. Drescher; 13° (MZB), Tjipanas, 19.xii.1930; 39° (MZB), Soekanegara, alt. 400–1000 m, ii.1940, native coll.; 13° (MZB), Pelaboean Ratoe, 16-17.iv.1933, M.A. Lieftinck; $13^{\circ} 29^{\circ}$ (MZB), Priangan, Mt. Limboeng, alt. 900 m, 30.vii.1934, M.A. Lieftinck; 13° (MZB), Cikaniki, Gn. Halimun, Sukabumi, alt.



Figures 1–9. *Calligaster* species. 1–9 Female 1, 2, 6 *C. viridipennis* 3, 7 *C. cyanoptera* 4, 8 *C. williamsi* 5, 9 *C. himalayensis* 1 Body, lateral view 2 Head, frontal view 3–5 Metasomal segments I–II, lateral view 6–9 Metasomal tergum I, dorsal view. Scale 1 mm.

950 m, 8.viii.1997, Zamilah et al.; 1 (MZB), Cikaniki, Gn. Halimun, Sukabumi, alt. 950–1000 m, 26.iv–2.v.1999, T. Ueno, M.R. Sofyan; 1 (MZB), 2.v.1937, Mt. Salak; 1 (MZB), Mt. Gede, i.1935; 1 (MZB), Djasinga, 2.viii.1952, Amsari; 1 (MZB), Gn. Tjimerang, 600 m, Bodjongkulong, Djampang Tengah, iii.1941,

native coll.; $5 \ 3 \ 3$ (MZB), Mt. Gede, 1000 m, i.1935, native coll.; $1 \ 3$ (MZB), Gn. Halimun Nat. Park, Cikaniki, 06°45'04"S 106°31'31"E, alt. 925 m, 15.ix.1999, W.A. Noerdjito; $1 \ 3$ (MZB), Sukabumi, Jampang, Bojong Pari, 07°10'S 106°37'E, 29.iii.2002, R. Ubaidillah; $1 \ 3$ (MZB), Penandjoeng bay, Kalipoetjang, alt. 300 m, vi.1936, M.A. Lieftinck; $1 \ 3$ (MZB), Batoerraden, Gn. Slamat, Java, 23.xii.1928, F.C. Drescher; $1 \ 3$ (MZB), Batoerraden, Gn. Slamat, Java, 9.vii.1939, F.C. Drescher; $3 \ 1 \ 3$ (MZB), Cisompet, Garut, W. Java, 4.vii.2013, H. Nugroho & J. Kojima. BALI: $2 \ 3$ (MZB), Baturiti, Tabanan, 13.ix.2013, H. Nugroho et al.

Distribution. Sumatra Is. (Marang), Java Is., Bali Is. (new record).

Remarks. In his monograph on solitary vespid wasps, de Saussure (1852) described *Calligaster cyanoptera* based on at least two (the body length was mentioned as "20 á 25 mill. [20 to 25 mill.]") females from "Java". The syntypes were indicated to be in "Musée de Leyde" (de Saussure 1852: 24), but no one has referred to the syntypes. Gribodo (1892: 261) described *Zethus (Calligaster) javanus* based on a single male from "Kaliparè [in Malang] (Giava orientale [East Java])", and van der Vecht (1937: 262) synonymized it under *C. cyanoptera*, stating "... GRIBODO's species is undoubtedly conspecific with *C. cyanopterus* ... the shape of the clypeus is very different in the two sexes". Meade-Waldo (1914: 204) published, as a synonym of *C. cyanopterus* de Saussure, 1852, "*Zethus erythrostomus* Cameron", which was actually an unpublished Cameron's manuscript name for a female specimen from Lawang, East Java (Bequaert 1928: 157).

This species have so far been recorded from Sumatra Is. (Gribodo 1892: 260) and Java Is. (de Saussure 1852, Gribodo 1892, van der Vecht 1937, 1938; our own data as listed below), and we herewith firstly record the species from Bali Is. We also collected a couple of nests made on tree twigs along the creek at Baturiti, Bali; their structure is basically the same as that from the south of Garut, West Java, described by van der Vecht (1938).

Calligaster etchellsii (Cameron, 1909)

- Zeuthus [!] etchellsii Cameron, 1909: 206, ♂, "Kuching, Borneo", holotype [by mono-typy] (BMNH).
- Calligaster etchellsii; Bequaert 1928: 157 (holotype examined; notes).

Remarks. This species was described based on a single male specimen from "Kuching, Borneo" in combination with *Zethus* (Cameron 1909: 206) and Bequaert (1928: 157) moved it to the genus *Calligaster*. Neither other records of this species have so far been published nor have we collected any wasps of this species in our rather intensive field collection at several places in Kalimantan.

Bequaert (1928: 157), having examined the holotype (by monotypy), stated "... quite a distinct species in the shape of the clypeus, which is unusually wide (twice as broad as high) and ends in a deep semi-elliptic emargination." Such a deep semi-



Figures 10–18. Calligaster species. 10–13 Female. 14–18 Male 10, 14, 17 C. cyanoptera 11 C. viridipennis 12, 15, 18 C. williamsi 13, 16 C. himalayensis 10–13 Female clypeus 14–16 Male clypeus 17, 18 Apex of male antenna. Scale 1 mm.

elliptical emargination at the ventral margin of the male clypeus is also found in *C. cyanoptera*, while the male clypeus in the latter is about 1.5 times as wide as high.

Material examined. No specimen examined.

Distribution. Only the type locality [Kuching in Sarawak, Borneo Is.].

Calligaster himalayensis (Cameron, 1904)

Figs 5, 9, 13, 16

Zethus himalayensis Cameron, 1904: 13, ♀, "Sikkim" (BMNH).
Calligaster himalayensis; Bequaert 1928: 157 (holotype examined; possibly a valid species).
Zethus hymalayensis [!]; Giordani Soika 1941: 216 (incorrect spelling of Zethus himalayensis Cameron; syn. of C. cyanopterus de Saussure).

Diagnosis. The characters which may allow us to differentiate *C. himalayensis* from *C. cyanoptera* are as follows [characters for *C. cyanoptera* are given in the brackets]: Metasomal segment I in dorsal view shorter and stouter (Fig. 9), about 1.8 times as long as its maximum width [slender, about 2.5 times as long as its maximum width (Fig. 7)]; tergum I with dorsal striae inconspicuous, in consequence of strong and distinct punctures [dorsal striae conspicuous; tergum with nearly no punctures]; mesoscutum strongly punctured, also in areas along notauli [strongly punctured, but areas along notauli with no punctures]; scutellum and metanotum with denser, larger and deeper punctures than those in *C. cyanoptera*; dorsal face of propodeum with strong

punctures along the border with the posterior face [glossy, nearly without punctures]; lateral face of propodeum with denser and deeper punctures [punctures sparser, interspaces between punctures wider than diameter of a puncture]; male antennal scape yellow ventrally [black entirely]; interantennal space with paired yellow spots [usually absent in female, rarely absent in male]; female clypeus black entirely [black with wide reddish-brown transverse band ventrally]; male clypeus with large yellow spot occupying nearly entire disk of clypeus [closely paired yellow spots in ventral part, but occasionally lacking].

Material examined. VIETNAM: 1 (IUNH), Me Linh, emerged from a nest collected on 9.iii.2005, F. Saito et al. [the nest, in its structure, is similar to that of *C. cyanoptera* we observed and that of *C. williamsi* described by Williams (1919)]; $1 \stackrel{\circ}{\hookrightarrow} 1$ (IEBR), Kim Hy National Park, Bac Kan, 5.viii.2012, L.T.P Nguyen et al.

Distribution. Sikkim, China, Laos, northern parts of Vietnam.

Remarks. Cameron (1904: 13) proposed *Zethus himalayensis* for a single female from "Sikkim [India]" and Bequaert (1928: 157) moved it to the genus *Calligaster*. Bequaert (1928: 157), having examined the holotype, mentioned that "Although similar to *C. cyanopterus*, it appears to differ in the shape of the clypeus and is possibly a valid species." Based on the comparison of our specimens from Vietnam [given under "Material examined"] with those of *C. cyanoptera* from Java and Bali, we recognized that *C. himalayensis* differs from the latter in having stronger and more distinct punctures.

Other than the locality given in the original description (Sikkim in India), *C. himalayensis* has been recorded from China (Giordani Soika 1960; without giving any specific localities). We have herein firstly recorded the species from northern parts of Vietnam (new record), suggesting that *C. himalayensis* may occur along the eastern slope of the Himalayas from Sikkim to northern parts of Vietnam, and probably to southeastern parts of China.

Calligaster viridipennis Giordani Soika, 1960

Figs 1, 2, 6, 11

Calligaster viridipennis Giordani Soika, 1960: 72, fig. 11 (nos. 7–8), 74, ∂, "*Celebes*: Enrekang", holotype (ZMB).

Remarks. Giordani Soika (1960: 72, 74) proposed *Calligaster viridipennis* for a single male from "*Celebes*: Enrekang". Since then, no information on this species has been added.

Based on the specimens recently collected in Central and Southeast Sulawesi we describe below the female of this Sulawesi-endemic *Calligaster* wasp for the first time.

The female can be associated with the male by the combination of the following characters: posterior face of propodeum strongly and reticulately punctured; basal fossa of metasomal sternum II deep and distinct, with dense fulvous hairs; wings fuscous, with strong greenish-purple iridescence.



Figures 19–22. *Calligaster cyanoptera.* **19** Female from Garut, West Java **20** Single cell nest from Garut, West Java **21** Nest with a newly constructed cell (made of cuts of fresh leaves) from Garut, West Java **22** Nest from Bali.

Female characters. Body length (head + mesosoma + metasomal segments I and II) 21–22 mm; fore wing length 20 mm. Head in frontal view subcircular, slightly wider than high, 1.2 times as wide as high (Fig. 2). Clypeus in profile smoothly and weakly convex; in frontal view about 1.5 times as wide as high (Fig. 11), with dorsal margin deeply emarginate medially and ventral margin slightly convex.

Mesosoma flattened dorsoventrally, 1.5 times as long as high in lateral view (Fig. 1); in dorsal view 1.4 times as long as wide. Propodeum with posterior face strongly and reticulately punctured (instead of rugosely striated). Metasomal segment I shorter than mesosoma, 0.8 times as long as mesosoma; tergum I strongly convex dorsally (Fig. 1) [moderately convex in *cyanoptera*]; tergum in dorsal view strongly convex along lateral margins, with faint oblique striae (Fig. 6). Metasomal sternum II with basal fossa as in *C. cyanoptera*, but distinct and deeper, with dense fulvous hairs.

Body densely covered with dense whitish pubescence; tibia and tarsi with golden pubescence. Head strongly punctured, but vertex and gena only sparsely with smaller punctures. Mesosoma strongly punctured; mesoscutum, scutellum and metanotum with punctures sparser and smaller, as those on vertex and gena. Metasomal segment I with punctures slightly stronger than those on *C. cyanoptera*; tergum I with punctures smaller than those on mesonotum; tergum II with small and superficial punctures, regularly arranged from base to apex.

Body black, without markings. Wings fuscous, with greenish-purple iridescence.

Material examined. SULAWESI: $3 \[Gamma] 1$ (NMST), Palu, Palolo, $[2 \[Gamma] 1$, vii.1995; $1 \[Gamma]$, i.1991], Mokuyosha; $1 \[Gamma] (MZB)$, North Kolaka, Tinukari, Mekongga, $03^{\circ}38'17''S$, $121^{\circ}11'31''E$, alt. ca. 1430 m, 17.vii.2011, R. Ubaidillah et al.; $1 \[Gamma] (MZB)$, Luwuk timur, Towuti, Soroako, $03^{\circ}35'10''S$, $121^{\circ}24'06''E$, alt. ca.450 m, 1–5.i.2007, A. Suwito & E. Cholik.

Distribution. Sulawesi Is. (central, south, and southeast Sulawesi).

Calligaster williamsi Bequaert, 1940

Figs 4, 8, 12, 15, 18

Zethus (Calligaster) cyanopterus; Williams 1919: 157–164 (natural history). *Calligaster* n. sp.; van der Vecht 1937: 263.

Calligaster williamsi Bequaert, 1940: 124, fig. 1 A–D, ♀♂, "Los Baños, Luzon, Philippine Is.", holotype female (MCZ).

Diagnosis. *Calligaster williamsi* can be distinguished from its congeners by the combination of the following characters: metasomal tergum I in lateral view barely convex dorsally, with preapical dorsal depression weakly produced (Fig. 4), in dorsal view weakly and evenly convex laterally (Fig. 8); longitudinal striae on tergum I strong, more or less regularly arranged (Fig. 8); apex of male terminal antennal flagellomere rounded [Fig. 18; bluntly pointed in *C. cyanoptera* (Fig. 17)].

Material examined. LUZON: 1 \bigcirc (IUNH), Los Banos, Laguna, 31.iii.1978, T. Murota; 2 \bigcirc 1 \checkmark (IUNH), Los Banos, Laguna, 2-5.viii.1978, H. Kurokawa; 1 \bigcirc (IUNH), Univ. Phil. Los Banos, Laguna, 21.iii.1980, J. Kojima; 1 \checkmark (IUNH), Univ. Phil. Los Banos, Laguna, 10.iii.1980, J. Kojima; 1 \checkmark (IUNH), Univ. Phil. Los Banos, Laguna, 1 \checkmark (IUNH), Univ. Phil. Los Banos, Laguna, 1 \checkmark (IUNH), Univ. Phil. Los Banos, I. Kojima; 1 \checkmark (IUNH), III (III), III), III), III), III (III), III), III),

18.vi.1977, Y. Kurosawa. MINDANAO: 1♀ (NSMT), N. Zamboanga, 5.xii.1994, J. Abella, Nagase coll.; 1♀ (NSMT), Aras-asan, Surigao, S. Mindanao, x.1978.

Distribution. Philippines: Luzon Is., Mindoro Is., Mindanao Is.

Remarks. Van der Vecht (1937: 262) pointed out that the Philippine species of *Calligaster*, of which life history was described by Williams (1919) under the name of *Zethus (Calligaster) cyanopterus*, was "not conspecific with *C. cyanopterus*" and mentioned that the species "will be described in a forthcoming paper by Prof. J. Bequaert." Bequaert (1940: 124–126) proposed *Calligaster williamsi* for the females and males from several places on Luzon Is. and Mindoro Is., with designation of a female from "Los Baños, Luzon" as the holotype.

As listed above, we examined specimens also from Mindanao Is., suggesting this species would be distributed throughout the Philippines Islands except for Palawan Is.

Calligaster zetteli Gusenleitner, 2006

Calligaster zetteli Gusenleitner, 2006: 1353, ♀, "Philippinen ... Bais Forest, Negros-Oriental Province", holotype (USC).

Material examined. No specimen examined.

Remarks. Gusenleitner (2006: 1353–1355) proposed *Calligaster zetteli* for females from Negros, Bohol, and Mindanao Islands, as a species similar to *C. williamsi*. According to Gusenleitner (2006), this species may be differentiated from *C. williamsi* by the characters given in the key to *Calligaster* species [for complete comparison see Gusenleitner (2006: 1354)].

Distribution. Philippines: Negros Is., Bohol Is., Mindanao Is.

Acknowledgments

This study is supported by the JSPS–LIPI Bilateral Research (2012–2015). We are thankful to A. Shinohara (NSMT) for arranging a loan of specimens and the ICBG Project, University California-Davis – LIPI for the specimens from southeast Sulawesi. We thank to J. M. Carpenter and an anonymous reviewer for comments on the manuscript.

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RESEARCH ARTICLE



Taxonomy, distribution and bionomics of Celonites tauricus Kostylev, 1935, stat. n. (Hymenoptera, Vespidae, Masarinae)

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Academic editor: <i>M. Ohl</i>	Received 18 October 2015	Accepted 30 December 2015	Published 1 March 2016
	http://zoobank.org/388B0CD9-07()B-4409-AAEC-B0E5C8ACDFBD	

Citation: Mauss V, Fateryga AV, Prosi R (2016) Taxonomy, distribution and bionomics of *Celonites tauricus* Kostylev, 1935, stat. n. (Hymenoptera, Vespidae, Masarinae). Journal of Hymenoptera Research 48: 33–66. doi: 10.3897/JHR.48.6884

Abstract

Male and female of *Celonites abbreviatus tauricus* Kostylev, 1935 are redescribed and a neotype is designated. Based on morphological characters *Celonites a. tauricus* is synonymized with *Celonites spinosus* Gusenleitner, 1966 and *Celonites abbreviatus invitus* Gusenleitner, 1973. The taxon is hypothesized to be reproductively isolated from *Celonites abbreviatus* Villers, 1789 by differences in the male genitalia and in the colour pattern of the male antennae and is therefore regarded as a separate biospecies named *Celonites tauricus*. *Celonites tauricus* is allopatrically distributed with regard to *C. abbreviatus* and has been recorded from the Crimea, Kos, Asia Minor and Cyprus. Within this range six intraspecific taxa can be separated by morphological characters and colour patterns. Habitat, flower association, flower visiting behaviour, mate seeking behaviour and nesting of *C. tauricus* are almost similar to *C. abbreviatus*.

Keywords

Hymenoptera, Vespidae, Masarinae, *Celonites*, taxonomy, bionomics, Palaearctic, Crimea, Asia Minor, Cyprus, flower association, Lamiaceae, female brood care

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Introduction

Nearly 100 years ago the first specimen of a species of the pollen wasp genus *Celonites* Latreille, 1802 was recorded from the Crimea. It was a single female collected by V.N. Wuczeticz on 13 June 1916 on the southern slope of Karagach in the Karadag (Kostylev 1928; original spelling "Karagatsh") which is a small mountain massive on the south-eastern coast of the Crimea. Kostylev (1928) identified the specimen as Celonites abbreviatus (Villers, 1789). Seven years later he formally described the Celonites taxon from the Crimea as a new subspecies of C. abbreviatus named Celonites abbreviatus tauricus Kostylev, 1935. He noted that specimens from the Crimea differed from specimens from the Caucasus by finely serrate margins of the second and subsequent terga and concluded that they possibly belong to a different subspecies (Kostylev 1935). Kostylev did not designate any type specimens of the subspecies either in his original description or in any further publication. Moreover, it is unknown how many specimens were available to him, when he described the taxon. In his world checklist of masarine wasps Carpenter (2001) recognized C. a. tauricus as a valid taxon. He speculated that the holotype of C. a. tauricus might be in the collection of the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg (Russia), but we could not find it there, though carefully searching for it. The holotypes of all other wasp species described by Kostylev are deposited in the Zoological Museum of the Lomonosov Moscow State University in Moscow (Russia). These types are stored in a separate box apart from the main collection. There is no specimen of *Celonites* from the Crimea in the "type box" or in the main collection, whereas all other wasps from the Karadag listed by Kostylev (1928) are there. It can be assumed, that Kostylev (1935) based his description on the female collected by Wuczeticz. Therefore, the type locality was probably situated in the Karadag Mountains (as reported by Kostylev 1928). Evidently Wuczeticz's specimen and any further material (if it had ever existed) have been lost.

In 1966 Gusenleitner described a new species belonging to the *Celonites abbreviatus*-complex from western Turkey, named *Celonites spinosus*. He argued that this taxon could not be identical with *C. a. tauricus* Kostylev, based on the incorrect translation or interpretation of Kostylev's description, that antennal article A3 should not be longer than A4+A5 in *C. a. tauricus*. In fact, Kostylev attributed this character state explicitly to a specimen from Spain and stated that A3 is longer than A4+A5 in *C. a. tauricus*, which is similar to *C. spinosus*. Moreover, in both taxa the posterior margins of the metasomal terga II–V were described as "serrated" or "spine-like crenulated" respectively (Kostylev 1935, Gusenleitner 1966), indicating further similarity between them.

Another subspecies of *Celonites abbreviatus* named *invitus* was described by Gusenleitner in 1973 from central Turkey and Armenia. He separated this taxon from *C. abbreviatus* by the very shiny cuticula of vertex and mesosoma and the incomplete colour banding on the metasomal terga III–V. As a result of the investigation of further material, Gusenleitner in 1985 recognized *C. a. invitus* as an eastern form of *C. spinosus* and synonymized both taxa formally.

A specimen of *Celonites abbreviatus tauricus* was first collected from the Crimea in 1916, but none were recorded in the following 86 years. Then in 2002 two specimens were collected in the Karadag Nature Reserve (Fateryga and Ivanov 2009). Following this find intensive field research led to the discovery of nine localities of *C. a. tauricus* on the Crimean peninsula (Fateryga and Ivanov 2010). In addition, it was discovered that a previously unnoticed specimen of *C. a. tauricus* had been collected in the Crimea in 1963 (Ivanov and Fateryga 2009), indicating the continuous existence of an endemic *C. a. tauricus* population in the area. Further field observations provided some bionomical data concerning flower associations and nesting (Ivanov and Fateryga 2009, Fateryga 2010, Fateryga and Ivanov 2010). However, until now the taxonomic identity and status of *C. a. tauricus* with regard to *C. abbreviatus* and *C. spinosus* had not been studied and remained uncertain.

The purpose of the study presented below was to revise the taxonomic status of *Celonites abbreviatus tauricus*, to designate a neotype, to describe both sexes and to summarize and discuss what is known of the distribution, geographical variation and bionomical characters of the taxon.

Material and methods

The specimens of *Celonites* studied belong to the public collections of the Taurida Academy of the Vernasdskiy Crimean Federal University (Simferopol, Russia) (VTNU), the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia) (ZIN), the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine (Kiev, Ukraine) (IZAN), the Kharkov Entomological Society (Kharkov, Ukraine) (KHEO), and the Upper Austrian State Museum (Linz, Austria) (OLML), as well as to the private collections of A.V. Amolin (Donetsk, Ukraine) (AA), J. Gusenleitner (Linz, Austria) (JG), V. Mauss (Michelfeld, Germany) (VM), S.A. Mosyakin (Simferopol, Russia) (SM), D.V. Puzanov (Yevpatoriya, Russia) (DP), C. Saure (Berlin, Germany) (CS), C. Schmid-Egger (Berlin, Germany) (CSE) and E. Yildirim (Erzurum, Turkey) (EY). Without success we searched for material of the taxa under consideration in the collections of the Zoological Museum of the Lomonosov Moscow State University (Moscow, Russia), the Bavarian State Collection of Zoology (Munich, Germany) and the Stuttgart State Museum of Natural History (Stuttgart, Germany).

The specimens were investigated under a WILD M3 stereo microscope (maximum magnification 80 times). Measurements of the exoskeleton were made using an ocular micrometer (highest resolution 0.011 mm). The genitalia of all males were extracted after re-softening the specimens and were then studied in 80% ethanol. Drawings were made with a drawing tube (WILD Type 308700). Micro-photos were taken with a Leica IC 80 HD camera mounted on a Leica MS 5 stereomicroscope. Multifocus-pictures were generated with Leica Application Suite (LAS) software. The scapus of the antenna is referred to as antennal article A1 and the pedicellus as A2, the flagellum consists of the articles A3–A12.

Systematic bionomical observations were made on the Crimea population by A. Fateryga at Cape Aya in 2004, in the vicinity of Veseloye near Sudak in 2004, and in Lisya Bay from 2005 until 2014 (for details see material studied), and documented using a Canon Powershot A570 IS.

The Kos population was studied by V. Mauss from 25 May to 4 June 2015 (for details see material studied). Observations were made with a close-up binocular (Pentax Papilio 8.5×21) and documented with a Canon EOS 70D with a 180 mm macro-lens (scale up to 1:1, resolution 20 mega pixel) and macro flash-lights. Time intervals were measured using a digital stop-watch. Specimens of flowering plants were collected and preserved dried. The material was placed in the herbarium of the Stuttgart State Museum of Natural History (Herbarium STU). The plant taxa were identified following Pils (2006) and Tutin et al. (1964–1980). Flower preferences of imagines were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the area at six localities (total investigation time 11.30 h). Flower visiting behaviour of the imagines at Satureja thymbra and Thymus capitata was investigated at various patches of these plants at six localities for 19.45 h in total. From three localities pooled pollen samples from the crops of up to three females previously fixed in Duboscq-Brasil solution (Romeis 1989) were prepared using the method outlined by Westrich and Schmidt (1986). The different pollen types were ascertained under a light microscope at magnifications of 400× or 1000× and determined to generic level with the aid of a reference collection consisting of pollen samples of 500 mainly Mediterranean plant species.

Systematics

Celonites tauricus Kostylev, 1935, stat. n.

- Celonites abbreviatus tauricus Kostylev, 1935, Arch. Mus. Zool. Univ. Moscou 2: 108 [Since the original type material is lost, we hereby designate a new specimen as a Neotype: 1♀ (dbM 4305), Crimea, Vicinity of Feodosiya: Lisya Bay, 44°54'N 35°09'E, leg. A. Fateryga 16.06.2010, coll. OLML, figs 1a, 2, 5]
- *Celonites spinosus* Gusenleitner, 1966, Polskie Pismo Entomol. 36: 359–362, figs 2a, b, c [Holotype: 1♀ (dbM 4665), Turkey, Kusadasi, leg. J. Gusenleitner 11.06.1964, coll. JG]
- Celonites abbreviatus invitus Gusenleitner, 1973, Boll. Mus. Civ. Stor. Nat. Venezia 24: 58, fig. 2b [Holotype: 12 (dbM 4662), Turkey, Gürün, 44°54'N, 35°09'E, leg. J. Gusenleitner 05.06.1970, coll. JG]
- *Celonites abbreviatus* (Vill.) *invitis* Gusenl.; Schmidt 1984, Steir. Entomologenrunde 18: 89, misspelling

Material studied. Taxon 1 (Crimea, "tauricus")

Russia: *Crimea:* Alushta, 44.666667°N, 34.41667°E, 06.07.1963, 1♀ IZAN; Simferopol, Marino, 44.91667°N, 34.11667°E, 31.07.2007 1♀ leg. A. Fateryga VTNU;
Vicinity of Feodosiya: Karadag Nature Reserve, 44.91667°N, 35.21667°E, 07.07.2002 1∂ (dbM No. 4704) 1♀ (dbM No. 4702) leg. S. Ivanov VM; Vicinity of Feodosiya: Lisya Bay, 44.90000°N, 35.15000°E, 22.06.2003 1^Q (dbM No. 4306) leg. S. Ivanov VM 1º leg. S. Ivanov VTNU 1º leg. S. Ivanov IZAN, 06.07.2005 1º leg. A. Fateryga VTNU 1♀ leg. A. Fateryga IZAN, 13.06.2007 2♀♀ leg. A. Fateryga VTNU, 25.06.2009 1♀ leg. S. Ivanov VTNU 1♀ leg. S. Ivanov ZIN, 27.06.2009 1♀ (dbM No. 4701) leg. A. Fateryga VM 1º leg. A. Fateryga VTNU, 12.06.2010 1d (dbM No. 4308) leg. A. Fateryga VM, 16.06.2010 1^Q (dbM No. 4305) leg. A. Fateryga VM, 09.07.2012 1º (dbM No. 4304) leg. A. Fateryga VM; Vicinity of Opolznevoye in the Yalta Mountain Forest Reserve, 44.40000°N, 33.93333°E, 04.07.2006 1♀ leg. S. Ivanov VTNU; Vicinity of Sevastopol: Cape Aya, 44.41667°N, 33.65000°E, 05.07.2004 1 (dbM No. 4705) leg. A. Fateryga VM 1 leg. A. Fateryga VTNU 1 leg. A. Fateryga IZAN 1 A. Fateryga KHEO 1 leg. A. Fateryga AA 1 S. Ivanov VTNU, 07.07.2004 1 leg. S. Naumenko DP, 08.07.2004 1 (dbM No. 4703) leg. A. Fateryga VM 1∂ leg. A. Fateryga ZIN 1∂ leg. A. Fateryga DP 1♀ leg. A. Fateryga VTNU, 07.2004 1 \bigcirc leg. L. Svolynskaya SM 1 \bigcirc V. Gromenko AA 1 \bigcirc V. Gromenko KHEO; Vicinity of Veselove near Sudak, 44.86667°N, 34.88333°E, 02.07.2004 1 leg. D. Puzanov VTNU; Yalta, Sovetskoye, 44.51667°N, 34.18333°E, 05.06.2010 1 (dbM No. 4307) leg. S. Ivanov VM.

Taxon 2 (Kos)

Greece: Dodekanes, Island Kos: SE Mastichari, 36.833333°N, 27.083333°E, 31.05.-01.06.2003 222 (dbM No. 3607, 3608) leg. J. Tiefenthaler OLML; 1 km SE Mastichari, Hang mit Phrygana Fragment unterhalb Kapelle, 36.841317°N, 27.085367°E, 50 m, 26.05.2015 2♀♀ (dbM No. 4776, 4777) leg. V. Mauss VM; 2 km N Kefalos, Phrygana E des Berges Korakies, 36.765583°N, 26.960067°E, 110 m, 27.05.2015 299 (dbM No. 4778, 4797) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana W Agia Anastasia, 36.719300°N, 26.924533°E, 40 m, 31.05.2015 2♀♀ (dbM No. 4783, 4795) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana W Agia Anastasia, 36.719983°N, 26.930767°E, 90 m, 31.05.2015 1♀ (dbM No. 4782) V. Mauss VM, 02.06.2015 222 (dbM No. 4792, 4793) leg. V. Mauss VM, 04.06.2015 2♂♂ (dbM No. 4789, 4790) 3♀♀ (dbM No. 4788, 4794, 4798) leg. V. Mauss VM; 4 km SW Kefalos, Phrygana in sandigem Trockenflusstal N Cape Kata, 36.727733°N, 26.922833°E, 20 m, 31.05.2015 1∂ (dbM No. 4785) 1♀ (dbM No. 4784) leg. V. Mauss VM, 03.06.2015 1^Q (dbM No. 4796) leg. V. Mauss VM; 4 km W Andimachia, Phrygana Fragment nahe "Hippokrates Garden", 36.813783°N, 27.051233°E, 60 m, 28.05.2015 1∂ (dbM No. 4780) 1♀ (dbM No. 4779) leg. V. Mauss VM, 31.05.2015 1 (dbM No. 4781) 1 (dbM No. 4791) leg. V. Mauss VM, 04.06.2015 1♂ (dbM No. 4787) 1♀ (dbM No. 4786) leg. V. Mauss VM.

Taxon 3 (Western Asia Minor, "spinosus")

Turkey: Ankara: 15 km S Ankara, Beynam, 39.685958°N, 32.895143°E, 23.07.1987 1♀ (dbM No. 4682) leg. Kl. Reinhold JG; Kizilcahamam N of Ankara, 40.470123°N, 32.648873°E, 09.07.2000 3♂♂ (dbM No. 3597, 3598, 3599) leg. M. Halada OLML. – Antalya: 100 km E Antalya: S von Taskesigi, 36.753821°N,

31.633813°E, 1998 3♂♂ (dbM No. 3586, 4511, 4512) leg. M. Halada OLML; 50 km NE Antalya, 37.183333°N, 31.183333°E, 550 m, 17.06.2001 1Q(dbM No. 3585) leg. J. Straka OLML; Alanya, 36.558341°N, 31.997983°E, 20–24.05.1993 1 (dbM No. 3431) leg. A. Kudrna OLML; Arapsuyu, 36.874761°N, 30.653459°E, 5 m, 30.06.2002 1^Q (dbM No. 4526) leg. H. Özbek EY. – *Aydin:* Kusadasi, 37.857802°N, 27.257981°E, 11.06.1964 3♂♂ (dbM No. 4693, 4694, 4695) 1♀ (dbM No. 4665) leg. J. Gusenleitner JG. - Bilecik: wn. Osmaneli, 40.356692°N, 30.001768°E, 14.06.1997 1º (dbM No. 3429) leg. M. Halada OLML. - Burdur: 28 km SEE Burdur, 37.6666667°N, 30.4666667°E, 1350 m, 08.07.2006 1♀ (dbM No. 3591) leg. M. Halada OLML. -Denizli: Cardak, 37.826119°N, 29.672490°E, 07.06.1964 1∂ (dbM No. 4697) leg. J. Gusenleitner JG; Pamukkale, 37.921213°N, 29.114931°E, 31.05.1966 1♀ (dbM No. 4674) leg. K. Kusdas JG. - Izmir: 10 km NE Ödemis, 38.333333°N, 28.0666667°E, 1200 m, 03.07.2006 1 (dbM 3596) 1 (dbM No. 3592) leg. M. Halada OLML; Izmir, 38.417154°N, 27.129925°E, 12.06.1964 12 (dbM No. 4666) J. Gusenleitner JG 1♂ (dbM No. 4696) 2♀♀ (dbM No. 4670, 4681) leg. H.H.F. Hamann JG; Tar.Ars.Enst. Menemen, 38.613484°N, 27.077789°E, 02.07.1992 12♀♀ (dbM No. 4530, 4531, 4532, 4533, 4534, 4535, 4536, 4537, 4538, 4539, 4540, 4541) leg. H. Özbek EY. – *Kayseri:* 25 km S Kayseri, 38.540470°N, 35.490265°E, 23.07.2003 1♀ (dbM No. 3593) leg. J. Straka OLML. - Konya: 30 km S of Aksehir, 38.188770°N, 31.495138°E, 24.06.1998 2♂♂ (dbM No. 3587, 4510) 1♀ (dbM No. 3428) leg. J. Halada OLML; Alti-Napa-Baraji, 37.880339°N, 32.303139°E, 12.06.1978 1 (dbM No. 4675) leg. J. Schmidt JG; Sille bei Konya, 37.929344°N, 32.420692°E, 09–17.06.1975 1^Q (dbM No. 4667) leg. J. Schmidt JG, 08.06.1978 1^Q (dbM No. 4676) leg. J. Schmidt JG, 12.06.1978 299 (dbM No. 4677, 4678) leg. J. Schmidt JG; W Seydisehir, 37.423314°N, 31.824113°E, 1800 m, 04.08.1991 1♀ (dbM No. 3632) leg. K. Warncke JG. - Nevsehir: Göreme, 38.642663°N, 34.830003°E, 1000 m, 20.07.1986 1^Q (dbM No. 4684) leg. Blank JG. – Usak: 7 km NW Sivasli, 38.58333°N, 29.58333°E, 21.05.1983 3♀♀ (dbM No. 4687, 4688, 4689) leg. Aspöck, Rausch, Resel JG; Between Usak and Sivasli (= 27 km SE Usak), 38.61667°N, 29.58333°E, 830 m, 21.05.1983, 1^Q (dbM No. 4686), leg. E. Hüttinger JG. – Region unkown: Versilkogy oberhalb, 31.05.2007 1♀ (dbM No. 4725) CSE.

Intermediate between Taxon 3 and 4

Turkey: Agri: 40 km N Muradye, 39.246612°N, 43.67878°E, 2200 m, 05.07.2000 1 \bigcirc (dbM No. 3602) leg. M. Halada OLML. – Artvin: Yusufeli Taskiran, 40.803573°N, 41.551595°E, 1350 m, 06.07.2003, 1 \bigcirc (dbM No. 4545) leg. I. Aslan EY; Yusufeli, Morkaya, 40.729267°N, 41.602720°E, 700 m, 15.06.2010 1 \bigcirc (dbM No. 4528) leg. E. Yildirim EY. – Erzincan: W Refahiye, 39.900486°N, 38.759372°E, 2200 m, 23.08.1991 2 \bigcirc \bigcirc (dbM No. 3682, 3683) leg. Halada OLML. – Erzurum: Aribahçe, 40.073708°N, 41.167181°E, 2400 m, 20.07.2001 1 \bigcirc (dbM No. 4529) leg. E. Yildirim EY; Caliyazi-Pasinlei, 40.124501°N, 41.669960°E, 2400 m, 10.07.1997 1 \bigcirc (dbM No. 4543) leg. E. Yildirim EY; Camibel, Oltu,

40.488294°N, 41.762214°E, 1700 m, 14.07.1996 1 \bigcirc (dbM No. 4521) leg. E. Yildirim EY; Dikyar / Uzundere, 40.532510°N, 41.547963°E, 08.09.1996 1 \bigcirc (dbM No. 4522) leg. I. Aslan EY; Pazaryolu, Kumaskaya, 40.531839°N, 40.751973°E, 1800 m, 20.07.2011 1 \bigcirc (dbM No. 4527) leg. S. Çoruh EY; Umudum Yayl., 40.027957°N, 41.246457°E, 2100 m, 08.08.1991 1 \bigcirc (dbM No. 4525) leg. H. Özbek EY. – *Icel:* Sertavul-Ort, 36.885202°N, 33.277297°E, 1300 m, 11.06.1977 1 \bigcirc (dbM No. 4685) leg. J. Schmidt JG. – *Kayseri:* 10 km S Kayseri, 38.616667°N, 35.516667°E, 1660 m, 20.07.2003 1 \bigcirc (dbM No. 3594) leg. J. Straka OLML. – *Nigde:* NO Çamardi, 37.832838°N, 34.986299°E, 2100 m, 10.08.1991 1 \bigcirc (dbM No. 4683) leg. Warncke JG. – *Sivas:* Gürün, 38.720560°N, 37.278278°E, 05.05.1970 1 \bigcirc (dbM No. 4662) leg. J. Gusenleitner JG, 07.06.1970 1 \bigcirc (dbM No. 4663) leg. K. Kusdas JG; 20 km E Gürün: Mezikiran Gecidi, 38.747021°N, 37.151695°E, 10.07.1997 1 \bigcirc (dbM No. 3601) leg. Ma. Halada OLML. – *Tokat:* Tokat, 40.324460°N, 36.553842°E, 900 m, 19.08.1992 1 \bigcirc (dbM No. 4542) leg. E. Yildirim EY.

Taxon 4 (Eastern Asia Minor, "invitus")

Iran: *Elburs:* 50 km S (90 km Straße) Chalus, 36.326699°N, 51.360601°E, 2800 m, 26.07.1977 1 $\stackrel{\circ}{O}$ (dbM No. 3656) 7 $\stackrel{\circ}{Q}$ Q (dbM No. 3649, 3650, 3651, 3652, 3653, 3654, 3655) leg. J. Gusenleitner JG; 75 km S Chalus, 36.142606°N, 51.446689°E, 2400 m, 13.07.1977 2 $\stackrel{\circ}{Q}$ Q (dbM No. 3648, 4664) leg. J. Gusenleitner JG.

Turkey: Adiyaman: Karadut, Nemrut Dag, 37.980373°N, 38.747183°E, 09.06.1998 1 (dbM No. 3430) leg. M. Halada OLML. - Bayburt: Bayrampasa, Demirözü, 40.1729804°N, 39.8201781°E, 31.07.1992 1♀ (dbM No. 4524) leg. H. Bastan EY. - Bitlis: Nemrut Dag, 38.650366°N, 42.218203°E, 2300 m, 15.08.1991 1 $\stackrel{?}{\circ}$ (dbM No. 3630) 1 $\stackrel{\circ}{\downarrow}$ (dbM No. 3629) leg. K. Warncke JG 1 $\stackrel{\circ}{\downarrow}$ (dbM No. 3681) leg. M. Halada OLML. - Erzurum: Palandöken Dagi südwestlich Erzurum: Dutçu, Komyolu, 39.84492°N, 41.25075°E, 2190 m, 28.07.2003 1♀ (dbM No. 2795) leg. V. Mauss & E. Yildirim VM; Palandöken, 39.84492°N, 41.25075°E, 16.08.1987 1♀ (dbM No. 4519) leg. H. Özbek EY, 17.07.1990 1♀ (dbM No. 4520) leg. E. Yildirim EY; Pehlivanli, Tortum, 40.513101°N, 41.484767°E, 29.06.1990 1♀ (dbM No. 4518) leg. E. Yildirim EY. - Hakkari: Tal S Gevria-Pass, 37.499257°N, 43.958866°E, 3000 m, 04.08.1986 1♀ (dbM No. 3634) leg. K. Warncke JG. – Icel: Mut, Passhöhe, 36.630138°N, 33.466345°E, 1520 m, 09.06.1966 1♀ (dbM No. 3578) leg. K. Kusdas JG. – Kars: 50 km S Kars: Pasli, 40.287056°N, 42.964613°E, 01.07.1997 13 (dbM No. 3595) leg. Ma. Halada OLML. - Tunceli: Esil, 39.5667°N, 40.1883°E, 12.06.1983 1♀ (dbM 3631) leg. J. Schmidt JG.

Intermediate between Taxon 4 and 5

Turkey: *Bitlis:* Nemrut Dag, 38.650366°N, 42.218203°E, 2850 m, 08.08.1986 1 \bigcirc (dbM No. 3627) leg. K. Warncke JG, 2300 m, 15.08.1991 1 \bigcirc (dbM No. 3628) leg. K. Warncke JG; Nemrut Dagi, 38.650366°N, 42.218203°E, 2800 m, 07.08.1986 1 \bigcirc (dbM No. 3626) leg. Blank JG; Tatvan, Nemrut Mt. 38.644449°N, 42.214363°E, 2000 m, 23.07.2003 1 \bigcirc (dbM No. 4544) leg. H. Özbek EY. – *Hakkari:* S Varegös / Mt. Sat, 37.3333°N, 44.25°E, 1700 m, 04.08.1982 1 \bigcirc (dbM No. 3633) leg. K. Warncke JG.

Taxon 5 (South-east of Taurus range)

Syria: North Syria: Marbij [Manbij], 36.528792°N, 37.935693°E, 09.05.1996 1♀ (dbM No. 3690) leg. M. Halada OLML.

Turkey: *Icel*: Mut, 36.6464°N, 33.4375°E, 13.06.1965 1 \bigcirc (dbM No. 4668) leg. M. Schwarz JG, 27–30.05.1967 1 \bigcirc (dbM No. 4672) leg. J. Schmidt JG, 28.05.1967 1 \bigcirc (dbM No. 4690) 1 \bigcirc (dbM No. 4673) leg. J. Gusenleitner JG, 06.06.1968 1 \bigcirc (dbM No. 4679) leg. J. Gusenleitner JG 1 \bigcirc (dbM No. 4680) leg. J. Schmidt JG, 19.05.1970 1 \bigcirc (dbM No. 4691) leg. J. Gusenleitner JG. – *Şanliurfa:* Birecik / Urfa, 37.066514°N, 38.104280°E, 22.05.1983 1 \bigcirc (dbM No. 3635) leg. K. Warncke JG; Urfa, 37.165902°N, 38.795883°E, 31.05.1968 1 \bigcirc (dbM No. 4669) leg. J. Gusenleitner JG; Urfa: Urfa Umgebung, 37.165902°N, 38.795883°E, 30.05.1978 1 \bigcirc (dbM 4692) 1 \bigcirc (dbM No. 4671) leg. M. Schwarz JG.

Taxon 6 (Cyprus)

Cyprus: *Troodos:* Mt. Olympos, 34.93°N, 32.86°E, 1900 m, 19.06.2013 $7 \bigcirc \bigcirc$ (dbM No. 4875, 4876, 4877, 4878, 4879, 4880, 4881) leg. C. Saure CS, 20.06.2013 6 $\bigcirc \bigcirc$ (dbM No. 4719, 4720, 4721, 4722, 4723, 4724) $4 \bigcirc \bigcirc$ (dbM No. 4715, 4716, 4717, 4718) leg. C. Schmid-Egger CSE.

Field observations, records from literature. Armenia: Erevan, Monti desertici, Aighpat 40 km SE, 23.07.1963 1 \bigcirc 1 \bigcirc leg. Giordani Soika coll. Giordani Soika det. J. Gusenleitner, GUSENLEITNER 1973 [intermediate between Taxon 4 and 5].

Russia: *Crimea:* Echkidag, 44.89667°N, 35.12167°E, 07.06.2014 field obs. A. Fateryga; Vicinity of Feodosiya: Lisya Bay, 44.90200°N, 35.15805°E, 02.07.2011 nest record A. Fateryga, 27.06.2013 28.06.2013 11.07.2013 10.06.2014 all field obs. A. Fateryga; Vicinity of Sevastopol: Cape Aya, 44.42367°N, 33.66133°E, 05.07.2004 field obs. A. Fateryga; Vicinity of Veseloye near Sudak, 44.86667°N, 34.88333°E, 02.07.2004 nest record D. Puzanov det. A. Fateryga [all Taxon 1].

Diagnosis. Axilla of mesoscutellum with short blunt lateral projection that only slightly projects over adjacent posterior part of tegula. Frons and clypeus covered with pale, stiff pollen collecting setae, about as long as diameter of median ocellus. In females most of these setae with tiny spherical enlargement at tip ("knob"), in males setae with distal enlargement only present in centre of frons. Cuticula of frons and clypeus dull and densely shagreened. Males with only two oval-shaped tyloids situated ventral on articles A9 and A10 of club-shaped antennae and small spine anterior at distal end of midcoxa. Posterior margin of metasomal tergum VII divided into four lobes.

Separated from *Celonites abbreviatus* by distinctly different colouration of club of antenna: Club has a dark tip, that is, at least distal end of A12 is blackish markedly contrasting on ventral side to adjacent light reddish brown area of antennal club. On dorsal side blackish marking extends usually over distal parts of A11 fading gradually towards proximal end. In *C. abbreviatus* club of individuals from Balkan populations completely orange, in some dark coloured individuals from western populations club becomes darker dorsally, while immediate tip and especially ventral side of A12 remain lighter. Male genital broader than in *C. abbreviatus*, in dorsal view transverse width

of each stipes larger than distance between dorso-medial margins of stipites. Medial process of volsella larger than in *C. abbreviatus*.

Description. Female. Colour: Black. The following are weakly yellowish white (Fig. 1a): two spots on frons; small narrow streak on occiput along occipital carina at dorso-lateral corner of head (absent in two specimens); large spot on antero-dorsal angle of pronotum (humeral spot); stripe along dorso-medial (inner) margin of pronotum, slightly enlarged anteriorly, interrupted in the middle by zone of reddish-brown colour; large spot on dorsal mesopleura; median spot on scutellum of moderate size; dorsal and ventral side of propodeal lamella; continuous posterior band on tergum I extending over lateral margin on ventral part of tergum; posterior bands interrupted on each side of middle into median and two lateral markings on terga II-V (in two specimens not completely interrupted on tergum II). Reddish-brown are: distal two third of mandible; labrum; zone in the middle of whitish stripe along dorso-medial margin of pronotum; tegula except small blackish marking at antero-medial margin; distal part of femora, tibiae and tarsi; sternum I; sternum II, becoming slightly darker posteriorly. Dark to blackish brown are: strongly sclerotized parts of labio-maxillary complex; propleura; coxae, trochanters and proximal part of femora; sterna III-V. Antenna with A1–2 black, distal margin of A2 dark brown, A3 proximally dark brown distally reddish brown, A4-11 reddish brown. A12 at least with distal tip black, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, dorsally extending over distal part of A11 (except in one specimen) fading gradually towards proximal end. Wings translucent blackish-brown.

Structure: Head in front view slightly longer than broad. Clypeus a little broader than long; dull with somewhat sparsely weak macropunctation; densely shagreened; covered with pale, stiff setae arising from weak macropunctures; setae about as long as diameter of median ocellus, with tiny spherical enlargement at tip ("knob") (Fig. 2), few somewhat shorter; some setae on ventro-lateral corners with distal ends curved towards median axis of clypeus; dorso-lateral vertical parts of clypeus more shiny not shagreened with moderately spaced micropunctures. Frons with very weak moderately spaced macropunctation; cuticula dull, densely and strongly shagreened; covered with pale outstanding knobbed setae arising from macropunctures; frontal line weak or absent, not raised to form medial carina. Vertex with close macropunctation becoming more distinct and closely reticulate behind ocelli (Fig. 3), where longitudinal interstices are more strongly raised forming lines; cuticula of interstices shiny, weakly longitudinally striated anterior to ocelli, completely smooth behind them; covered with short setae arising from macropunctures. Compound eye sparsely covered with small setae (Fig. 2). Gena narrow, preoccipital carina sharp. Antennal articles A8-12 forming ventrally flattened club (Fig. 2) slightly more than 2 times as long as broad (viewed dorsally).

Anterior margin of pronotum raised to carina distinctly present along anterior margin of pronotum, especially sharp medially (erroneously termed anterior pronotal carina by Mauss 2013). Short anterior pronotal carina (sensu Carpenter 1988) distinctly present at antero-ventral angle of pronotum running parallel to anterior margin, preceding crenate groove; distance between anterior pronotal carina and anterior



Figure 1a. Specimens of *Celonites tauricus* from populations from different geographical regions in lateral view (insect pins and in a few specimens also protruded proboscis were retouched with photo software to improve comparability of the pictures), Crimea female dbM No. 4305 male dbM No. 4307, Kos female dbM No. 4776 male dbM No. 4790, Western Asia Minor female dbM No. 3585 male dbM No. 3586.

margin of pronotum about width of fore metatarsus. Posterior pronotal carina forms low narrow translucent sinuate crest on humeral angle of pronotum. Pronotum with anterior side nearly vertical; dorso-medially slopes down towards mesoscutum, resulting in slight depression along the dorso-medial margin; posterior margin raised to short carina dorsally in front of upper half of tegula; cuticula shiny, with close, reticulate macropunctation, interstices smooth, rounded, without micropunctures; horizontally striated due to more strongly raised longitudinal interstices, becoming more coarsely punctured postero-ventrally with interstices raised to knife-like edges. Cutic-



Figure 1b. Specimens of *Celonites tauricus* from populations from different geographical regions in lateral view (insect pins and in a few specimens also protruded proboscis were retouched with photo software to improve comparability of the pictures), Eastern Asia Minor female dbM No. 3629 male dbM No. 3430, South-east of Taurus range female dbM No. 4671 male dbM No. 4690, Cyprus female dbM No. 4717 male dbM No. 4720.

ula of mesoscutum shiny, reticulate with close deep macropunctation and narrow, distinctly raised interstices. Postero-medial cuticula of mesoscutum and mesoscutellum with longitudinal interstices more strongly raised leading to striated appearance; finely longitudinally wrinkled, postero-medially with, in addition, moderately spaced micropunctures especially along posterior margin. Mesoscutellum laterally with distinct carina along posterior margin, carina medially increasingly reduced so that cuticula of medial lobe continues evenly into the margin. Carina along posterior margin of



Figure 2. *Celonites tauricus* female (dbM No. 4305) head in lateral view, clypeus and frons covered with "knobbed setae".

metanotum medially with small tooth-like projections. Axilla with short blunt lateral projection only slightly projecting over adjacent posterior end of tegula. Tegula shiny, closely covered by macropunctures except completely smooth central convex area.

Mesepisternum with pronounced epicnemial carina deflexed backwards to run transversely in front of mid coxa; cuticula shiny, with close macropunctation; horizontally striated by raised interstices; area ventral to scrobal groove coarsely punctured with some interstices strongly raised to knife-like edges forming coarse honeycomblike sculpture. Process at mesepisternal scrobal groove of moderate size, cuticula on posterior side faintly shiny, finely but densely shagreened with irregularly moderately spaced micropunctation. Basal horizontal propodeal triangle laterally delimited by a perpendicular declivity, somewhat laterally produced at postero-lateral edge, posteriorly bordered by serrated carina; cuticula shiny, coarsely punctured, interstices almost



Figures 3–6. *Celonites tauricus* **3–4** head in dorsal view **3** female (dbM No. 4304) **4** male (dbM No. 4307) **5–6** metasoma in dorsal view **5** female (dbM No. 4305) **6** male (dbM No. 4307).

knife-like. Posterior surface of propodeum striated by strong vertical cuticula-folds; cuticula shiny, weakly coriaceous and covered with fine pale setae. Cuticula of sides of propodeum and metepisternum shiny, densely horizontally wrinkled. Lateral lamella broad, somewhat convex; lateral margin almost straight; posterior margin straight, not crenate; medially where lamella joins central part of propodeum with a rounded emargination, ventro-medial edge of which produced to a small blunt protrusion; dorsal cuticula of lamella shiny, with moderately spaced macropunctation, interstices weakly wrinkled. Claws ventral with small tooth.

Metasomal terga with posterior two-fifth separated from anterior part by slight declivity especially laterally (Fig. 5); postero-lateral corners slightly produced; posterior margin of tergum I weakly crenulated, crenulation not produced into spines and not projecting over smooth translucent lower posterior margin of tergum; posterior margin of terga II–V strongly crenulated (Fig. 5), crenulation produced into distinct spines raised at an angle of approximately 30° projecting distinctly over the translucent lower posterior margin of terga (Fig. 5); cuticula with silken sheen, densely covered with coarse macropunctation, with about nine micropunctures along median axis of tergum III; single thin seta arises from bottom of each macropuncture, only slightly protruding over rim of puncture; interstices finely shagreened, moderately covered with very tiny, decumbent, pale setae, all setae orientated towards caudal end. Tergum VI with sides converging almost as straight lines, posterior margin with curved protrusion over central two-thirds (Fig. 5), laterally transverse, forming distinct angle to side.

Metasomal sternum I shiny, finely shagreened, with tiny setae but without punctures. Sterna II–V posteriorly with broad stripe of asetose, translucent cuticula adjacent to posterior margin of more strongly sclerotized cuticula; small sparse band of setae along posterior sclerotized margin somewhat projecting over anterior part of translucent strip of cuticula; sclerotized cuticula shiny, finely shagreened, on posterior half of sternum II–V with dense to moderate punctation of shallow micropunctures from which short pale setae arise, becoming sparser anteriorly, on sternum II antero-laterally with a few shallow macropunctures, on sternum III–V anteriorly with moderate to sparse shallow macropunctation. Sternum VI tapering towards distal end; with outer margin raised to bulged rim, posteriorly protruded into little blunt spine; cuticula with rather narrow smooth mid-line slightly raised to weak keel at distal end, at sides with strong macropunctures from which pale setae arise.

Male. Colour: Resembles female, except as follows (Fig. 1a). White (less yellowish than female): basal spot on mandible (absent in one specimen); labrum; clypeus except small reddish brown ventral margin; sinuate band at frons laterally extending towards upper inner margin of eye where it bends ventrally into ventral half of ocular sinus (shortly to broadly interrupted medially in two specimens); humeral spot posterolaterally extended to posterior margin of pronotum (except in one specimen), dorsomedially lengthened towards enlarged anterior part of stripe along dorso-medial margin of pronotum (fused with it into complete dorso-anterior pronotum band in two specimens); stripe along lateral part of dorso-medial margin of pronotum interrupted in the middle by zone of black colour; posterior bands on terga II-VI interrupted on each side of middle into median and two lateral markings; broad band on posterior four-fifth of sternum II; (in one specimen postero-lateral spot on each side of sternum III-IV). Antenna with A1-2 black; A3-6 anteriorly with whitish stripe otherwise dark brown at basal end changing continuously into reddish-brown to orange towards A6; A7 reddish-brown to orange; antennal club (A8-12) orange, ventrally with distinct blackish marking on A12 extending on distal parts of A11 well set off from orange of adjacent ventral area, orange on dorso-posterior parts of A8-A12 can be darkened to variable extend.

Structure: Resembles female, except as follows. Clypeus longer than broad, distal margin deeply emarginated; cuticula shiny, with moderately spaced, shallow macropunctation, interstices on apical third weakly shagreened becoming smooth distally; pale stiff setae arising from macropunctures without distal "knob", distal ends of setae frequently curved in distal-medial direction. Frons with moderately spaced macropunctation; interstices densely obliquely shagreened; bearing pale stiff setae, mainly with curved distal end, in centre few with distal "knob" (Fig. 4); frontal line can be raised to form small carina or protuberance in centre of frons. Antenna with two oval shaped, perhaps sensory, depressions (tyloids) on concave, ventral side of club, situated within antennal articles A9 and A10. Midcoxa with small but distinct spine at distal end on anterior side close to anterior-medial angle. Posterior margin of tergum VII with three deep emarginations, resulting in two lateral lobes that continue laterally into lateral margins of tergum VII and two lanceolate medial projections (Fig. 6). Sternum VIII with distinct little spine on each side of posterior margin; even concavely emarginated, surface not much sunk in towards emargination (Fig. 7).

Male genitalia as in Figs 7, 8. Genital broad, in dorsal view distance between dorso-medial margins of stipites smaller than transverse width of adjacent part of stipes. Dorso-medial shovel-like lobe of harpide large, densely covered ventrally with long setae. Dorso-posterior margin of stipes only slightly curved, without distinct dorsomedial concavity. Stipes with dorso-medial margin running nearly parallel to sagittal plane. Sides of stipites converging continuously anteriorly towards cupula. Volsella large and broad reaching antero-medial margin of dorso-medial lobe of harpide; dorsal area with strongly sclerotized large, dark tubercles; distances between tubercles moderate; medial process large, trapeziform due to more or less truncate apex, continuing posteriorly into posterior process at a blunt angle. Sides of thyrsoi only slightly converging towards posterior (apical) end of aedoeagus. Each thyrsos continues anteriorly into apodema thyrsos with a distinct outwardly directed curve. On ventral side cupula medially clearly protruded anteriorly, completely projecting over dorsal margin of cupula in ventral view of genital capsule.

Measurements. Measurements of the exoskeleton are listed in Table 1.

Geographic distribution and variation. The geographic range of *Celonites tauricus* is shown in Fig. 9. Based on morphological differences six intraspecific taxa can be separated (Table 2, Figs 10–13) belonging to different geographic regions (Fig. 9). Distinct population groups exist in the Crimea, Kos, western Asia Minor, eastern Asia Minor up to the Elburs mountains, south-east of the Taurus range and in Cyprus.

Individuals from western Asia Minor are large and strongly built (Fig 1a), their metasomal terga are coarsely punctured and bear distinct pointed spines at the posterior end that project well beyond the lower posterior margin (Fig. 10). The specimens are dark with reduced whitish markings and reddish brown legs (Fig.1a). The posterior bands on the metasomal terga are laterally interrupted, usually from T2 to T5 but at least from T3 to T5. The population from the Crimea differs only slightly in that the individuals are a little less robust and the terga are somewhat less coarsely punctured. The population from Kos varies from the mainland population in that the crenulation along the posterior margin of the metasomal terga is reduced to short, weakly pointed, horizontal processes that do not project beyond the posterior margin (Fig. 12). The members of the populations to the south-east of the Taurus range are distinguished from individuals from western Asia Minor by their yellowish colour and considerably

Parameter	Female			Male				
	x	min	max	n	x	min	max	n
lateral ocelli distance	0.42	0.40	0.45	5	0.39	0.32	0.41	5
front./lat. ocellus distance	0.17	0.14	0.17	5	0.14	0.11	0.14	5
compound eyes distance	1.28	1.17	1.33	5	1.06	0.92	1.10	5
A1 length	0.20	0.19	0.21	5	0.19	0.18	0.20	5
A3 length	0.30	0.25	0.31	5	0.23	0.21	0.25	5
A3 width	0.12	0.10	0.12	5	0.11	0.11	0.13	5
A4-5 length	0.14	0.11	0.21	5	0.19	0.17	0.21	5
A8-12 length	0.79	0.77	0.86	5	0.97	0.92	1.05	5
A8-12 width	0.37	0.35	0.39	5	0.47	0.44	0.51	5
antennal sockets distance	0.74	0.66	0.76	5	0.50	0.47	0.53	5
clypeus max. width	1.12	1.03	1.14	5	0.84	0.80	0.88	5
clypeus apical width	0.48	0.45	0.52	5	0.42	0.39	0.44	5
clypeus length	0.95	0.85	0.97	5	0.73	0.68	0.76	5
mesonotum width	2.81	2.55	2.90	5	2.32	2.16	2.46	5
mesoscutum length	2.07	1.82	2.13	5	1.51	1.41	1.68	5
wing length	5.61	5.11	5.68	5	4.90	4.83	5.04	3
R+Sc length	3.13	2.85	3.22	5	2.60	1.71	2.80	5
number of hamuli	10	8	12	5	10	8	10	5
femur I length	1.50	1.41	1.55	5	1.19	1.14	1.26	5
tibia I length	0.97	0.96	1.01	5	0.84	0.78	0.88	5
metatarsus I length	0.58	0.54	0.61	5	0.45	0.41	0.46	5
tergum I width	2.85	2.55	2.99	4	2.44	2.30	2.60	5
tergum I length	1.26	1.12	1.31	5	0.99	0.90	1.07	5
tergum II width	2.92	2.66	2.99	4	2.35	2.30	2.55	5
total length	7.8	7.1	8.3	5	7.5	6.8	7.8	4

Table 1. Measurements of the exoskeleton of imagines of *Celonites tauricus* from the Crimea (x = median; min = minimum, max = maximum; measurements were made with a Wild M3 stereomicroscope with maximum magnification 80×, maximum accuracy 0.011 mm, all distances in mm).

more extensive markings (Fig. 1b), including a spot on the clypeus of the females. The individuals from eastern Asia Minor are smaller and daintier than individuals from the western populations. The macropunctures on their metasomal terga are much smaller and the crenulation along the posterior margins of the terga consists of short, horizontal, truncated processes (Fig. 13). The light colour is yellowish and the markings are more extensive than in specimens from the western populations with, at least, complete posterior bands on the terga T1 to T3 (Fig. 1b). Populations with at least some specimens intergrading between the taxa from western and eastern Asia Minor exist in a zone extending from the Taurus range in the south-west to north-east Turkey and Armenia (Fig. 9). Such individuals reveal an intergrading pattern of various morphological and colour traits, but also transient characters like, for example, little spines along the posterior margins of the metasomal terga or macropunctures of intermediate size on the metasomal terga. Likewise there are populations in south-east Turkey with



Figure 7. Male genitalia in dorsal (left) and ventral view (middle) and metasomal sternum VIII of male in ventral view (right) of *Celonites abbreviatus* (dbM No. 3451), *C. tauricus* from the Crimea (dbM No. 4307) and *C. tauricus* from Western Asia Minor (dbM No. 3431).

specimens, intergrading between the taxon from eastern Asia Minor and the taxon to the south-east of the Taurus range (Fig. 9), that are characterized by little spines along the posterior margins of the metasomal terga and a yellowish spot on the clypeus of the females. The specimens from Cyprus are distinguished by their small size, comparatively dark coloured dorsal side of the antennae (Fig. 1b), deeper yellow colour, and the crenulation of the metasomal terga that, at least laterally, consists of short but more or less pointed processes.

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Taxon No.	1 Crimea	2 Kos	3 Western Asia Minor	4 Eastern Asia Minor	5 SE of Taurus range	6 Cyprus
antenna	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal dub, on dorsal side fading more gradually into reddish brown colour of proximal area of club; four specimen with dorsal side dark reddish brown	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown of club; one specimen with dorsal side dark reddish brown	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light reddish brown proximal area of antennal club, on dorsal side fading more gradually into reddish brown colour of proximal area of club	tip dark, at least A12 with distal end blackish, on ventral side markedly contrasting to adjacent light proximal area of antennal club, on dorsal side fading gradually into dark brown to dark brown colour of proximal area of club
shade of light colour	faintly yellowish-white	faintly yellowish-white	faintly yellowish-white; in two specimens light yellowish	light yellowish to yellow	light yellowish to yellow	light yellow to yellow
clypeus (female)	black; one specimen with two tiny spots	black	black	black	black with dorsal spot, that may reach the dorsal margin and can expand on ventral half of clypeus, at minimum little isolated spot	black
tempora	short stripe to completely black	short stripe	short stripe to completely black	long stripe to completely black	long stripe	long to short stripe
tegula	reddish brown	reddish brown	reddish brown	light yellowish to yellow with small reddish brown translucent centre or reddish brown	light yellowish to yellow; in two specimens with small reddish brown translucent centre	light yellowish to yellow with small reddish brown translucent centre
pronotum	narrow stripe along dorsal margin, brownish interrupted in the middle of dorso-lateral margin	narrow stripe along dorsal margin, blackish interrupted in the middle of dorso-lateral margin; in one specimen brownish interrupted	narrow stripe along dorsal margin, brownish or blackish interrupted in the middle of dorso-lateral margin	continuous stripe along dorsal margin; in three specimens brownish interrupted in the middle of dorso-lateral margin	continuous stripe along dorsal margin; in two specimens brownish interrupted in the middle of dorso-lateral margin	broad continuous stripe along dorsal margin

of Taurus range 6 Cyprus	tterally expanding lium-sized medial spot spot		ad continuous ga L-V; in two mens on tergum rally interrupted; o specimens on interrupted	ad continuous terior band on ga I–V; in two mens on tergum rally interrupted; o specimens on interrupted interrupted interrupted k. basally with Marcal stripe; hat has basally with narrow marcal stripe; hat has basally with narrow interrupted black, basally with narrow meteral stripe; hat has black basally with narrow meteral stripe; hat has black basally with harrow	ad continuous rerior band on mens on tergum mens on tergum naly interrupted o specimens on interrupted interupted interrupted interupted interupted interrupted interrupted in	ad continuous ereior band on ga I–V; in two mens on tergum rally interrupted; o specimens on interrupted interupte	ad continuousad continuousga I-V; in twomens on tergumrally interrupted;oo specimens oninterruptedinterruptedinterruptedinterruptedk, basally withblack, basally with narrowwalateral stripe;interly black, basally with narrowwalateral stripe;profecimen completely blackyellowisharge, strongsmall, more daintycoarse to coarsemoderate
laterally expanding large laterally ex	medial spot; in one or medium-sized pecimen completely spot black	broad continuous sterior band on terga V; in three specimens in tergum V laterally N laterally in two specimens on in two specimens	cimens on terga IV–V terga III–V lat laterally interrupted interrupte	cimens on terga IV–V terga III–V lat laterally interrupted interrupte black, basally narrow lateral in one speci completely t	cimens on terga IV–V aterally interrupted interrupted black, basally narrow lateral in one speci completely t reddish brown yellowisł	cimens on terga IV–V terga III–V lat laterally interrupted interrupte black basally black in one speci completely treddish brown yellowist edium-sized to small, large, stro more dainty large, stro	cimens on terga IV–V terga III–V lat laterally interrupted interrupte black basally black interrupteral in one speci completely tellowist edium-sized to small, large, strou more dainty very coarse to moderate very coarse to
E	medium-sized to small medial spot	continuous posterior band on tergum I, posterior band on terga II–V laterally interrupted; in two specimens tergum II with continuous band; in seven specimens band on tergum I interrupted; o in one specimen band on	tergum II continuous; in six spec specimens posterior band on lergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe	tergum II continuous; in six spec specimens posterior band on spec tergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe black	tergum II continuous; in six specimens posterior band on tergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe black black reduced to medial stripe teduced to medial	tergum II continuous; in six specimens posterior band on tergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe black black large, very strong to strong mm large, very strong to strong to strong to strong the speciment of th	tergum II continuous; in six specimens posterior band on tergum V reduced to medial stripe; in three specimens posterior band on terga III–V reduced to medial stripe black black reddish brown reddish brown me large, very strong to strong me coarse (in specimens from Antalya very coarse)
	medium-sized medial m spot	E posterior band on terga I–V laterally interrupted; ba four specimens with	continuous band on tergum I si si tu	continuous band on tergum I sl	continuous band on tergum I sl sl sl tu	continuous band on tergum I sl tu black black reddish brown large, strong	continuous band on tergum I sl tu black black reddish brown large, strong coarse coarse
	medium-sized medial spot	continuous posterior band on tergum I, posterior band on terga II–V laterally	interrupted; in two specimens tergum II with continuous band	interrupted; in two specimens tergum II with continuous band black	interrupted; in two specimens tergum II with continuous band black black reddish brown	interrupted; in two specimens tergum II with continuous band black reddish brown large, strong	interrupted; in two specimens tergum II with continuous band black reddish brown large, strong coarse
	scutellum	metasomal terga		metasomal tergum VI (female)	metasomal tergum VI (female) legs	metasomal tergum VI (female) legs size, physique	metasomal tergum VI (female) legs size, physique macropunctation of terga II–IV

6 Cyprus	crenate, at least laterally crenulation consists of short horizontal ± pointed processes, posteriorly not projecting beyond the translucent lower posterior margin, medially processes posteriorly truncate to variable extend
5 SE of Taurus range	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures); in one specimens spines projecting only moderately beyond posterior margin
4 Eastern Asia Minor	crenate, crenulation consists of very short horizontal processes, posteriorly truncated not projecting over the translucent lower posterior margin sompletely the translucent margin remains completely
3 Western Asia Minor	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures); in seven specimens spines projecting only slightly beyond posterior margin
2 Kos	crenate, crenulation consists of short ± pointed horizontal processes, posteriorly not projecting beyond the translucent lower posterior margin; in one specimen a few processes on tergum III projecting beyond posterior margin
1 Crimea	crenate, crenulation produced into distinct spines raised at an angle of approximately 30° distinctly projecting beyond the translucent lower posterior margin of terga (spines approximately as long as diameter of macropunctures)
Taxon No.	sculpture of posterior margin of tergum II–IV



Figure 8. Male genitalia of *C. tauricus* (dbM No. 4307) in dorsal (left) and ventral view (right). (Setae only shown on one side of each drawing; Nomenclature follows that of Birket-Smith (1981): ad, aedoeagus; cu, cupula; ha, harpide; mp, medial process of volsella; pp, posterior process of volsella; sl, shovel-like dorso-medial lobe of harpide; sp, stipes; ty, thyrsos; vo, volsella).



Figure 9. Geographical records of *Celonites tauricus*. The intraspecific taxon affiliation of the local populations is marked by different colours; a population is regarded as "intermediate" when at least one individual shows intermediate character states. [OpenStreetMap contributors]



Figures 10–13. Cuticula structure of metasomal terga II and III of females belonging to different intraspecific taxa of *Celonites tauricus* in dorsal view. **10** Western Asia Minor (dbM No. 4681) **11** South-east of Taurus range (dbM No. 4673) **12** Kos (dbM No. 3607) **13** Eastern Asia Minor (dbM No. 3653).

Bionomics of Celonites tauricus

Habitat

Eight out of nine localities of *Celonites tauricus* in the Crimea are situated in the habitat zone of submediterranean vegetation of the south coast (Fig. 14), and it can be presumed that the taxon is distributed along the whole south coast of the peninsula. A single record comes from the zone of forest steppes of the Crimean foothills. In the Crimea *C. tauricus* is confined to dry light forests and shrubs or rocky steppe and phrygana slopes (Fig. 15). The highest abundance of the taxon was recorded in Lisya Bay where in some years 1.5–2 foraging females per 100 m² were observed on average



Figure 14. Distribution of localities of Celonites tauricus in different habitat zones in the Crimea.

at the same time (the size of the whole sample area was 2500 m²). The distribution of *Celonites tauricus* in the Crimea seems to be not only affected by the distribution of *Teucrium chamaedrys*, as its main forage plant, since this plant is very common and abundant on the entire peninsula. Probably *C. tauricus* does not occur both in higher altitudes of the mountains and in the plains of the Crimea for climatic reasons, since e.g. the mean winter temperatures are lower in these regions in comparison with the foothills and slopes on the south coast (Ved' 2000).

In Kos *Celonites tauricus* was found in areas from 20 to 110 m above sea level that were covered with phrygana vegetation characterized by larger patches of flowering plants of *Satureja thymbra* (Fig. 20).

Flower associations

Flower visiting records of *Celonites tauricus* are summarized in Table 3. In all investigated populations males and females of *C. tauricus* were exclusively recorded from flowers of Lamiaceae, but there are distinct regional differences with regard to the species of Lamiaceae utilized. In the Crimea females of *Celonites tauricus* visiting flowers were primarily observed to collect pollen and nectar from flowers of *Teucrium chamaedrys* (Figs 16, 17). This flower association was confirmed at all localities where *C. tauricus* was studied and in every study period. Occasionally females were also recorded at



Figures 15–19. Bionomics of *Celonites tauricus* in the Crimea 15 Habitat 16 Female visiting flower of *Teucrium chamaedrys* 17 Female brushing pollen from the frons towards the mouthparts by alternating movements of the fore legs subsequent to regular flower visit at *Teucrium chamaedrys* 18 Nest under construction on the underside of a stone (brood cell on the left removed) 19 Old nest attached to the underside of a stone with emergence holes of *Celonites* imagines in the walls of three brood cells.



Figures 20–24. Bionomics of *Celonites tauricus* in Kos **20** Habitat (qs = potential quarry site of females) **21** Male perching on stone **22** Male visiting flower of *Satureja thymbra* **23** Female standing on the ground near a plant of *Satureja thymbra* brushing with the fore legs over her frons **24** Male visiting flower of *Thymus capitatus* (p = protruded proboscis).

plant taxon	Σ sightings of flower visiting individuals						
	Cri	mea	Palan	döken	K	os	
	Ŷ	8	Ŷ	8	Ŷ	8	
Lamiaceae							
Satureja thymbra L.					52	11	
Teucrium chamaedrys L.	35	10					
Teucrium polium L.	1	2					
Thymus capitatus (L.) Hoffmanns. & Link					1	6	
Thymus tauricus Klokov & DesShost.	8						
Ziziphora clinopodioides Lam.			1*				
other plant taxa							

Table 3. Flower-visiting records of males and females of *Celonites tauricus* from different geographic regions.

*dbM No. 2795

flowers of Thymus tauricus and Teucrium polium. However, visiting flowers of these two plant species is probably not typical for C. tauricus in the Crimea and was only observed in Lisya Bay in 2013. In that year the spring was unusually dry and flowering plants of *Teucrium chamaedrys* were very scarce whereas flowering *Thymus tauricus* were much more abundant and widespread. In five out of the eight visits to Thymus tauricus and also in the visit to *Teucrium polium* the females switched over to these plants from Teucrium chamaedrys and afterwards returned to visit flowers of T. chamaedrys. Females of C. tauricus were only observed to visit plants of Thymus tauricus growing in close proximity to flowering plants of *Teucrium chamaedrys*. Males of *C. tauricus* also were observed mainly at flowers of T. chamaedrys at Cape Aya in 2004 and in Lisya Bay in each year of observation. In contrast, the Kos population was mainly associated with Satureja thymbra and to minor extend also with Thymus capitatus, though in addition, at least at some localities two Teucrium species (T. divaricatum and T. polium) were in flower. However, the proportion of visits to Thymus capitatus may increase during the on-going flight season, since at the end of the investigation period Th. capitatus had just started flowering whereas S. thymbra was nearly over.

During flower visits at *Satureja thymbra* and *Teucrium chamaedrys* the females always stood on the lower lip of a flower and took up nectar and pollen simultaneously. The proboscis was protruded deeply into the corolla tube while the female performed at a high frequency slight back and forth movements of the anterior parts of her body, rubbing her head over the nototribic anthers (Figs 16, 25, 26). In this manner pollen grains were removed from the pollen sacs with the stiff knobbed setae on the frons, which form a pollen-collecting apparatus, accumulating on frons and clypeus (Fig. 27). The median duration of the visits of females to flowers of *Satureja thymbra* was 2.6 s (range 0.8–6.3 s, n = 43). At *Thymus capitatus* the flower visiting behaviour was very similar to the behaviour described above, except that the female orientated her body axis at an angle to the longitudinal plane of the zygomorphic flower both to the left and to the right so that her frons was directed towards the anthers that are situated



Figures 25–30. Flower visiting behaviour of *Celonites tauricus* at *Satureja thymbra* in Kos **25–26** Regular flower visit for the simultaneous uptake of nectar and pollen with the proboscis protruded into the corolla tube and the knobbed setae on the frons making contact with the nototribic anthers **25** Viewed from ventral-posterior **26** Viewed from dorso-lateral **27** Proboscis partly retracted shortly before leaving the flower, in lateral view **28–29** Female standing on the lower lip and an adjacent flower brushing pollen from her frons with alternating movements of her fore legs **30** The fore legs are brought between the mouthparts for pollen ingestion during pollen transfer from the frons by brushing movements towards the mouthparts.

further laterally in this flower. Periodically flower visiting was interrupted and the pollen grains were transferred from the frons to the mouthparts by alternating brushing movements of the fore legs (Figs 17, 28, 29) which were brought between the mouthparts while the pollen was being ingested (Fig. 30). This from brushing behaviour took place on flowers (Figs 17, 28, 29) and also on the ground in the close vicinity of the plants (Fig. 23).

On the Crimea, individual females of *C. tauricus* usually visited flowers over a period of 20–40 minutes. After about 10–15 minutes they regularly interrupted flower visiting and alighted on stones or grass. They remained there for several minutes repeatedly regurgitating and withdrawing again a mass of pollen and nectar that became visible as a drop of liquid between the mouthparts. This behaviour probably served to thicken the pollen and nectar mass.

During flower visits males always inserted their proboscis into the corolla tube (Figs 22, 24) indicating the uptake of nectar. At flowers of *Satureja thymbra* males, like the females, performed slight back and forth movements in addition rubbing with their frons over the anthers, so that they probably collected pollen as well. This rubbing behaviour was not observed at flowers of *Thymus capitatus*.

More than 99% of the pollen from the crops of females from Kos consisted of hexacolpat pollen grains of Lamiaceae. This pollen type occurs in several genera of Lamiaceae including *Satureja* and *Thymus*.

Nesting

Three nests of *Celonites tauricus* were recorded in the Crimea. The first nest was investigated on 2 July 2004 in the vicinity of the village of Veseloye near Sudak. The nest site was a rocky slope with steppe vegetation predominated by *Melica taurica* K. Koch and Teucrium chamaedrys along with individual trees of Celtis glabrata Steven ex Planch. The nest was located in a small cavity underneath a stone situated in the shadow of one of the Celtis trees. The nest under construction contained two brood cells. The cells were placed on the underside of the stone and were made of fine clayey soil with a few tiny stones (Fig. 18). The cells were cylindrical, rounded at the closed (basal) and truncate at the open (apical) end (Fig. 18) measuring 9 mm in length and 4 mm in width. The cell wall was 0.25 mm thick. The outer cell surface, typically for Celonites, showed a distinct "fish scale" pattern. The first cell was sealed with mud. The cell seal was positioned slightly in from the edge of the cell opening and was of the same thickness as the cell wall. The cell was provisioned with a pollen loaf and contained an egg at the basal end. Basally the loaf was situated close to the egg, while the apical end of the loaf was further away from the seal resulting in an empty space between the pollen loaf and the seal at the apical end of the cell. The pollen loaf was attached to the cell wall with numerous spike-like projections. The second cell was open and contained the female owning the nest.

The second nest was studied on 2 July 2011 in Lisya Bay. The nest site was a slope covered with phrygana vegetation predominated by *Elytrigia caespitosa* subsp. *nodosa* (Nevski) Tzvelev, *Atraphaxis replicata* Lam., *Thymus tauricus* and *Teucrium chamae-drys*. The nest was also situated in a small cavity on the underside of a small stone. The

nest was old and contained three cells covered with an additional layer of mud forming a nest covering (Fig. 19). All cells were sealed at the apical end and had a large frontal opening that covered the apical third of the cell, which had probably been made by an emerging imago of *Celonites tauricus* (Fig. 19). Every cell contained an empty, thin, whitish *Celonites* cocoon and a meconium.

The third nest was found in Lisya Bay on 11 July 2013. It was also situated on the underside of a small stone and it was also old. The nest consisted only of a single cell covered with an additional layer of mud. The cell was sealed at the apical end and had a frontal opening at the apical part, which had probably been made by an emerging imago of *C. tauricus*. Inside the cell were a *Celonites* cocoon and meconium.

Females of *C. tauricus* were never observed at water collection sites. Therefore the mud used for cell construction was probably made by mixing clay particles with regurgitated nectar.

Male behaviour

Males performed patrol flights along the preferred forage plants of the females, i.e. *Teucrium chamaedrys* in the Crimea as well as *Satureja thymbra* and *Thymus capitatus* in Kos, and over nearby stones in a low constant flight. Patrolling was regularly interrupted by perching in the immediate vicinity of the forage plants, mainly on stones but also on the ground or on the plants themselves (Fig. 21). Moreover, patrolling was occasionally interrupted by flower visits. On one occasion a male was observed pouncing on a female resting on a stone between consecutive flower visits. The male alighted on the back of the female for a short moment and flew off again. On another occasion a male pounced on a female while it was visiting a flower of *Satureja thymbra*. Courtship and copulation were not observed.

Phenology

The species is univoltine. In the Crimea males were observed from 5 June to 8 July and females from 7 June to 31 July indicating slight proterandry.

Discussion

The rediscovered *Celonites* taxon from the Crimea, assigned to *C. abbreviatus tauricus*, can be consistently identified as a member of the *Celonites abbreviatus*-complex (sensu Mauss 2013) by the existence of a pollen collecting apparatus composed of knobbed setae on clypeus and frons, the outstanding autapomorphic character of this group (Mauss 2013). Moreover, the Crimean taxon also shares all apomorphies of the *C. abbreviatus*-group (Mauss 2013), that is, the males have only two oval-shaped tyloids

on the antennal club, they bear a small spine at the distal end of the midcoxa, their tergum VII is posteriorly markedly lobed and the posterior margin of sternum VIII of the males is specifically emarginated.

Within the Celonites abbreviatus-complex the members of the taxon Celonites a. tauricus from the Crimea are in the main similar to individuals of Celonites spinosus from western Asia Minor in both the colouration and morphology of the exoskeleton and in the structure of the male genitalia. Because of this high degree of similarity it is hypothesized that both taxa are not reproductively isolated from each other and thus belong to the same biospecies (sensu Mayr 1967). The existence of populations of Celonites in Central and East Anatolia that include at least some individuals with intermediate characters between typical spinosus- and typical invitus-forms indicate that these eastern populations are not reproductively isolated from the western *spinosus*-like populations. This is in agreement with the findings of Gusenleitner (1985), who as a result formally synonymized both taxa. In the same way, the distinct yellowish populations that occur to the southeast of the Taurus range are connected to the northeastern *invitus*-form by populations that contain individuals with intermediate characters in southeast Anatolia. For that reason it can be hypothesized that they also are not reproductively isolated from the other taxon and therefore belong to the same biospecies. All members of this biospecies are characterized by an antennal club with dark tip and male genitalia with a broad stipes and a large medial process of the volsella. The colour pattern on the ventral side of the antennal club that is in contrast richly coloured might be associated with mate recognition, since it has been demonstrated by Mauss and Müller (2014) that in an allied *Celonites* species the tips of the male antennae are held above the female compound eyes for a short time during mating prior to the insertion phase. Therefore the colour pattern of the club could be part of a mating signal and therefore may act as a reproductive isolation mechanism. This is also likely for the observed differences in the proportion and structure of the male genitalia. Since the *Celonites* populations from Kos and from Cyprus are mainly similar in regard to these particular characters there is no evidence that they may be reproductively isolated from the mainland populations. For that reason, they are regarded as allopatric populations of a single biospecies. Due to priority the name of this biospecies has to be *Celonites tauricus*.

Celonites tauricus resembles *Celonites abbreviatus* in many characters and is therefore in all probability closely related to this species, as already established by Gusenleitner (1966). Despite some differences in specific characters of particular populations, both taxa differ mainly in the colour pattern on the ventral side of the antennal club and in the proportion of the stipes and the form of the volsella. As discussed above these characters are associated with the mating system and might act as a reproductive isolation mechanism. It is of note that neither *Celonites abbreviatus* nor any other species of the *C. abbreviatus*-complex could be demonstrated to occur within the geographic range of *C. tauricus*. All former records of *C. abbreviatus* from this region, for which voucher specimens were examined, turned out to belong to *C. tauricus*. Therefore *C. tauricus* and *C. abbreviatus* seem to be allopatric taxa that have evolved from a common stem species.

The areas inhabited by *Celonites tauricus* in the Crimea and in Kos are comparable to habitats of *Celonites abbreviatus* in Central Europe (Bellmann 1995, pers. obs.), southern France (pers. obs.), Spain (pers. obs.) or the Peloponnese (Mauss 2006). The flower associations of C. tauricus are very similar to those of C. abbreviatus, in that both taxa specialize in utilizing Lamiaceae with nototribic flowers that serve as the sole pollen source (Bellmann 1984, 1995, Mauss 2006, Müller 1996, Schremmer 1959). Moreover, as in C. tauricus in the Crimea, a Teucrium species seems to be of particular importance for the occurrence of C. abbreviatus in Central Europe (Bellmann 1995), and Satureja thymbra, which is the main forage plant of C. tauricus in Kos, is also the mainly visited plant of C. abbreviatus in the Peloponnese (Mauss 2006). The flower visiting behaviour of both species appears identical (cf. Bellmann 1984, 1995, Mauss 2006, Müller 1996, Schremmer 1959). The construction of the brood cell, the position and shape of the egg and the provision, as well as the frontal orientation of the emergence hole in old cells of C. tauricus are similar to C. abbreviatus (cf. Bellmann 1984, 1995). Nests constructed on the underside of stones, as in C. tauricus, do also exist in C. abbreviatus (Bellmann 1995), though nests of the latter, at least in Central Europe, are more frequently aerial, attached to stones or twigs (Bellmann 1995). Finally, males of both taxa search for females in the vicinity of forage plants (cf. Mauss 2006). In summary, the ecology and behaviour of C. tauricus and C. abbreviatus seem to be similar in all investigated parameters and their ecological niches are probably mainly identical. This is in congruence with the perceived allopatric distribution of both taxa, as their comparable ecological requirements should prevent sympatry.

The observed distribution pattern of the intraspecific taxa of *C. tauricus* in Asia Minor (Fig. 9) can be biogeographically explained by the isolation of small populations in cold periods of the Pleistocene in secondary glacial refuges that have already been characterized by Lattin (1967). The ancestors of the western *spinosus*-like populations probably subsisted in the eastern part of the Pontomediterranean refuge, the ancestors of the populations south-east of the Taurus range in the Syrian refuge and the ancestors of the eastern *invitus*-like populations in the Caspian refuge sensu Lattin (1967). As a result of the post glacial warming the three populations expanded their range again and hybridized with each other where they secondarily came into contact as is indicated by individuals with intergrading characters.

It can be hypothesized that *C. tauricus* colonized the Crimea from the west of Asia Minor, since the Crimean population of *Celonites tauricus* is morphologically much more similar to the *spinosus*-like populations of *C. tauricus* from the western parts of Asia Minor than to the *invitus*-like populations in the east. Probably, the colonization took place in a phase of low sea-level when today's extensive western shelf of the Black Sea was situated above the level of the ancient Black Lake, resulting in a large area along the western coast of the Black Lake covered with Sub-Mediterranean vegetation that connected the Sub-Mediterranean areas on the Crimea with the north-west end of Asia Minor (Yena et al. 2005, and references therein). During the Würm glacial this western costal zone was an extensive refuge harbouring the Mediterranean flora (Yena et al. 2005). Major et al. (2006) showed that intense meltwater pulses at the end of the

Würm glacial between 18 and 16 ka BP raised the level of the Black Lake, probably to its outflow, so that lower parts of the shelf were drowned. But during the following warm post glacial periods of the Bølling-Allerød (15–13 ka BP) and the Preboreal (11.6–9.4 ka BP) the complete shelf was again well above the sea level (Major et al. 2006). Consequently it seems likely that finally this entire area was inhabited by the western *spinosus*-like population of *C. tauricus*. The range was disrupted when the Black Sea shelf was flooded with water from the Marmara Sea as a result of the post glacial rise of the global sea level about 9.4 ka BP (Major et al. 2006). The flooding led to the separation of the recent relict population on the Crimea from the main *spinosus*-like population of *C. tauricus* in the western part of Asia Minor. A comparable biogeographical pattern exists, for example, in *Pinus brutia* Ten. (Yena et al. 2005) and some species of spiders (Kovblyuk 2014). Similarly, the population of *C. tauricus* in Kos probably has been isolated from the *spinosus*-like mainland population by the post-glacial rising of the sea level of the Aegean that separated the island from Asia Minor.

In contrast, Cyprus is a primarily oceanic island of volcanic origin, that probably has been connected to the mainland only for a period of approximately 600000 years during the Messinian Salinity Crisis of the upper Miocene (5.9–5.3 Ma BP), when a land bridge existed that joined the island with continental areas of Asia Minor and Syria (Poulakakis et al. 2013, and references therein). Since the re-flooding of the Mediterranean basin in the early Pliocene Cyprus has been separated from Asia Minor as the nearest mainland by a distance of at least 30 km (Hadjisterkotis et al. 2000). Therefore, the existence of a morphologically distinct Cyprian population of *C. tauricus* is probably the result of dispersal, but it is uncertain whether this occurred over a land bridge or transmarine, as the divergence time from the mainland population is unknown. Based on morphological similarity the migration probably started from an eastern, more *invitus*-like population of *C. tauricus*.

Acknowledgments

We are greatly indebted to Sergey P. Ivanov and Dmitriy V. Puzanov (Taurida Academy of the Vernadskiy Crimean Federal University, Simferopol) for help with collecting material in the field; to Alexander V. Antropov (Zoological Museum of the Lomonosov Moscow State University, Moscow) for help with access to the collection with Kostylev's type specimens in Moscow, to Sergey A. Belokobylskij (Zoological Institute of the Russian Academy of Sciences, Saint Petersburg) for help with access to the collection of the type specimens of Vespidae in Saint Petersburg, and James M. Carpenter (American Museum of Natural History, New York) for his consultation concerning the whereabouts of the type of *C. a. tauricus* and his careful review of the manuscript. Josef Gusenleitner (Linz), Erol Yildirim (Atatürk University, Department of Plant Protection, Erzurum), Christoph Saure (Berlin) and Christian Schmid-Egger (Berlin) generously provided material from their collections. Annette Rosenbauer (Stuttgart State Museum of Natural History, Stuttgart) identified the collected plants from Kos and Andreas Müller (Zürich) determined the pollen samples. We are especially grateful to Sarah Gess (Albany Museum, Grahamstown) for valuable comments on the manuscript and improvement of our English.

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RESEARCH ARTICLE



A new species of *Temelucha* Förster from Malta with an updated and revised identification key to the Western Palaearctic *Temelucha* species (Hymenoptera, Ichneumonidae, Cremastinae)

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Academic editor: G. Broad	Received 5 October 2015	Accepted 11 December 2015	Published 1 March 2016
,	http://zoobank.org/FEAF7AC2-9E)81-430E-A1CF-0A76752E132E	

Citation: Vas Z (2016) A new species of *Temelucha* Förster from Malta with an updated and revised identification key to the Western Palaearctic *Temelucha* species (Hymenoptera, Ichneumonidae, Cremastinae). Journal of Hymenoptera Research 48: 67–84. doi: 10.3897/JHR.48.7094

Abstract

A new species, *Temelucha rea* **sp. n.**, of the ichneumon wasp subfamily Cremastinae is described from Malta. Since the last published keys to the Western Palaearctic species of *Temelucha* are outdated and lack several species, an updated and revised identification key is provided for the 47 known *Temelucha* species of the region.

Keywords

Taxonomy, species description, ichneumon wasp, Mediterranean region, Europe

Introduction

Temelucha Förster, 1869 is a moderately species-rich genus of the ichneumon wasp subfamily Cremastinae. The definition of the genus was summarized by Townes (1971). According to Yu et al. (2012), 235 valid species belong to this genus, with worldwide distribution, and 46 species have been known from the Western Palaearctic region. The early keys provided for the Western Palaearctic species of *Temelucha* (i.e. in combination with *Cremastus* Gravenhorst, 1829 at that time) are seriously outdated by now and cover only a very limited set of species (e.g. Szépligeti 1905, Schmiedeknecht 1910). The only comprehensive taxonomic revision of the European species was published by Šedivý (1971). In his work he not only provided a useful key for the 23 European *Temelucha* species known at that time but also gave detailed descriptions for all the species. As several, previously described species were published with insufficient morphological descriptions, Šedivý's (1971) work is still a base-line for the European species.

Since Šedivý's (1971) revision, several new species have been described from the Western Palaearctic region, mainly from the Balkan Peninsula and the Mediterranean area (Aubert 1977, 1981, Narolsky 1987, Kolarov 1989, Šedivý and Schwarz 1993, Kolarov 1995, 1996, Kolarov and Beyarslan 1999, Narolsky 2004). Kolarov (1997) provided a new key for 36 species of the region with a valuable zoogeographical discussion. His key includes many but not all species that have been described since Šedivý (1971) and it was a good attempt to simplify the distinguishing characters; however, some mistakes could be revealed by comparing the distinguishing characters of some species in that key with the original descriptions and type specimens (e.g. a species known only from males could only be keyed out by choosing between ovipositor characteristics, or a species with a yellow scutellum was keyed in the section of species with a black scutellum, etc.). Additionally, some species described long ago, such as *Temelucha corsicator* Aubert, 1961, *T. picticollis* (Hellén, 1949), and *T. minuta* (Morley, 1912) were included in neither previous key.

Recently, by finding a new *Temelucha* species from Malta, I realized the necessity of an updated identification key which covers all the species of the region and corrects the errors of the previous keys. In this paper, along with the description of a new species, an identification key is provided for the 47 currently known Western Palaearctic *Temelucha* species (including the one described here).

Methods

Ichneumonidae taxonomy and nomenclature follow Yu and Horstmann (1997) and Yu et al. (2012). The morphological terminology follows Gauld (1991), and Gauld et al. (1997). The updated and revised key is based on previous keys (Šedivý 1971, Kolarov 1997), original descriptions and descriptions given by Šedivý (1971), Narolsky (1990), Kolarov and Beyarslan (1999), Kolarov and Yurtcan (2009), and Rousse et al. (2011). The key was tested on the material of the Hungarian Natural History Museum (HNHM), Budapest. The author examined the types of species described by Szépligeti (deposited in HNHM), and of *T. picticollis* (Hellén) (borrowed from the Finnish Natural History Museum, Helsinki). Distribution notes are not given in the key; it would just repeat Kolarov's (1997) work, and are well summarized in Yu et al. (2012). The specimens were examined using Nikon SMZ645 and Olympus SZX9 stereoscopic microscopes. Photos were taken by T. Németh (HNHM Coleoptera Col-

lection) with Nikon D5200 and Nikon AF Micro Nikkor 60mm lens and Mitutoyo M Plan Apo 5X microscope lens. Exposures were stacked in Zerene Stacker, post image work was done with Photoshop CS5.

Results

Taxonomy

Temelucha rea sp. n.

http://zoobank.org/349622C9-A95A-426A-9B02-27207B713487

Material examined. Holotype: female, Malta, Mellieha, Il-Prajjet, 14.viii.2014, leg. M. Zammit. Paratype: female, same locality, collecting date, and collector. The holo-type and the paratype are deposited in the HNHM Hymenoptera Collection (HNHM Id. No. 23011, 23012, respectively).

Diagnosis. The new species belongs to the morphological group of *Temelucha* species with the following characters in combination: mainly yellow head and thorax, at least the basal part of the hind coxa dark, the second discal cell more than $1.5 \times as$ long as the first sub-discal cell, and the second recurrent vein (2m-cu) postfurcal. Within this group it most resembles *T. decorata* (Gravenhorst, 1829) due to its colour pattern; however, it is significantly smaller than *T. decorata*. Another such small species within this group is *T. picticollis* (Hellén, 1949); however, *T. picticollis* differs from the newly described species by its black propodeum, the absence of notauli, and colour pattern.

Description. Female (holotype) (Figs 1–4). Body length 4.7 mm, fore wing length 2.7 mm, ovipositor sheath 2.0 mm.

Head. Antenna with 26 flagellomeres. First flagellomere $3.3 \times as$ long as wide. Gena short, strongly constricted behind eyes. Occipital carina dorsomedially incomplete. Occiput smooth and shiny. Vertex, frons, gena and malar space finely coriaceous. Middle of face punctate, punctures separated from each other by usually less than a puncture diameter. Clypeus with fewer punctures, convex in profile, and with curved apical margin. Inner eye orbits parallel. Ocellus diameter slightly smaller than distance between lateral ocellus and eye. Malar space about 0.75 × as long as basal width of mandible. Mandibular teeth of equal length.

Mesosoma. Mesosoma densely punctate; distance between punctures on mesonotum and mesopleuron generally smaller than puncture diameter. Pronotum less densely punctate and with fine wrinkles. Epomia distinct. Notaulus distinct, reaching middle of mecoscutum. Scutellum punctate with lateral carinae not reaching its middle. Sternaulus indistinct. Speculum shiny and almost impunctate. Epicnemial carina present, reaching above middle of hind edge of pronotum. Posterior transverse carina of mesosternum complete. Metanotum (including postscutellum) with longitudinal wrinkles and a few punctures. Metapleuron densely punctate. Legs slender, hind femur about 5 × as long as wide. Tarsal claws small and thin, only slightly longer than aro-



Figures 1–4. Holotype of *Temelucha rea* sp. n., female. I lateral view 2 dorsal view 3 frontal view 4 anteroventral view.

lium. Propodeum long, only very weakly convex in profile with its apical edge reaching middle of hind coxa. Pleural carina complete, its distance from circular propodeal spiracle about equal to diameter of spiracle. Spiracle connected to pleural carina by a raised ridge. Lateromedian and lateral longitudinal carinae and basal transverse carina complete. Median section of apical transverse carina indistinct. Pleural areas strongly punctate. Lateral areas with dense punctures and sparse transverse wrinkles. Area basalis very small with almost parallel lateral carinae on its basal half. Area superomedia and area petiolaris indistinctly separated; both areas narrow, almost parallel-sided and with dense transverse striation, except basal part of area superomedia, which is almost triangular-shaped and less striate, rather shiny with a few punctures.

Wings. Wing membrane with dense short hairs. Fore wing with vein *cu-a* interstitial. Vein 2m-*cu* postfurcal with a wide bulla. Distal abscissa of *Rs* almost completely straight. Second discal cell about $2 \times as$ long as first sub-discal cell (measured at front margins). Pterostigma slightly shorter than front margin of marginal cell. Hind wing with vein *cu-a* + abscissa of *Cu*1 between *M* and *cu-a* almost straight, not intercepted. Distal abscissa of *Cu*1 spectral.

Metasoma. First metasomal segment slightly longer (about $1.15 \times$) than second segment. Ventral margins of first tergite touching each other ventrally. Lateromedian carinae of first tergite relatively weak. Second tergite with longitudinal striation characteristic of many Cremastinae. Third tergite coriaceous. Following tergites mainly punctate. Metasoma strongly laterally compressed, especially from third tergite on. Ovipositor sheath twice as long as hind tibia (or as long as fore wing from base to middle of marginal cell). Ovipositor straight, laterally compressed with distinct subapical notch. Apex smooth and straight, with subapical part somewhat widened in profile.

Colour. Head yellow except following parts. Upper face with brownish patch in midline. Black parts are: mandible teeth, middle of frons, ocellar area, posterior half of gena and occiput. Maxillary and labial palpi yellowish brown. Antennal flagellomeres dark brown with lighter apical bands on first few basal flagellomeres. Scapus and pedicellus mainly dark brown with some yellowish brown colouration on ventral side. Wings hyaline, venation and pterostigma brownish. Pronotum reddish with wide yellowish edges and hind corner. Mesoscutum yellow with an anteromedian black patch and two posterolateral brownish patches. Hind edge of mesoscutum and scutellar groove black. Scutellum entirely yellow. Mesopleuron mainly reddish and yellowish with black patches on ventral parts. Metanotum dark brown, its center somewhat lighter reddish brown. Metapleuron reddish and yellowish, its anterior ventral corner black. Propodeum almost entirely pale reddish, only basally black, medially reaching only basal part of area superomedia.

Fore and mid legs: coxae yellow with brownish patches basally; trochanters and trochantelli yellow; femora, tibiae and tarsomeres pale reddish except brown apical tarsomeres. Hind leg: coxa basally black; trochanter and trochantellus brown with yellowish apical parts; femur brown, basally and apically yellowish brown; tibia yellowish brown in middle, basally and apically brown; tarsomeres brown with yellowish brown base of first tarsomere; apical tarsomere dark brown.



Figures 5–8. Paratype of *Temelucha rea* sp. n., female. 5 lateral view 6 dorsal view 7 frontal view 8 anteroventral view.
First tergite reddish brown laterally as well as dorsally in middle and in most apical part. Basal part of tergite and basal part of postpetiolus almost black dorsally. Second tergite reddish brown with irregular brown patches in middle. Following tergites dark brown (almost black) basally, reddish brown apically with yellowish brown lateral and posterolateral edges. Ovipositor sheath dark brown (almost black); ovipositor reddish brown with paler apex.

Variation. The paratype female (Figs 5–8) is identical to the holotype in all the characteristics described above except that it is darker than the holotype. The brownish patch in the midline of the upper face is larger and black; pronotum more reddish; the posterolateral dark patches of the mesoscutum are black; mesopleuron with less yellowish and more reddish colouration and almost black around the speculum; metanotum almost black; propodeum darker, the basal half black, apical half pale reddish; hind tibia darker brown in the middle; the first and second tergites are darker, the light edges of the apical tergites are slightly darker.

Male. Unknown.

Distribution. Currently known only from Malta.

Ecological note. Adult wasps emerged on 14.viii.2014 from flowers of *Limbarda crithmoides* (Linnaeus) collected on 8.ix.2014. Several adult moths of *Eublemma parva* (Hübner) (Lepidoptera: Noctuidae) also emerged from the flowers; most probably it is the host species.

Etymology. Arbitrary combination of letters, feminine gender.

Identification key to Temelucha in the Western Palaearctic region

Supporting but not distinguishing characters are given in parentheses, comments in brackets. Figures 9–18 depict some important characteristics. Only some specific figures are cited in the key; other features used throughout the key such as ovipositor (Figs 9–11) and propodeum (Figs 14–15) shapes are recommended to be checked before using the key.



Figures 9–11. Ovipositor apex characteristics, lateral view. 9 straight, *Temelucha rea* sp. n. 10 down-curved, *Temelucha interruptor* (Gravenhorst, 1829) 11 sinuous, *Temelucha discoidalis* (Szépligeti, 1899).

	male ocellus almost as long as distance between lateral ocellus and eye) [female
	unknown] <i>T. tibialis</i> Kolarov, 1995
_	Spurs on hind tibia not unusually short, longer spur is longer than apical
	width of hind tibia4
4	Fore wing venation partly unpigmented, basal abscissa of M+Cu spectral,
	other veins (except most apical ones) are more or less pigmented, not spec-
	tral; mesosoma predominantly black (ovipositor apex very weakly sinuous, not
	down-curved; male ocellus large, its diameter longer than distance between
	lateral ocellus and eye; body length 2.4-4 mm) T. minuta (Morley, 1912)
_	Fore wing venation pigmented, or if (partly) unpigmented, then pattern of
	depigmentation not the same as described above5
5	Mesothorax in greater part yellow and/or reddish coloured (usually both fe-
	male and male face mainly yellow; propodeum often with yellowish/reddish
	colouration)
_	Mesothorax in greater part black (usually female face mainly dark, male face
	either mainly yellow or mainly dark; propodeum usually black)18
6	Frons with a pair of tubercles; hind femur elongate, $7.5 \times as$ long as wide
	medially (ovipositor apex straight with distinct dorsal subapical notch; fore
	wing ~6 mm long) [male unknown]
_	Frons without a pair of tubercles; hind femur not so elongate7
7	Second discal cell 1.5–2 × as long as first sub-discal cell8
_	Second discal cell shorter, less than $1.5 \times as$ long as first sub-discal cell15

8	All coxae entirely yellow and/or reddish (ovipositor apex down-curved; body
	length 7–8 mm) <i>T. schoenobia</i> (Thomson, 1890)
_	At least hind coxa basally dark9
9	Propodeum short, curved in lateral view10
-	Propodeum long, not curved in lateral view11
10	Male ocellus small, its diameter shorter than distance between lateral ocellus
	and eye; vein 2 <i>m</i> - <i>cu</i> weakly postfurcal (ovipositor sheath as long as fore wing
	from base to the base of marginal cell; ovipositor apex straight; body length
	7-9 mm) [the lightest specimens key out here, for the darker specimens see
	also couplet 47] <i>T. lucida</i> (Szépligeti, 1899)
_	Male ocellus large, the lateral one almost touching eye; vein 2 <i>m-cu</i> interstitial
	(fore wing 6.3 mm long) [female unknown] T. ocellaris Kolarov, 1995
11	Fore wing vein 2m-cu interstitial (female ocellus large, its diameter about the
	same as distance between lateral ocellus and eye; male ocellus large, its diameter
	longer than distance between lateral ocellus and eye; body length 6.5–7 mm)
_	Fore wing vein 2 <i>m-cu</i> distinctly postfurcal (ocellus shorter than or about the
	same as distance between lateral ocellus and eye)
12	Following characters in combination: malar space $0.4 \times as$ long as basal width
	of mandible; inner eye orbits weakly convergent ventrally; ocellus small, its
	diameter shorter than distance between lateral ocellus and eye; fore wing -4
	mm long [female unknown] T. pagliani Kolarov, 1995
_	Not exactly as above (either female or male with distinctly longer malar space
	and parallel inner eye orbits, as in T. decorata (Gravenhorst, 1829), or with
	distinctly shorter fore wing, as in <i>T. picticollis</i> (Hellén, 1949))13
13	Propodeum black; ovipositor apex weakly sinuous; notaulus absent (male
	ocellus small, its diameter shorter than distance between lateral ocellus and
	eye; body length 4-5 mm) [lighter female specimens key out here, for the
	darker females and males see also couplet 53 and 59]
	T. picticollis (Hellén, 1949)
_	Propodeum extensively yellowish/reddish coloured; ovipositor apex straight
	to very weakly down-curved; notaulus well developed
14	Female body 7-10 mm, fore wing 3.5-4 mm long; first tergite relatively
	stout, postpetiolus distinctly swollen (ovipositor sheath relatively shorter, less
	than $0.4 \times$ as long as body length; male ocellus relatively small, its diameter
	slightly shorter than or about the same as distance between lateral ocellus and
	eye; body length 6–10 mm) <i>T. decorata</i> (Gravenhorst, 1829)
_	Female body 4-5 mm, fore wing less than 3 mm long; first tergite slender,
	postpetiolus not distinctly swollen (ovipositor sheath relatively longer, 0.4 or
	more × as long as body length) [male unknown] <i>T. rea</i> sp. n.
15	Body length 3-4 mm; fore wing venation mostly depigmented (ovipositor
	apex slightly down-curved) T. anatolica (Šedivý, 1968)
_	Body length 8–11 mm, fore wing venation pigmented16



Figures 12–13. Fore wing characteristics. **12** *Rs* curved near the front margin of the wing, *Temelucha signata* (Holmgren, 1860) **13** *Rs* straight, not curved near the front margin of the wing, *Temelucha inter-ruptor* (Gravenhorst, 1829).



Figures 14–15. Propodeum characteristics, lateral view. **14** short and curved propodeum, *Temelucha lucida* (Szépligeti, 1899) **15** not short, not curved, 'usual' propodeum, *Temelucha discoidalis* (Szépligeti, 1899).

16	Ocellus small, its diameter as long as or shorter than the distance between
	lateral ocellus and eye (ovipositor sheath about as long as fore wing from base
	to the apex of marginal cell; body length 8–12 mm)
	T. dorsonigra (Hedwig, 1957)
_	Ocellus large, its diameter longer than the distance between lateral ocellus
	and eye
17	Hind tarsal claws distinctly longer than arolium; fifth tarsal segment of hind
	leg $4.2 \times as$ long as wide; ovipositor sheath about as long as fore wing (body
	length ~10 mm) T. afghana Šedivý, 1968
_	Hind tarsal claws as long as arolium; fifth tarsal segment of hind leg shorter,
	$3.2-3.4 \times$ as long as wide; ovipositor sheath about as long as fore wing from
	base to the base of marginal cell (body length 8–11 mm)
	T. observator Aubert, 1966

18	Front edge of clypeus almost straight to weakly convex; clypeus flat or very weakly convex in lateral view (cf. Fig. $16-17$).
_	Front edge of clypeus distinctly curved, convex; clypeus moderately to strong- ly convex in lateral view (cf. Fig. 18)
19	Ventral margins of first tergite not touching each other 20
_	Ventral margins of first tergite touching each other 22
20	Mesosoma distinctly elongate 2.6 x as long as high in lateral view slightly
20	concave ventrally (ovinositor anex straight: male ocellus diameter shorter than
	distance between lateral ocellus and eve: fore wing length 2.5–2.7 mm)
	<i>T cylindrator</i> Narolsky 1987
	Mesosome not so elongate and not surved; fore wing > / mm long 21
- 21	Ovinesiter sheath long distinctly longer than fore wing (ovinesiter aper
Δ1	weakly down curved, male acellus large its diameter langer than the distance
	between leteral coeffus and even bedy length 0, 11 mm)
	between lateral ocenus and eye; body length $9-11$ mm/
	Origonitation of anti-alignment of a state of the state o
_	$T_{\rm resc}$ (role wing length 4.2
22	mm) [male unknown]
LL	Maiar space black (eye orbits mostly black, a pair of spots on the vertex and
	patches on the inner orbits below toruli are yellowish; ovipositor apex not
	down-curved; ovipositor sheath about as long as fore wing from base to the
	apex of marginal cell; diameter of male ocellus shorter than the distance be-
	tween lateral ocellus and eye; body length $4-7 \text{ mm}$)
	<i>I. guttifer</i> (Inomson, 1890)
-	Maiar space at least partiy yellow, eye orbits partiy or entirely yellow
23	Fore wing with vein Rs almost straight, not curved near the front margin (cf.
	Fig. 13); ovipositor sheath as long as fore wing from base to apex of marginal
	cell (diameter of male ocellus shorter than the distance between lateral ocellus $T = \frac{1}{2} \frac{1}{2}$
	and eye; body length ~5 mm) <i>I. albipennis</i> (<i>Letterstedt</i> , 1838)
-	Fore wing with <i>Rs</i> curved near the front margin of the wing (cf. Fig. 12) 24
24	Ovipositor sheath as long as fore wing from base to base of marginal cell (the
	diameter of male ocellus shorter than the distance between lateral ocellus and
	eye; body length 5–9 mm) <i>T. signata</i> (Holmgren, 1860)
-	Ovipositor sheath longer, as long as fore wing or at least as long as fore wing
	from base to apex of marginal cell (body length ~5 mm) [male unknown]
	T. subsignata Kolarov, 1989
25	Clypeus distinctly separated from face, strongly convex and nose-shaped in
	lateral view; propodeum convex in lateral view (ovipositor apex sinuous; male
	ocellus large, its diameter distinctly longer than the distance between lateral
	ocellus and eye; body length 6–8 mm) T. subnasuata (Thomson)
_	Clypeus weakly separated from face, moderately convex and not nose-shaped
	in lateral view
26	Soutollum block (to a maximum beautich as mucht laterally) 27
	Scutenum black (to a maximum brownish of fusty laterally)2/



Figures 16–18. Clypeus characteristics, frontal view. **16** edge of clypeus almost straight, *Temelucha caudata* (Szépligeti, 1899) **17** edge of clypeus weakly convex, *Temelucha signata* (Holmgren, 1860) **18** edge of clypeus distinctly convex, *Temelucha lucida* (Szépligeti, 1899).

18

	the distance between lateral ocellus and eye; fore wing 4.4–4.9 mm long) <i>T. tobiasi</i> Narolsky, 2004
_	Not exactly as above
29	Female [note that females of <i>T. elongata</i> Kolarov, 1995 and <i>T. szepligetii</i> (Dalla Torre, 1901) are unknown] 30
_	Male [note that male of <i>T. thoracica</i> Kolarov, 1989 is unknown]
30	Mesonotum short, only $1.1 \times as$ long as wide; ovipositor apex rather strongly down-curved (body length ~7 mm)
_	Mesonotum more elongate; ovipositor apex either straight or sinuous, or very weakly down-curved
31	Malar space entirely or partly yellow
-	Malar space black to reddish
32	Scutellum without lateral carinae; malar space yellow (ovipositor apex straight; body length 4–5 mm) <i>T. tenerifensis</i> Šedivý, 1993
_	Scutellum carinate to its apex; malar space only partly yellow (ovipositor apex straight to very weakly down-curved; body length ~5 mm) [there are only a few females with partly yellow malar space; the majority have black malar space, hence they key out at couplet 35] <i>T. arenosa</i> (Szépligeti, 1899)
33	Ovipositor apex not sinuous (straight or weakly down-curved)
_	Ovipositor apex sinuous
34	Ovipositor sheath longer than fore wing (ovipositor apex straight and sharp; body length 6–7 mm)
_	Ovipositor sheath shorter than fore wing
35	Scutellum carinate to its apex (body length ~5 mm)
_	Scutellum not carinate to its apex (body length 5–6.5 mm)
	<i>T. meridionellator</i> Aubert, 1981
36	Scapus entirely dark brown (body length 7–8 mm)
_	Scapus with yellow or reddish colouration
37	Thorax matt; propodeum elongate, not curved in lateral view; lateromedian cari- nae of first tergite reaching the middle of the tergite; petiolus basally depressed; outer surface of hind tibia brown (body length 5–6 mm)
	<i>T. ophthalmica</i> (Holmgren, 1860)
-	Thorax shiny; propodeum short, curved in lateral view; lateromedian carinae
	of first tergite missing or faint; petiolus basally cylindrical; outer surface of
	hind tibia whitish (body length ~7 mm)
38	Ocellus diameter longer than the distance between lateral ocellus and eye 39
_	Ocellus diameter shorter than the distance between lateral ocellus and eye41
39	Scutellum without lateral carinae (body length 4–5 mm)
_	Scutellum with lateral carinae

40	Thorax matt; propodeum elongate, not curved in lateral view; outer surface of
	hind tibia brown (body length 5–6 mm) <i>T. ophthalmica</i> (Holmgren, 1860)
_	Thorax shiny; propodeum short, curved in lateral view; outer surface of hind
	tibia whitish (body length ~7 mm) T. marocator Aubert, 1977
41	Malar space yellow
_	Malar space black to reddish
42	Fore wing veins indistinctly pigmented, pale yellowish, the wing membrane
	lactescent; scapus in greater part and ventral side of basal flagellomeres yellow
	(body length ~5 mm)
_	Fore wing veins pigmented, brown, the wing membrane more hyaline; scapus
	in greater part and ventral side of basal flagellomeres black or dark brown
	(body length ~5 mm)
43	Propodeum short, curved in lateral view (body, except the legs, black; body
-0	length 6–7 mm)
_	Propodeum longer, not curved in lateral view
44	Mesosoma elongate. 2.2 x as long as high (fore wing 4.7 mm)
	<i>T. elongata</i> Kolarov. 1995
_	Mesosoma not so elongate
45	Fore femur mainly vellowish/reddish (body length ~7 mm)
1)	T annulata (Szépligeti)
_	Fore femur mainly black anterior surface and anex vellowish or reddish (body
	length 5–6.5 mm) [note that this couplet does not allow safe identification due
	to the poorly described males in the original description of this species]
	T moridionallator Aubert 1981
46	Propodeum short, curved in lateral view (male ocellus small, its diameter
10	shorter than distance between lateral ocellus and eve)
_	Propodeum long, not curved in lateral view (male ocellus either small or
	large)
47	Head and mesosome not covered with unusually dense white hairs: vein 2m
T /	a weakly postfurgal; ovipositor sheath relatively short, as long as fore wing
	from base to the base of marginal cells ovipositor apex straight, usually mes
	accutum mesopleuron and propodeum with rich vellow colouration (body
	length 7, 9 mm) [for the lightest specimens see also couplet 10]
	T lucida (Szópliczti 1800)
	Head and marganeous covered with distinct dense white hairs wain 2m au postfur
_	all avinagitat charth distinctly langer avinagitat and weakly down gurud bady.
	cal, ovipositor sheath distinctly longer, ovipositor apex weakly down-curved, body
	with more restricted yellow, propodeum black, mesopleuron only with small yel-
40	
4ð	Following characters in combination: malar space swollen, $1.3 \times as$ long as
	basal width of mandible; notauli present as transversely striate shallow con-
	cavities; area superomedia pentagonal, closed posterioriy (ocellus diameter
	snorter than the distance between lateral ocellus and eye; body length $-/$
	mm) [temale unknown] I. notaulata Kolarov, 1989

_	Not exactly as above
49	Female
_	Male [note that males of <i>T. arenosella</i> Kolarov, 1989, <i>T. notata</i> Kolarov, 1989, <i>T. corsicator</i> Aubert, 1961 are unknown] 58
50	Ovipositor apex down-curved
_	Ovipositor apex not down-curved (straight or sinuous)
51	Head very strongly and almost rectilinearly constricted behind eyes; hind
	femur reddish, usually somewhat darker basally (body length 6–9 mm)
	<i>T. interruptor</i> (Gravenhorst, 1829)
-	Head strongly but roundly constricted behind eyes; hind femur yellowish
	apically (body length ~5 mm) <i>T. notata</i> Kolarov, 1989
52	Ovipositor apex sinuous (strongly or weakly but distinctly)
-	Ovipositor apex straight, not sinuous
53	Ovipositor sheath as long as fore wing; body length 8–9 mm; ovipositor apex strongly sinuous (head mainly black) <i>T. discoidalis</i> (Szépligeti, 1899)
-	Ovipositor sheath distinctly shorter than fore wing; body length 4-5 mm;
	ovipositor apex weakly sinuous (head mainly yellow) [for lighter female speci-
	mens see also couplet 13] <i>T. picticollis</i> (Hellén, 1949)
54	Following characters in combination: malar space slightly longer than basal
	width of mandible; second discal cell $2 \times as$ long as first sub-discal cell; area
	superomedia shiny with or without punctures; lateromedian carinae on first
	tergite short and weak or absent (body length 5–7 mm)
	<i>T. mohelnensis</i> Sedivý, 1971
-	Not exactly as above (malar space at a maximum as long as basal width of
	mandible; second discal cell less than 2 × as long as first sub-discal cell; latero-
	median carinae on first tergite usually distinct)
<i>55</i>	Following characters in combination: body length ~4.5 mm; notauli absent
	or indistinct; first tergite as long as second tergite; lateromedian carinae on
	hirst tergite well developed
_	Not exactly as above; body length 6–10 mm (first tergite either longer than
5(Second tergite, or if equal then notauli present)
30	(i.e. the years short transverse strike among the punctures of the mesoscietum)
	(i.e. the very short transverse strike among the punctures of the mesoscutum)
	x = 1, 2, 3 where $x = 1, 3$ and
	cell (area superomedia entirely or partly striate: body length 6, 9 mm)
	T united superformedia entitiety of party strate, body length 0^{-1} mm/
_	Notauli absent or indistinct: inner eve orbits parallel: second discal cell less
	than $1.5 \times (-1.2 \times)$ as long as first sub-discal cell (area superomedia not en-
	tirely striate)
57	Head roundly constricted behind eves: lateral areas of propodeum mainly
- 1	striate: metasomal tergites brown to black. tergites 2–7 with lighter posterior
	edges (body length ~10 mm)

-	Head more strongly constricted behind eyes; lateral areas of propodeum
	mainly punctate; tergites black, only the apical tergites with lighter posterior
	edges (body length ~10 mm) <i>T. corsicator</i> Aubert, 1961
58	Ocellus diameter longer than the distance between lateral ocellus and eye
	(head, as in females, very strongly and almost rectilinearly constricted behind
	eyes; body length 6–9 mm) <i>T. interruptor</i> (Gravenhorst, 1929)
-	Ocellus diameter shorter than the distance between lateral ocellus and eye 59
59	Following characters in combination: body length < 5 mm; second discal
	cell ~1.5 × as long as first sub-discal cell; lateromedian carinae of first tergite
	absent; pronotum and mesoscutum almost entirely black with little yellow
	colouration
_	Not exactly as above; body length > 5 mm60
60	Second discal cell 2 × as long as first sub-discal cell (area superomedia shiny with
	or without punctures; body length 5–7 mm) T. mohelnensis Šedivý, 1971
-	Second discal cell less than $2 \times as$ long as first sub-discal cell61
61	Lateral areas of propodeum mainly striate; second discal cell less than 1.5 \times
	$(-1.2 \times)$ as long as first sub-discal cell (body length -8 mm)
-	Lateral areas of propodeum mainly punctate; second discal cell at least ~1.5 \times
	as long as first sub-discal cell
62	Notauli present [although not very easy to recognize but usually easier than
	in females: the different sculpture (i.e. the very short transverse striae among
	the punctures of the mesoscutum) helps to reveal the shallow line of the no-
	taulus]; inner eye orbits slightly divergent ventrally; area superomedia entirely
	or partly transversely striate (body length 6–8 mm)
_	Notauli absent or indistinct; inner eye orbits parallel; area superomedia shiny
	and distinctly punctate, not striate (body length 8–9 mm)

Acknowledgements

I would like to express my gratitude to D. Mifsud (University of Malta, Msida) for donating the Maltese ichneumon wasp specimens to the HNHM Hymenoptera Collection and for his activity in our co-operation about the Maltese ichneumon wasp fauna, as well as to M. Zammit for collecting the specimens. I am especially grateful to G. R. Broad (Natural History Museum, London) for his valuable professional and linguistic corrections on the manuscript, as well as to J. A. Kolarov (University of Plovdiv, Plovdiv) and to an anonymous reviewer for their valuable comments. I thank S. A. Belokobylskij (Zoological Institute of the Russian Academy of Sciences, St. Petersburg), G. R. Broad (Natural History Museum, London), and J. Paukkunen (Finnish Museum of Natural History, Helsinki) for helping my work with relevant papers and/

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or with borrowed type specimens. I am grateful to T. Németh (HNHM, Budapest) for the taking the photos and to Z. György (HNHM, Budapest) for post-processing some of them. This study was supported by Hungarian Scientific Research Fund (OTKA, Grant no. 108571).

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RESEARCH ARTICLE



Variation of fore wing shape in Melipona mandacaia Smith, 1863 (Hymenoptera, Meliponini) along its geographic range

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Academic editor: <i>H. Baur</i>	Received 17 September 2015 Accepted 10 December 2015 I	Published 1 March 2016
	http://zoobank.org/AD1A9A01-3B36-4013-BF24-68D1DA331347	

Citation: Prado-Silva A, Nunes LA, de Oliveira Alves RM, Carneiro PLS, Waldschmidt AM (2016) Variation of fore wing shape in *Melipona mandacaia* Smith, 1863 (Hymenoptera, Meliponini) along its geographic range. Journal of Hymenoptera Research 48: 85–94. doi: 10.3897/JHR.48.6619

Abstract

Melipona mandacaia is a stingless bee species responsible for the pollination of many native plants in Brazil, South America. In spite of its ecological and economic importance, natural populations of *M. mandacaia* have been depleted because of deforestation. In order to evaluate the interpopulation morphometric structure of remaining populations, we carried out geometric morphometric studies based on fore wing shape in this native bee species. The grouping analysis by UPGMA revealed three distinct clusters and significant differences in fore wing size were observed (p<0.001) among populations. The three groups were also reflected in the first two principal components explaining about 60% of the total variation. These results indicate differentiation among populations, which can be regarded as unique management units. Therefore, efforts should be directed to the conservation of local populations of *M. mandacaia* to avoid the negative impacts of loss in pollination over plant species and environmental services.

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Keywords

Bees, Apidae, principal component analysis (PCA), Meliponini, geometric morphometrics, Procrustes superimposition

Introduction

Stingless bees play a key role in natural and agricultural systems (Eardley et al. 2006) as they account for about 30% to 90% of pollination in native flora (Kerr 1997). Besides, these bees produce high-quality honey, propolis, pollen and wax used as food sources and/or as pharmaceutical products. However, human activities, such as deforestation and habitat loss, are a potential threat to these insects, leading to population declines (Fortuna and Bascompte 2006).

In Brazil, the stingless bees of the tribe Meliponini encompass most of native social bee taxa, in which *Melipona* is the species-richest genus (Michener 2007, Camargo and Pedro 2013). *Melipona mandacaia* Smith, 1863 is an endemic bee species from semiarid regions in northeastern Brazil, including one of the poorest Brazilian regions, named the "drought polygon". Being typical of the caatinga (dry bushland) biome, *M. mandacaia* is well adapted to high temperatures and reduced rainfall conditions (Carvalho et al. 2003, Batalha-Filho et al. 2011). The nests of this species are built in tree holes (Camara et al. 2004) and some populations have been raised in boxes by local farmers for honey production, representing a major portion of economy and food in traditional agriculture (Carvalho et al. 2003).

Because of its importance and vulnerability to deforestation, populations of stingless bees have been intensively studied using molecular (Francisco and Arias 2010, Tavares et al. 2013), behavioral (Kuhn-Neto et al. 2009, Palacio et al. 2010) and traditional morphometric methods (Nunes et al. 2007, Diniz-Filho and Bini 1994, Hepburn et al. 2005). Recently, the utilization of geometric morphometrics has increased in population (Tilde et al. 2000, Francoy et al. 2006, Nunes et al. 2008, Nunes et al. 2012), heritability (Monteiro et al. 2002), evolutionary (Bonatti et al. 2014) and reproductive (Carvalho et al. 2011) studies of bees. These reports have shown that geometric morphometric data are effective in the identification of groups and lineages (Francoy et al. 2008, Francoy et al. 2009, Bischoff et al. 2009).

In fact, morphometric analyses based on landmarks allow evaluating homologous morphological features that are independent of size (Francoy and Fonseca 2010). Furthermore, the geometric morphometrics of wings have been useful to establish the geographic origin of individuals of a single species (Bischoff et al. 2009, Nunes et al. 2012).

In spite of being a precise and simple technique to assess population diversity (Adams et al. 2004), no geometric morphometrics reports are available in *M. mandacaia*. Therefore, we focused on analyzing morphogenetic traits in populations of *M. mandacaia* in order to examine how populations are structured throughout their range.

Material and methods

The samples were collected in 15 localities (3–26 colonies per collection site) along the semiarid regions of the state of Bahia, northeastern Brazil. Right after collection, the specimens were stored in absolute ethanol for further morphometric analyses. The right fore wings were removed from 9 to 13 adult workers per colony, totaling 127 colonies and 1199 specimens (Table 1). Afterwards, they were placed onto glass slides and photographed using a stereomicroscope equipped with an image capture system (Leica Application Suite version 3.4.1).

Based on high-resolution images, two dimensional landmarks were digitized with the software TPSDIG2 (Rohlf 2006). A total of 12 landmarks were recorded in each fore wing for morphometric analyses (Figure 1).

Based on Cartesian coordinates, Procrustes superimposition and Principal Component Analysis (PCA) were performed using the software MORPHOJ version 2.0 (Klingenberg 2011) based on mean values of colonies. Subsequently, a cluster analysis using UPGMA (Unweighted Pair-Group Method with Arithmetic Average) was carried out with the software Past (Paleontological Statistics) version 1.81 (Hamer 2008). The cophenetic correlation coefficient was also calculated using Past.

A variance analysis (ANOVA) followed by a Tukey test was performed to evaluate centroid size. Shape and size of fore wings from each population were compared to altitude and geographic distance of colonies via a Mantel test in the software NTSYS version 2.02 (Rohlf 1993).

Locality	Altitude (m)	Latitude (S)	Longitude (W)	Number of colonies	Number of specimens
Casa Nova	397	9°59'56.2"	42°28'50.5	10	100
Hidrolândia	492	11º15'45.4	42°07'26.1	10	100
Itaguaçu	44	11°00' 42"	42°23' 58"	6	60
Juazeiro	368	9°24'42"	40°29'55"	26	168
Macururé	357	9°10'03"	39°03'27"	7	82
Morpará	405	11°33'31"	43°16'51"	6	66
Morro do Chapéu	609	13°12'0"	40°19'18.1"	10	100
Muquem de São Francisco	560	12° 11' 55''	43° 49' 58''	4	41
Ourolândia	560	10°58'13"	41°04'59"	3	31
Paulo Afonso	243	9°24' 28"	38°13' 19"	5	50
Pilão Arcado	394	9°53'57.6	42°29'11.1"	7	68
Remanso	388	9°12'44.1"	42°01'29.2"	11	111
São Gabriel	692	11º13'44"	41°54'43"	15	150
Serra do Ramalho	438	13°33'45"	43°35'48"	3	32
Uibaí	582	11°20'13"	42°07'58"	4	40
TOTAL				127	1199

Table I. Sampling sites of *Melipona mandacaia* with altitude, geographic coordinates and number of samples colonies and specimens.



Figure 1. Right fore wing of Melipona mandacaia with 12 landmarks.

Results

The first two principal components explained about 60% of the variation in fore wing shape. Three groups were distinguished according to collection site in PCA, as follows: 1 – Pilão Arcado, Remanso and Casa Nova; 2 – Juazeiro, Macururé and Paulo Afonso; and 3 – Ourolândia, Morro do Chapéu, Serra do Ramalho, São Gabriel, Morpará, Itaguaçu da Bahia, Muquém de São Francisco, Uibaí and Hidrolândia (Figure 2).

Similarly, the dendrogram based on UPGMA (Figure 3) revealed three distinct clusters. It should be pointed out that the third group is composed of colonies from both sides of the São Francisco river (Serra do Ramalho and Muquém de São Francisco are located on the left margin while Morro do Chapéu, São Gabriel, Morpará, Itaguaçu da Bahia, Ourolândia, Uibaí and Hidrolândia are located on right margin of São Francisco River) with a cophenetic correlation coefficient of 84% (Figure 4).

Fore wing size was significantly different among colonies from distinct collection sites (p<0.001) (Figure 5) by the Tukey test. However, the fore wing shape was more informative in discriminating the groups than size, thus demonstrating the efficiency of geometric morphometrics.

	es, altitude and snape and size of fore wings
using Mantel's test with 5000 permutations.	

1.1.1

Variables	R	р
Geographic distance × forewing shape	0.349	0.0122*
Geographic distance × forewing size	0.438	0.0008**
Altitude × forewing size	-0.149	0.8420ns
Altitude × forewing shape	-0.19	0.9236ns
forewing size × forewing shape	0.884	0.0002**

ns (p>0.05); * (p<0.05); ** (p<0.001)



Figure 2. Analysis of Principal Components and Minimum Spanning Tree of fore wings of Melipona mandacaia.



Figure 3. UPGMA dendrogram of morphological relatedness of fore wings based on Euclidean distance among colonies of Melipona mandacaia with bootstrap values (after 10,000 repetitions).



Figure 4. Map of Bahia, in Brazil, with sampling sites of Melipona mandacaia.

The Mantel test revealed no correlation between both size x altitude and shape x altitude (p>0.05) (Table 2). On the other hand, both shape (p<0.05) and size (p<0.001) were weakly but significantly correlated to geographic distance in *M. mandacaia*.

Discussion

The present analyses indicated gene flow among individuals from the three morphogenetic groups of *M. mandacaia* (Figure 2) inasmuch as populations are weakly structured. This result suggests that São Francisco River should not act as an effective geographic barrier to the dispersal of individuals from both river margins.

Similarly, molecular markers revealed a moderate genetic structuring (Φ ST = 0.2961) among these populations (Miranda et al. 2012). Only the Sobradinho



Figure 5. Boxplot of fore wing centroid size of *Melipona mandacaia* and comparison of mean values by a Tukey test (same letters represent no significant statistical differences).

reservoir (about 320 km of extension and a water surface of 4.214 km²) seems to disrupt gene flow between groups 1 and 2, as identified in this study (Figure 4). Thus, the construction of dams related to human disturbance seems to be responsible for the population structure associated with decreased genetic variation and high inbreeding in colonies of *M. mandacaia*. A similar result was reported in *Apis mellifera* L. (Miguel et al. 2007) and rodents (*Calomys expulsus* Lund, 1841) (Nascimento et al. 2011). Additional support to this hypothesis is that the Sobradinho dam was built about 40 years ago. This relatively long period is compatible with, at least, 10 generations of queen bees that could potentially lead to both fixation and losses of alleles (i.e. reduced genetic variation).

Moreover, previous reports have shown that fore wing size and shape of some *Melipona* species are influenced by both geographic distance and altitude, like that observed in *M. scutellaris* Latreille (Nunes et al. 2007), *M. quadrifasciata anthidioides* Lepeletier (Nunes et al. 2013) and *M. subnitida* Duke (Lima et al. 2014). Nonetheless,

no significant morphometric differences were observed in *M. mandacaia* in relation to altitude (p>0.05), but both fore wing size and shape were correlated to geographic distance (p<0.001 and p<0.05, respectively). This isolation-by-distance model in *M. mandacaia* can be explained by the eusocial behavior of these bees and their short flight range (about 2,000 m) (Araújo et al. 2004), causing restricted gene flow among populations.

Therefore, the morphometric analysis based on fore wingsis useful to evaluate the interpopulation genetic divergence of *M. mandacaia*, once they seem to be less susceptible to environmental influence. In this sense, studies of geometric morphometrics are useful to the identification of variation in populations and species of bees (Oleksa and Tofilski 2015) that are essential to conservation plans.

Acknowledgments

The authors are grateful to Fundação de Amparo à Pesquisado Estado da Bahia (FAPESB) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support.

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Case series of 23 deaths from Hymenoptera stings among United States Air Force populations

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Academic editor: <i>Jack Neff</i>	Received 25 January 2016	Accepted 18 February2016	Published 1 March 2016
ht	tp://zoobank.org/A31F8C69-FDE	D-450C-8FC6-3F974D0CDE70	

Citation: Voss JD, Kugblenu R, Salter K, Johnson L, Reeves WK (2016) Case series of 23 deaths from Hymenoptera stings among United States Air Force populations. Journal of Hymenoptera Research 48: 95–99. doi: 10.3897/JHR.48.7905

Abstract

Medical conditions arising from hymenopteran sting allergy or mass envenomation are a serious health concern, particularly in austere environments. Both practicing allergists and entomological pest control personnel should consider the relevance of stinging insects when responding to problems with Hymenoptera. Recent occupational reviews of civilian deaths from insect bites and stings prompted our review of the US Air Force Mortality Registry to determine the relevance of insect stings and bites as a cause of death in the US Air Force. After reviewing over 40 years of death records we identified 23 death records, among US Air Force Active duty, guard, or retirees that arose directly from hymenopteran stings.

Keywords

Hymenoptera, bees, wasps, stings, mortality, military, Air Force Mortality Registry

Introduction

Public health aspects of pest control have substantially improved since the days when flea-infested rats helped transmit the Black Death that decimated medieval Europe (Tulchinsky and Varavikova 2014). Advancements in military medicine are also striking; vector-borne diseases such as malaria were once shaping military battles, but are now manageable with integrated pest control pioneered by the military (Ockenhouse et al. 2005). In the early 1900s, then Colonel (later General) William Gorgas virtually eliminated malaria and yellow fever at the Panama Canal Zone using a combination of vector control, medical prophylaxis, screens around living quarters, and other measures (Ockenhouse et al. 2005). Similarly, the discipline needed to ensure compliance with medical countermeasures for zoological or entomological diseases has also been a mainstay in the military approach to these threats. More recently, a soldier's death from rabies called to mind the public health role of command-directed interventions to protect the health of military members (Chretien 2012).

In modern times, this legacy of fleas, mosquitoes, and stray dog control makes it easy to overlook another threat envenomation from Hymenoptera (i.e., bees, wasps, and ants) or possibly other insects such as certain Lepidopteran caterpillars. While hymenopteran stings are known to cause allergic reactions, their medical importance is underestimated because their venom is often more irritating than lethal and they are not known as a vector for any infectious diseases.

Despite having a lower historical priority, there is growing evidence for the medical importance of ants, bees, and wasps. A recent review of mortality among workers in the United States found there were 52 occupational deaths from bees, 11 deaths from wasp stings, 4 from ant stings, and an additional 16 from spiders or other unknown insects from 2003–2010 and thousands of non-fatal lost work days attributable to insect stings (Pegula and Kato 2014). Less is known about mortality among military populations, but from a morbidity perspective, Hymenoptera were recently identified as an environmental threat to deployed military personnel throughout the world (Turbyville et al. 2013). This conclusion was based on the presence of medically important Hymenoptera species in Afghanistan and surrounding areas and a review of medical records in the deployed environment showing 1 in every 500 medical encounters was attributable to insect stings (Turbyville et al. 2013).

Methods

We evaluated the Air Force Mortality Registry (AFMR), which is the largest mortality registry within the Department of Defense. In the late 1990s, the Air Force began to compile death records from any member who died in the Active, Reserve, and Guard components of the Air Force and any retiree from these components. These records are still being collected from current times and now date back to 1970. There are over

350,000 deaths already registered within this database. The Air Force is the only service to assemble a long-term database of mortality records among retirees.

Within AFMR, deaths are classified by International Classification of Diseases (ICD) –10 codes based on the death certificate, casualty reports, ICD–10 codes obtained from the National Death Index, or a combination of sources. We defined cases as those having an ICD–10 of T63.4, which is the standardized coded designation for hymenoptera stings. All death certificates were reviewed individually to evaluate whether the individual died at home, on arrival, or after arrival to a medical facility.

Results and discussion

There were 23 deaths due to Hymenoptera stings representing <0.7 per 10,000 of all registered deaths within AFMR. A death certificate was available for 15 of the 23 identified cases. The number of stings was not reported so we could not determine if these were death from a single sting or mass envenomation. There is a significant difference between death from anaphylaxis or heart attack and massive toxin exposure. Eight individuals died after arrival to the emergency room, but before admission to an inpatient setting, and three died after being admitted to an inpatient setting. Thus, 11/15 deaths (73%) occurred after arrival to an emergency department.

Aggregate demographics are provided in Table 1. With less than one documented Hymenoptera sting death per year, these deaths are undoubtedly rare. In fact there were only three deaths in active personnel instead of retirees. This indicates that even with the higher risk jobs found in the military deaths from Hymenoptera stings are extremely rare despite the relatively common sting related medical encounters reported by Turbyville et al. (2013). This could be the result of military policy that excludes uniformed service in individuals with known anaphylactic allergies to insect bites or stings. Nevertheless, Hymenoptera sting deaths are more common in AFMR than other highly emphasized rare causes of death such as rabies and malaria (ICD–10s A82, Z20.3, and B50–B54; see Reeves and Bettano 2014), which could indicate that prior service increases the risk or exposure to Hymenoptera and thus allergic reactions later in life. When taken in the context of the overall US at work population a recent review by Pegula and Kato (2014) reported an average of 10 fatal injuries resulting from insects per year from 2003-2010 in the USA. In this regard while sting related deaths were rare among the USAF and retirees they are a potentially significant por-

Table I. Summary Characteristics of 23 Hymenoptera Death Cases in the US Air Force 1977–2013.

0	8
Sex 22 ma	es; 1 female
Status 20 reti	rees; 1 each from Active, Reserve, and Guard components

tion of the annual US deaths from Hymenopteran stings. Since the Army, Navy, and Marines Corps. do not have a similar mortality registry it is not currently possible to determine if their death rates were higher.

Clinical allergists could potentially play a role in secondary prevention of death or serious allergic reactions, such as screening individuals at risk for Hymenoptera sensitivity including at the time of retirement or separation from military service. Once identified, these individuals could carry medical countermeasures as recommended by their medical provider. Immunologic testing (e.g., specific IgE tests, basophil activation test, horseradish peroxidase, etc.) may help with identification and immunotherapy may provide therapeutic and quality of life benefits (Boyle et al. 2012, Eberlein et al. 2012). An even more intriguing observation for clinical allergists is that the majority of cases (73%) in this series of deaths were alive at the time they arrived for medical care. Most anaphylactic deaths take more than an hour after initial exposure. While we are not certain that improved medical care would have prevented any of the deaths, the death certificates clearly indicate that deaths rarely occur immediately after the sting without time for advanced medical treatment.

Conclusion

While a comprehensive approach to Hymenoptera control offers hope that these deaths are modifiable, these benefits have not yet materialized. In fact, despite the broad-based progress in mitigating medical effects of numerous pests, trends in occupational Hymenoptera deaths are fairly stable over the past decade (Pegula and Kato 2014). The unique challenges in mitigating medical consequences of Hymenoptera mark another opportunity for a public health approach.

Acknowledgements

The authors have no conflicts of interest to disclose. The views expressed in this article are those of the authors and do not necessarily reflect the official policy or position of the Uniformed Services University, United States Air Force, United States Navy, Department of Defense, or the U.S. Government. Distribution A: Approved for public release; distribution is unlimited. Case Number: 88ABW–2015-1032, 11 March 2015.

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Piercing of nectarless Hemerocallis (Xanthorrhoeaceae) flowers by Xylocopa varipuncta and X. virginica virginica (Apidae)

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Academic editor: J. Neff Received 1 September 2015 Accepted 28 September 2015	Published 1 March 2016
http://zoobank.org/33A2F42D-5E76-4170-B729-2EA6C83E547C	

Citation: Barrows EM (2016) Piercing of nectarless *Hemerocallis* (Xanthorrhoeaceae) flowers by *Xylocopa varipuncta* and *X. virginica virginica* (Apidae). Journal of Hymenoptera Research 48: 101–110. doi: 10.3897/JHR.48.6427

Abstract

The native carpenter bee *Xylocopa varipuncta* frequently made and re-used piercings in tubular corolla bases of nonnative, nectarless *Hemerocallis* 'Stella de Oro' (Stella de Oro Daylily, HSDO) in the César E. Chávez Memorial Plaza in downtown Sacramento, California. The bees frequently visited HSDO flowers from mid-morning through late afternoon in August 2014 during the 3-yr, severe California drought. Their foraging bouts were up to 10 floral visits, and they were evidently obtaining cell fluid. Nonnative *Apis mellifera* extended their proboscides through the piercings, acting as secondary cell-fluid robbers. They also may have pollinated HSDO when they collected its pollen. *Hemerocallis*-flower piercing by native *X. virginica virginica* is apparently rare, but in the Wehawken Nature Preserve in Bethesda, Maryland, a female pierced succulent, nectarless flowers of two other *Hemerocallis* cultivars and three unnamed seedlings, possibly obtaining cell-fluid, learning that the flowers did not have nectar, or both during the wet summer of 2015.

Keywords

Apis, Hemerocallis, Xylocopa, cell-fluid consumption, flower-piercing

Introduction

Some species of ants, bumble bees, carpenter bees, flowerpiercer birds, hummingbirds, mammals, stingless bees, and wasps are primary nectar robbers which make holes, piercings, and slits in floral corolla tubes through which they and secondary nectar robbers, which do not make such openings, imbibe nectar (Barrows 1980; Barrows et al. 2013). These robbers cannot reach nectar in long-corolla bases because their tongues are too short. *Xylocopa* pierces flowers using its bladelike galeae, and some *Bombus* species and a vespid-wasp species chew holes into flowers with their mandibles (Schremmer 1972, Michener 2007, Barrows et al. 2013, pers. obs.). Nectar robbing can increase, reduce, or have no significant effect on plant fitness, depending on environmental factors and plant species (Maloof and Inouye 2000).

In contrast, two *Xylocopa*-bee species pierce succulent corollas of nectarless *Hemerocallis* flowers with their proboscides. The main aim of this study is to describe the frequent flower piercing of such flowers by female *X. varipuncta* (Valley Carpenter Bee), proboscis probing of these piercings by workers of *Apis mellifera* (Western Honey Bee) in California, and rare piercing of such flowers by *X. virginica virginica* (Eastern Carpenter Bee) in Maryland. This study involves two native and one nonnative bee species and hybrid plants of nonnative parentage in an urban and suburban ecosystem, respectively. *Xylocopa varipuncta* evidently imbibed cell fluid, not nectar, from the nectarless flowers. To my knowledge, this is the first report regarding frequent nectarless-flower piercing and apparent cell-fluid feeding by bees.

Methods

Study sites

I observed *A. mellifera*, *X. varipuncta*, and *H.* 'Stella de Oro' (Stella de Oro Daylily, HSDO) on 11–15 August 2014 in the César E. Chávez Memorial Plaza in downtown Sacramento, California (Fig. 1) during the dry season of a 3-year extreme drought. All observation days were warm and sunny. The Plaza had four heavily mulched, automatically-watered HSDO beds: the north (38 clumps of HSDO shoots), north-northeast (44), south (53), and south-southwest (65) bed. There was no standing water in the fountain, or other place in the Plaza, which hymenopterans and other animals could drink. I also observed rare, daylily floral piercing by an unworn female *X. virginica virginica* on the warm, sunny day of 7 July 2015 during a wet summer in the Wehawken Nature Preserve in Bethesda, Maryland. The Preserve is within a residential neighborhood with many plant species, including large trees, and it contains about 600 cultivars and unnamed seedlings of *Hemerocallis* and several kinds of flowering plants used as nectar sources by this bee species. The focal bee was easily observed close up because she visited potted daylilies on two plant tables at about 30 cm above the ground.



Figure 1. César E. Chávez Memorial Plaza in Sacramento, California, view from the north. The northnortheast bed of yellow-orange *Hemerocallis* 'Stella de Oro' is in the background.

Bees

The only bee species I saw in the Plaza were *A. mellifera* and *X. varipuncta*. Many apid, colletid, halictid, and megachilid bee species occur in the Preserve. The native North American *X. varipuncta* occurs from Arizona, California, and Nevada through Baja California, and the native *X. virginica* occurs from southern Canada through Florida and west through Nebraska, Kansas, Oklahoma, and Texas (Krombein et al. 1979, Powell and Hogue 1980). *Apis mellifera* is an Old World species introduced into other parts of the world, including North America. All three of these species imbibe nectar from many plant species.

Hemerocallis

Hemerocallis is an insect-pollinated, Eurasian monocot genus with about 15 species, 80,000 registered cultivars, and thousands of unregistered hybrids derived from the species (American Hemerocallis Society 2015). These *Hemerocallis* occur in urban and other gardens worldwide, and some species, cultivars, and unregistered clones are nec-

tar and pollen sources of both pollinators and nonpollinators (Hirota et al. 2012, Billingslea 2015, pers. obs.). In general, each flower lasts only about 24 hr, whether or not it is pollinated. *Hemerocallis* flowers are succulent, and cell fluid appears at freshly cut tissue of their corollas (pers. obs.). In smaller-flowering kinds of *Hemerocallis*, which are the subjects of this study, corolla-tube walls are 1–1.5 mm thick.

The only kind of *Hemerocallis* I saw in and within 650 m of the Plaza was HSDO. In the Plaza, this daylily bloomed profusely, and its 200 clumps each had all or a combination of old, brown scapes with fallen capsules; scapes with green and ripe capsules; scapes with flower buds and flowers; and small, developing scapes with flower buds. In Maryland this same cultivar has a spring and summer flush of flowers, not the continuous bloom in the Plaza. Twenty Preserve HSDO flowers were 77 ± 4.9 SD (70–85) mm long and had corolla tubes 23.6 ± 0.9 SD (21–25) mm long. Preserve non-HSDO *Hemerocallis* flowers visited by the *X. v. virginica* were larger and longer than HSDO flowers.

In 2014–2015, the Preserve had about 600 *Hemerocallis* culivars and seedings, frequent visits from *A. mellifera* from three hives, about 30 m away, to other flowering-plant genera, and frequent *Hemerocallis* pollen collection by *Lasioglossum* bees. I measured piercing lengths in Plaza HSDO flowers with a mm rule. In looking for *Hemerocallis* nectar, I cut flowers from both study sites lengthwise and searched for nectar droplets, films, or both inside flowers using a magnification of 10×.

Flower-piercing frequency

To determine how the frequency of floral-piercing by *X. varipuncta* changed during a day, I sampled 193 new flowers in all four of the Plaza's beds in the morning (10:30–11:30 a.m.) and afternoon (4:30–5:30 p.m.) on 13 August 2014. I sampled all 43 flowers in the north bed and 50 flowers in each of the other three beds, which had up to 75 flowers per bed.

Results

Scores of new HSDO flowers were present in the Plaza, and *X. varipuncta* females pierced these flowers on all observation days. In late mornings and afternoons, they quickly flew about and landed on HSDO flowers, up to 10 flowers per foraging bout in a particular bed, and probed old and new piercings with their proboscides (Fig. 2). These bees landed on flowers in three ways: (1a) a bee landed on a flower tepal and then quickly crawled down into its base, (1b) backed out, (1c) crawled to the apical area of a tepal, (1d) crawled to the outside of a flower's floral tube, (1e) made a new piercing with her tongue or (1f) extended her tongue into a previously-made piercing; (2) a bee landed on a tepal facing away from a flower's center and then exhibited steps 1d–1f; and (3) a bee directly landed on a floral tube and exhibited steps 1e–1f. Piercings were 1.5 mm long. During one sampling day in California, floral-piercing frequency



Figure 2. A female *Xylocopa varipuncta* that fed on cell fluid of a *Hemerocallis* 'Stella de Oro' flower through a piercing in the flower's corolla tube.

Table 1. Percent pierced flowers and piercing number per flower. Flowers are those of *Hemerocallis* 'Stella de Oro' pierced by *Xylocopa varipuncta* on 13 August 2014 in the César E. Chávez Memorial Plaza, Sacramento, California.

Flower bed	Percent of flowers pierced [†]		Number flowers with 1 or 2 piercings ^{\ddagger}	
	Morning (10:30–11:30 a.m.)	Afternoon (4:30–5:30 p.m.)	Morning (10:30–11:30 a.m.)	Afternoon (4:30–5:30 p.m.)
North	28	49	12 (1)	18(1), 3(2)
North-northeast	0	26	0	13(1)
South	0	18	0	5(1), 4(2)
South-southwest	0	10	0	5(1)

 † N = 43 flowers in the north bed and 50 flowers for the other three beds totaling 193 flowers.

^{\ddagger} 12 (1) = 12 flowers with 1 piercing; 3(2) = 3 flowers with two piercings; etc.

increased from 15%–25% of 193 flowers (Table 1). Forty-one of the flowers had one piercing, and seven had two piercings by 5:30 p.m. I did not see *X. varipuncta*'s visiting the four other flowering species in the Plaza.

Apis mellifera workers showed two kinds of landings on HSDO flowers. In landing type-1, a worker landed on a tepal and then crawled into a flower's throat, presumably



Figure 3. An *Apis mellifera* worker on the corolla tube of *Hemerocallis* 'Stella de Oro'. Such bees extend their proboscides through piercings made by *Xylocopa varipuncta*.



Figure 4. An Apis mellifera worker that was collecting pollen of Hemerocallis 'Stella de Oro'.

in search of nectar. In landing type-2, a worker landed on the top of a tepal and then crawled to the outside of its flower where she probed an already-made piercing with her proboscis (Fig. 3). *Apis mellifera* workers also landed on anthers where they collected pollen (Fig. 4). Besides visiting HSDO flowers, *A. mellifera* visited flowers of *Rosmarinus officinalis* (Rosemary) in the Plaza. Elsewhere near the Plaza, *A. mellifera* visited flowers of both *Rosmarinus officinalis* (Rosemary) and a *Zinnia* cv.

Small ants were on corollas of three HSDO flowers, but were not seen entering corollas through piercings. A male *Colias* butterfly entered four HSDO flowers through their natural corolla openings, evidently looking for nectar, and did not extend his proboscis through piercings.

In Maryland, the female *X. v. virginica* first searched the inside of a flower of *H.* 'Violacea' and did not pierce the flower (Fig. 5). She then visited and pierced a flower of each of three unnamed seedlings (Fig. 6) and a flower of *H.* 'Brown Witch' before she left the *Hemerocallis* patch. She spent only a few seconds at each flower. I found no evidence of nectar in the flowers when I dissected them within 10 min after her visit.

Discussion

Xylocopa varipuncta frequently pierced HSDO flowers, and individuals often flew to many of these flowers during single foraging bouts. Their frequent visits and floral piercing indicate that they were obtaining cell fluid from the nectarless flowers. It is unclear whether the bees were seeking water alone, cell contents in general, or both when they pierced the flowers. In the Plaza, *A. mellifera* that extended their tongues into previously-made piercings likely obtained cell-fluid. The female *X. v. virginica* pierced four *Hemerocallis* flowers and then flew off. She seemed to have learned that the flowers did not have nectar, obtained enough cell fluid during her piercing bout, or both. In Maryland, unworn adult butterflies, *e.g., Papilio glaucus* and *P. troilus*, also visit different kinds of *Hemerocallis* flowers, and after visiting only a few flowers and likely finding no nectar, these butterflies leave *Hemerocallis* patches, evidently learning these flowers are not nectar sources (pers. obs.). However, butterflies and moths obtained nectar from two *Hemerocallis* species and their F1 and F2 hybrids in Japan (Hirota et al. 2012).

Although I have observed many insect species on thousands of kinds of *Hemerocallis* flowers since 1976 in seven U.S. states and Japan, I saw flower piercing only by *X. varipuncta* and *X. v. virginica*. This piercing was frequent in the California site and rare in the Maryland site. There, *X. v. virginica* often hovered over *Hemerocallis* flowers and sometimes rested on their tepals and anthers, but so far, I have seen only one individual pierce such flowers.

I have seen many workers of *A. mellifera* fly about *Hemerocallis* flowers, but have never seen this bee collect *Hemerocallis* pollen outside of California. In Eastern U.S., *Lasioglossum* bees are frequent *Hemerocallis* pollen foragers that are likely *Hemerocallis* pollinators. The California HSDO plants frequently produced fruit containing seeds,



Figure 5. A female *Xylocopa virginica virginica* that entered a flower of *Hemerocallis* 'Violacea'.



Figure 6. The same female *Xylocopa virginica virginica* which pierced a corolla base of an unnamed *Hemerocallis* hybrid.
which sprouted in flower pots (pers. obs.). *Apis mellifera* may have been a key pollinator of these plants.

The long California drought and dearth of nectar in Sacramento may have favored daylily floral-piercing and cell-fluid imbibing by *X. varipuncta*. It would be interesting to determine if these bees visit HSDO flowers during times of abundant nectar in flowers of other species used by this species. Determination of this was not possible in 2015, because the Sacramento area was in its forth year of extreme drought. In the Maryland case, a young female *X. v. virginica* evidently quickly learned that daylilies she visited did not have nectar. She may have imbibed cell-fluid although water was often on plants and in shallow plant trays in the Preserve, and nectar was available in other flowers. Although I have seen *X. v. virginica* fly over, land, and rest on daylily flowers scores of times, this was the only case of *Xylocopa Hemerocallis* piercing that I have seen in Eastern U.S. I have seen *A. mellifera*, but not *X. v. virginica*, drink water in the Preserve.

In conclusion, the California *X. varipuncta* behaved as if they were primary cell-fluid robbers, and *A. mellifera* behaved as if they were secondary cell-fluid robbers. The Maryland *X. v. virginica* exhibited one foraging bout during which she likely learned that *Hemerocallis* flowers she visited did not have nectar, obtained an adequate amount of cell fluid, or both. Given the high abundances of many kinds of *Hemerocallis* in gardens, parks, and rural areas in many parts of the world; the hundreds of *Xylocopa* spp.; and the cosmopolitan distribution of *A. mellifera*; there should be many other cases of *Apis-Hemerocallis-Xylocopa* interactions awaiting discovery.

Acknowledgments

I thank David Inouye and Jack Neff for comments on the manuscript. I dedicate this paper to Charles D. Michener for his 97th birthday and lifetime bee research and to the memories of activist César Estrada Chávez and *Hemerocallis* breeder Walter Jablonski who made this study possible.

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