RESEARCH ARTICLE



Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae)

Christophe J. Praz¹

I University of Neuchatel, Institute of Biology, Evolutionary Entomology, Emile-Argand 11, 2000 Neuchatel, Switzerland

Corresponding author: Christophe J. Praz (christophe.praz@unine.ch)

Academic editor: J. Neff	Received 18 November 2016	Accepted 20 February 2017	Published 28 April 2017
	http://zoobank.org/52609DE3-186	3-4183-B137-D7B377E30CD1	

Citation: Praz CJ (2017) Subgeneric classification and biology of the leafcutter and dauber bees (genus *Megachile* Latreille) of the western Palearctic (Hymenoptera, Apoidea, Megachilidae). Journal of Hymenoptera Research 55: 1–54. https://doi.org/10.3897/jhr.55.11255

Abstract

A new identification key is presented for the western Palearctic subgenera of the bee genus Megachile. In addition, the species composition of each subgenus is discussed, and for large subgenera, species groups are delineated to facilitate future taxonomic treatment. The nesting biology and floral associations of each subgenus are briefly reviewed. Lectotypes are designated for Megachile albocincta Radoszkowski, M. genalis Morawitz, M. hirsuta Morawitz, M. inornata Walker, M. luteipennis Friese, M. mandibularis Morawitz, M. melanogaster Eversmann, M. orientalis Morawitz, M. picicornis Morawitz, M. pilicrus Morawitz, M. sedilloti Pérez, M. thevestensis Ferton, M. vestita Giraud (=M. giraudi Gerstäcker) and M. villipes Morawitz. In addition, the following taxonomic changes are proposed: the subgenus Paracella is synonymized with the subgenus Anodonteutricharaea (syn. n.); three species, Megachile breviceps Friese, M. luteipennis and M. algira Radoszkowski are excluded from the Palearctic fauna as they were likely based on mislabeled specimens; *M. luteipennis* is newly placed in synonymy with *M. dimidiata* Smith (syn. n.), and *M. algira* with *M. opposita* Smith (syn. n.); *M. punctatissima* Spinola is considered an incorrect spelling of Stelis punctulatissima (Kirby) and not a valid species-group name. Heriades sinuata Spinola is newly placed in synonymy with H. truncorum (Linnaeus) (syn. n); M. boops Friese is transferred to the genus Hoplitis (comb. n.) and placed in synonymy with Hoplitis tigrina (Morawitz) (syn. n.); M. pyrsa Vachal is transferred to the genus Prodioxys (comb. n.) and placed in synonymy with Prodioxys carnea (Gribodo) (**syn. n.**); *Stelis megachiloides* Alfken is transferred to the genus *Megachile* (**comb. n.**) and placed

Copyright Christophe J. Proz. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

in synonymy with *M. marginata* Smith (syn. n); *M. larochei* Tkalců and *M. lanigera* Alfken are placed in synonymy with *M. albohirta* (Brullé), *M. albocincta* Radoszkowski with *cyanipennis* Guérin-Méneville, *M. rhodosiaca* Rebmann and *M. heinrichi* (Tkalců) with *M. doriae* Magretti, *M. vicina* Morawitz with *M. giraudi, M. picicornis* Morawitz and *M. albocincta* Pérez with *M. marginata, M. esseniensis* (Pasteels) with *M. maxillosa* Guérin-Méneville, *M. sexmaculata* Alfken, *M. sexmaculata thracia* Tkalců and *M. pilicrus flavida* Zanden with *M. melanogaster, M. transitoria* Benoist with *M. parietina* (Geoffroy), *M. judaea* (Tkalců) with *M. pasteelsi* (Zanden), *M. cyrenaica* Schulthess, *M. fumosa* Alfken and *M. fulvocrinita* Alfken with *M. sedilloti, M. insignis* Zanden with *M. soikai* Benoist, *M. mavromoustakisi* Zanden with *M. troodica* Mavromoustakis and *M. semipleta* Cockerell with *M. versicolor* Smith (syn. n.). *Megachile rhodoleucura* Cockerell is reestablished as a valid species (stat. rev.). *Megachile posti* Mavromoustakis is considered as a valid species (stat. n.) and not as a subspecies of *M. basilaris* Morawitz. *Megachile calloleuca* Cockerell is newly placed into the subgenus *Megachile, M. inornata, M. thevestensis, M. troodica* into the subgenus *Anodonteutricharaea*, and *M. hirsuta, M. pasteelsi* into the subgenus *Chalicodoma*.

Keywords

Megachile, classification, nesting biology, oligolecty, solitary bees

Introduction

The bee genus *Megachile* Latreille, 1802 accounts for a significant proportion of most bee faunas (Michener 2007). In its current delineation, this genus includes more than 1400 species (Ascher and Pickering 2016) in 55 subgenera (Michener 2007, Trunz et al. 2016, and references therein). These subgenera are distributed in two groups based on nesting biology: the leafcutter species (or group 1 subgenera), which cut leaf discs to line their brood cells; and the dauber bees (or group 2 subgenera), which use resin or mud to build their cells (Michener 2007, Trunz et al. 2016). The subgenus Creightonella Cockerell, 1908, the lone member of a third group according to Michener (2007), is considered to be a member of group 1 (Trunz et al. 2016). The dauber bees have sometimes been placed in a separate genus, Chalicodoma Lepeletier, 1841 (e.g. Michener 1965, Pasteels 1965, Tkalců 1969); Trunz et al. (2016) recently showed that the dauber lineages constitute a paraphyletic assemblage from which the leafcutters evolved, and the separation of the dauber bees into one (Chalicodoma) or a few well-delineated, monophyletic genera did not appear practical. Consequently, Trunz et al. (2016) advocated the use of a classification close to Michener's generic classification, with a large genus Megachile that includes both leafcutter and dauber lineages with the exception of three comparatively small tropical groups segregated as separate genera: Gronoceras Cockerell, 1907, Heriadopsis Cockerell, 1931 and Matangapis Baker & Engel, 2006 (Trunz et al. 2016). This classification is adopted here, placing all Palearctic species into one large genus Megachile that includes, among others, Chalicodoma, Creightonella and Pseudomegachile Friese, 1898 as subgenera. With respect to the Palearctic fauna, the following further changes were also made to Michener's classification by Trunz et al. (2016): the subgenus Parachalicodoma Pasteels, 1966 was merged with the subgenus Pseudomegachile; its species are considered here to form a species

group of *Pseudomegachile*, referred to as the *incana* group; *Eumegachile* Friese, 1899 (with only one species, Megachile bombycina Radoszkowski, 1874) was merged into the subgenus Megachile; Eurymella Pasteels, 1965 was recognized as a valid subgenus of the genus Megachile and not as a synonym of Eutricharaea Thomson, 1872. Lastly, the morphologically unusual species *M. giraudi* Gerstäcker, 1869, placed alternately in the subgenera Eutricharaea (e.g. Tkalců 1974) and Xanthosarus Robertson, 1903 (e.g. Özbek and Zanden 1994, Ornosa et al. 2007) is included here in Eutricharaea based on its phylogenetic position (Trunz et al. 2016). All these classificatory changes were based on highly supported topologies (100% bootstrap support in all maximum likelihood analyses) and are adopted here. Trunz et al. (2016) further considered Anodonteutricharaea Tkalců, 1993 and Paracella Michener, 1997 to be synonymous. Paracella was first described in 1965 (Pasteels 1965), although this description is not valid because no type species was designated. Michener (1997) used the same name to reestablish the subgenus. Consequently Anodonteutricharaea has priority and Paracella is placed here as a synonym of Anodonteutricharaea (syn. n.), and not the other way around as suggested by Trunz et al. (2016).

Palearctic leafcutter and dauber bees have not been recently revised, with the exception of the central European species for which identification keys are available (e.g., Benoist 1940, Dorn and Weber 1988, Banaszak and Romasenko 2001, Amiet et al. 2004, Scheuchl 2006). At the European scale no revision exists except that of Friese (1911); according to Nieto et al. (2014), 81 species are present in Europe but the taxonomic status of approximately a quarter of them remains in doubt. Most subgenera are in urgent need of revision in the Palearctic, and these taxonomic revisions are hampered by the uncertain subgeneric placement of several Palearctic species. Moreoever, no practical key to the subgenera exists (see comments on the key in Michener 2007: 565) and the classificatory changes mentioned above need to be implemented in identification keys.

As a first step towards a better taxonomic treatment of this important group of bees, a new key to the western Palearctic subgenera is proposed here; when needed, I delineate species groups within large subgenera. For some subgenera, I briefly comment on the species composition and highlight taxonomic problems associated with some species. For large subgenera such as Eutricharaea, the number of unpublished synonymies is so large that presenting a list of species, even tentative, does not seem appropriate at this point. I also verify and change if necessary the subgeneric placement of each of the western Palearctic species (Ascher and Pickering 2016, Kuhlmann et al. 2016), based on the examination of the type material of most species. A few lectotypes are designated, mostly when the identity of the species is currently unclear, and a few new synonymies are also proposed to avoid using names that will be placed in synonymy in the near future. I decided not to give distribution data for each species; such data will be presented in the online Checklist of the Western Palaearctic Bees (Kuhlmann et al. 2016) and on the Discover Life website (Ascher and Pickering 2016). Last but not least, what is known about the nesting biology and floral associations of each subgenus is summarized.

Materials and methods

Terminology and abbreviations

Terminology follows Michener (2007). In the key, the morphological characters are given in order of importance, with the most distinctive characters first. For simplicity, metasomal terga and sterna are commonly abbreviated as T and S, respectively, when they are numbered (e.g., T1 for metasomal tergum 1, S1 for metasomal sternum 1). When part of the integument is orange or red, I simply mention that the particular body part is orange or red; thus "front basitarsus yellowish-white" or "mandible or ange" means that the cuticula of these body parts is yellowish-white or orange. For convenience I often refer to a subgenus simply with its subgeneric name [e.g. *Eutricharaea* and not *Megachile (Eutricharaea*)]; thus throughout the manuscript, *Chalicodoma* refers to the subgenus *Chalicodoma* and not to the genus *Chalicodoma* of some authors; when the subgenus *Megachile* is meant, *Megachile s. str* is used.

Collections studied with abbreviations

BMNH	Natural History Museum, London, UK			
CSE	Private collection of Christian Schmid-Egger, Berlin, Germany			
DAAN	Department of Agriculture, Ministry of Agriculture and Natural Resour			
	Nicosia, Cyprus			
ETHZ	Eidgenössische Technische Hochschule, Entomologische Sammlung,			
	Zürich, Switzerland			
ISZP	Polish Academy of Sciences, Institute of Systematic Zoology, Krakow,			
	Poland			
MNHN	Muséum National d'Histoire Naturelle, Paris, France			
MSCA	Maximilian Schwarz Collection, Ansfelden, Austria			
NMPC	National Museum (Natural History), Prague, Czech Republic			
NMW	Naturhistorisches Museum, Wien, Austria			
OLML	Oberösterreichisches Landesmuseum, Linz, Austria			
OUMNH	University Museum of Natural History, Oxford, UK			
RMNH	Nationaal Natuurhistorisch Museum Naturalis, Leiden, Holland			
SEMC	University of Kansas, Snow Entomological Museum, Lawrence, USA			
SMFD	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main,			
	Germany			
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany			
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia			
ZMHB	Museum für Naturkunde, Berlin, Germany			

Geographic coverage of the key

The keys presented by Michener (2007) for the Palearctic subgenera of *Megachile* cover both the Palearctic and Oriental regions. They are difficult to use for non-specialists as they rely on few characters; moreover, several Palearctic species do not run properly through the key. For this reason, the present key relies on numerous alternative characters; some of these characters will be useful in other geographic regions, while others will not. This key covers all species known to me from the western Palearctic region. It also covers the faunas of Iran, central Asia and Siberia, which are essentially similar to the Western Palearctic fauna, but will progressively become less practical towards the Oriental zone (e.g. in Pakistan or in the Himalayas). It will not be useful in India, China and Japan: other, distinctive subgenera occur there (e.g., *Aethomegachile* Engel & Baker, 2006, *Chelostomoda* Michener, 1962 and *Megella* Pasteels, 1965) while some distinct Palearctic groups do not (e.g., the *incana* group of *Pseudomegachile*, or the *montenegrensis* group of *Chalicodoma*). Moreover Oriental members of some subgenera (notably *Anodonteutricharaea* or *Pseudomegachile*) are distinct from the Palearctic species and will not run properly through the present key.

As mentioned above, the key covers the northern parts of the Arabian Peninsula (Saudi Arabia north of Jeddah) as well as the United Arab Emirates but not the southern part (Yemen, Oman, southern parts of Saudi Arabia). The fauna of the southern part of the Arabian Peninsula is poorly known and rather distinct from the Palearctic fauna: temperate subgenera such as *Xanthosarus* or *Megachile s. str.* do not appear to occur there, while several taxa with Afrotropical affinities are found (e.g., *Amegachile* Friese, 1909, the *eurimera* group of *Eurymella*; and *Stenomegachile* Pasteels, 1965). These three lineages are not included in the key but are briefly described below; their inclusion would render this key less practical for the vast majority of its users.

Delineation of species groups within large subgenera

Informal "species groups" are particularly convenient for referring to groups of presumably related taxa sharing distinctive morphological features; such informal groups are not regulated by the code of zoological nomenclature and do not have to be monophyletic. Furthermore, it does not matter if the recognition of such groups renders the rest of the subgenus paraphyletic. I use species groups to facilitate the taxonomic treatment of large, diverse subgenera. Such subgenera typically appear in different couplets of the key and I find it useful to have a name to refer to these groups. Often, such groups have been given subgeneric rank in the past, for example "*Neoeutricharaea* Rebmann, 1967". This group could be referred to as the *Neoeutricharaea* group of *Eutricharaea*. I prefer to refer to this group as the *rotundata* group of *Eutricharaea*, as most people will be familiar with species names and not necessarily with subgenus names. For clarity, I list existing but not currently valid, subgeneric names for each species group.

Results

Taxa excluded from the Palearctic fauna or from the genus Megachile

The following three species descriptions were likely based on mislabeled specimens. First, Megachile breviceps Friese, 1898, described from a single specimen putatively collected in Spain and preserved in ZMHB, does not appear to belong to any known Palearctic taxon. Pasteels (1966) noted the peculiar morphology of *M. breviceps* and tentatively placed it into the subgenus Callomegachile Michener, 1962 due to its similarity to the *disjuncta* group of species. I consider *M. breviceps* as a member of *Callo*megachile with unclear geographic origin; its vestiture pattern (vestiture grey on head and mesosoma, orange-brown on metasoma) is reminiscent of some Australian taxa. In the same article Megachile luteipennis Friese, 1898 is described, supposedly from Algeria. A female preserved in ZMHB is designated here as a lectotype; it is labeled as follows: 1. "Algeria 1890"; 2. "Megachile luteipennis det. Friese 1897"; 3. "Lectotype Megachile luteipennis des. Zanden 1992"; this designation has not been published and is accepted here. Both the original description and the lectotype agree perfectly with the Oriental species M. (Lophanthedon) dimidiata Smith, 1853. I place M. luteipennis as a junior synonym of M. dimidiata (syn. n.) and consider its type locality to be an error. Lastly, several syntypes of *Megachile algira* Radoszkowski, 1874, supposedly from Algeria, are preserved in different institutions (ZMHB, ISZP, as well as BMNH according to Baker 2004). I have examined three syntypes (ZMHB and ISZP), which agree with Radoszkowski's original description. As noted by Baker (2004: 240), M. *algira* is not a Palearctic species but probably originates from Java; Baker (2004) further writes under *M. algira* "= Chalicodoma (Callomegachile) florale oppositum (Sm. 1853)". M. floralis (Fabricius, 1804) and M. opposita Smith, 1853 were considered as two distinct species by Gonzalez and Engel (2012) and I place *M. algira* as a junior synonym of *M. opposita* (syn. n). Note that *M. opposita* is not a member of *Callomegachile* but is considered here to be a member of the semivestita group of Pseudomegachile (Largella Pasteels, 1965).

The type of *Megachile boops* Friese, 1921, described from "Jaribaschi im Amanusgebirge" (Nur Mountains, Hatay Province, Turkey) could not be located in ZMHB or SMFD. The description does not match any known species of the genus *Megachile* but points to *Hoplitis* (*Megahoplitis*) tigrina (Morawitz, 1872). John Ascher and Eli Wyman (pers. comm., July 2014) located a specimen of *H. tigrina* (det. John Ascher) identified as *M. boops* by Friese, labeled "Amanusgeb., Jaribasch" (AMNH). Given that the original description mentions only one specimen, this specimen is probably the holotype of *M. boops*, which is here placed as a junior synonym of *Hoplitis tigrina* (syn. n). Similarly, the description of *Megachile pyrsa* Vachal, 1910, of which I was unable to locate the type, does not appear to match any existing species of the genus *Megachile*; rather, several features point to a Dioxyine bee: absence of pulvillus, first submarginal cell larger than second, T6 with apical margin simple (thus without preapical carina), T7 small, hidden under T6. Based on the original description, in particular the color of the integument, Maximilian Schwarz (pers. comm., May 2014) suggests placing *M. pyrsa* as a junior synonym of *Prodioxys carnea* (Gribodo, 1894), which I formally do here (syn. n). Megachile punctatissima Spinola, 1806 has been mentioned as a valid species of the genus Megachile (e.g. Nieto et al. 2014, Ascher and Pickering 2016). The entry in Spinola (1806: 135) under M. punctatissima is "3. MEGACHILE PUNCTATISSIMA. Latr. hist. des. inst. [SIC] 14. p. 54. n. 5" and was not meant as a species description. "M. punctatissima Latreille" is likely an incorrect spelling of "Apis punctulatissima Kirby, 1802, [=Stelis punctulatissima (Kirby, 1802)]", given that the entry in Latreille (1805) was "Apis punctatissima. Kirby, tab. 16, fig. 9", thus precisely referring to Kirby's species. Lastly, Heriades pusilla Spinola, 1808 and Heriades sinuata Spinola, 1808 have been included in the genus Megachile (Schletterer 1889, Ungricht et al. 2008); based on their original descriptions (no existing syntype is known: Casolari and Casolari-Moreno 1980) both are considered to belong to the Osmiini (see further details in Suppl. material 1). Based on its original description (axillae with spine) and especially on the account of its nesting biology (nests in Rubus stems, partitions made of masticated leaf material), H. pusilla likely refers to a species of the genus Osmia Panzer, 1806 subgenus Hoplosmia Thomson, 1872. Heriades pusilla is probably best placed in synonymy with Osmia (Hoplosmia) ligurica Morawitz, 1868 and treated as a nomen oblitum; however I do not formally transfer this species into Osmia for now as this would create a homonymy with the valid species Osmia pusilla Cresson, 1864. To resolve this case study of the Spinola collection and the designation of a lectotype or neotype appear to be necessary. The original description of the male of *H. sinuata* precisely refers to a species of *Heriades* (see details in Suppl. material 1; the identity of the female is unclear and may refer to either Hoplosmia or Heriades). Spinola apparently did not know the male of Heriades truncorum (Linnaeus, 1758): the entry in Spinola (1806) under "Megachile truncorum" was "Mas. [male]- Megachile campanularum Latr.". Consequently H. sinuata is placed as a junior synonym of H. truncorum (syn. n.).

New lectotype designations

A likely syntype of *Megachile inornata* Walker, 1871 could be located and examined (BMNH), a female labeled as follows: 1. "Garden around Mt Sinai [printed]"; 2. "F. Sm. Coll. 79 22"; 3. "*Megachile sp* f: ex Lord Colln and possibly a syntype of *inornata* Walker 1871: 48" [handwritten by D. Baker]; 4. "Lectotype *Megachile inornata* des. C. Praz 2015". This specimen agrees with Walker's short original description of the female; the species is valid and newly placed into the subgenus *Anodonteutricharaea*. A lectotype is also designated for *Megachile mandibularis* Morawitz, 1875 (ZIN); it is a male in good condition bearing the following labels: 1. "14" [printed]; 2. "3apBIII. AOA" [abbreviation for the Zeravshan Valley; both localities given in the original description are in present-day Uzbekistan according to Appendix B of Baker (2004)]; 3. "*Megachile mandibularis* F. Morawitz"; 4. "Lectotype *Megachile mandibularis* des. C. Praz 2015".

A lectotype is also designated for *Megachile villipes* Morawitz, 1875 (ZIN); it is a wellpreserved male labeled as follows: 1. "Кизиль Кум" [Kyzylkum (Desert); localities in the original description are in present-day Kazakhstan according to Appendix B of Baker (2004)]; 2. "villipes F. Morawitz"; 3. "Syntypus". 4. "Lectotype M. villipes des Tkalců". This designation has not been published and it is accepted here. As suggested by Tkalců (1993), both M. mandibularis and M. villipes are valid species of the subgenus Anodonteutricharaea. A lectotype is designated for Megachile thevestensis Ferton, 1908, a well-preserved female labeled as follows: 1. "voisine de flabellipes nouvelle? thevestensis" [handwritten by Ferton: "near flabellipes, new?" The word "thevestensis", written vertically, was probably added later by Ferton]; 2. "Tebessa 12/7 06 n sp?" [Tébessa, Algeria, 12 July 1906]; 3. "Mus. Paris Coll. Ferton"; 4. "Lectotype Megachile thevestensis des. C. Praz 2016". M. thevestensis is newly placed here into the subgenus Anodonteutricharaea. A lectotype is designated for Megachile hirsuta Morawitz, 1893, a male from "Masar-Boschara" bearing the additional label "Lectotype Megachile hirsuta des. B. Tkalců "; this designation is not published and is accepted here. The type locality cannot be located with precision, although it is in the "Sarawschan" region (Zeravshan valley) according to Becker (1917: 399); a locality named "Mazar" appears on old maps some 30 km westwards of the Zeravshan glacier in Tadjikistan. Given that M. hirsuta is a high-altitude species throughout its range, the lectotype was probably collected in the upper Zeravshan valley in the Sughd Region of Tadjikistan. M. hirsuta is newly placed into the subgenus Chalicodoma. A lectotype is also designated for Megachile melanogaster Eversmann, 1852 (ISZP), a well preserved female labeled as follows: 1. "melanogaster mihi"; 2. [a rounded, gold label]; 3. "Orenburg" [printed on pink label; Orenburg Region, Russia]; 4. "Lectotype Megachile melanogaster des. C. Praz 2013". A lectotype is designated for Megachile picicornis Morawitz, 1877, a well-preserved female labeled as follows: 1. "Kurgulutschaiskaja" [handwritten, black ink; in present-day Azerbaijan according to Astafurova and Pesenko 2006: 78]; 2. "picicornis Mor. Type"; 3. "Lectotype Megachile picicornis des. C. Praz 2015". A conspecific male from the same locality is designated as a paralectotype (des. C. Praz 2015). The original description of Megachile orientalis Morawitz, 1895 suggests that the female and male were not conspecific. The study of two syntypes (ZIN) confirms that the female is a Eutrichardea while the male belongs to the subgenus *Pseudomegachile*. I designate here the female specimen as the lectotype; it is a well-preserved specimen labeled as follows: 1. "Copet. D." [Kopet Dag, or Turkmen-Khorasan Mountain Range, Turkmenistan and Iran]; 2. "Nerduali (...)" [date not readable. I could not find this locality on maps; Volkovitsh and Kalashian (2002) cited it as the "Nerduali River" in the Khorasan Province, Iran]; 3. "Megachile orientalis f F. Moraw."; 4. "Lectotype Megachile orientalis des. C. Praz 2016" (ZIN). A lectotype is further designated here for Megachile sedilloti Pérez, 1895, a female from "Kairouan v. 1884" [Kairouan, Tunisia, May 1884] bearing the following label: "Lectotype Megachile sedilloti des. Baker 1990"; this designation has not been published and is accepted here. A further female from the same locality is designated as a paralectotype (it bears a label "Paralectotype *M. sedilloti* des Baker 1990"). A lectotype (MNHN) is also designated for Megachile vestita Giraud, 1863 (not vestita Smith

1853; the name *Megachile giraudi* has been proposed as a replacement name), a female labeled as follows: 1. "Suse [Susa, Italy]"; 2. "Lectotype Megachile vestita Giraud des. C. Praz 2010". Three further females (two from "Suse" and one from "Vall.", likely Vallouise, France) are designated as paralectotypes (des. C. Praz 2010). As indicated by Benoist (1940), the male described by Giraud (preserved in MNHN) is not conspecific. A well-preserved female originating from Egypt is designated as a lectotype for Megachile albocincta Radoszkowski, 1874; it bears the following label "Lectotype Megachile albocincta des. C. Praz 2013" (ISZP); an additional female (ISZP) is designated as a paralectotype. Lastly, lectotypes are designated for Megachile genalis Morawitz, 1880: a well-preserved female (both antennae are partly broken) labeled as follows: 1. [rounded, silver disc]; 2. "114506". 3. "genalis Mor.". 4. "Syntypus". 5. "Mor. 1880: 380 Tjan Shan (...)" [Tian Shan Mountains; according to the original description, which mentions "Im Tjan-Shan auf dem Plateau des kleinen Juldus", this is likely the Yulduz Valley, Xinjian autonomous region, China]. 6. "Lectotype Megachile genalis des. C. Praz 2015" (ZIN); and for Megachile pilicrus Morawitz, 1877: a-well preserved female labeled as follows: 1. "Borshom Siewers" [Borjomi, Georgia; leg. G. Sievers]; 2. "Lectotype Megachile pilicrus des. C. Praz 2015" (ZIN).

New synonymies, new taxonomic status and new subgeneric placement

The following new synonymies are proposed based on the examination of the type material, or if the type material could not be obtained or examined, on the original descriptions. Rationale and details on each of these synonymies are given in Suppl. material 1. Megachile larochei Tkalců, 1993 and M. lanigera Alfken, 1933 are placed in synonymy with M. albohirta (Brullé, 1839) (syn. n), which is newly placed into the subgenus Anodonteutricharaea. Megachile mavromoustakisi Zanden, 1992 is placed in synonymy with *M. troodica* Mavromoustakis, 1953 (syn. n), which is newly placed into the subgenus Anodonteutricharaea. Megachile judaea (Tkalců, 1999) is considered as a junior synonym of Chalicodoma pasteelsi Zanden, 1998 (syn. n), which is newly placed into the subgenus Chalicodoma. Megachile transitoria Benoist, 1934, of which the type appears to be lost (MNHN), is considered to have been based on an intersex specimen of *M. parietina* (Geoffroy, 1785) and is placed in synonymy with that species (syn. n). Megachile rhodosiaca Rebmann, 1972 and M. heinrichi (Tkalců, 1979) are placed in synonymy with *M. doriae* Magretti, 1890 (syn. n). *Megachile picicornis* and *M. al*bocincta Pérez, 1879 (not M. albocincta Radoszkowski, 1874; M. perezi Mocsáry, 1887 and M. provincialis Pérez, 1890 are replacement names) are placed in synonymy with M. marginata Smith, 1853 (syn. n) (the holotype of M. marginata is in OUMNH); the holotype (NMPC) and paratype (ZMHB) of Stelis megachiloides Alfken, 1942 are likely intersex specimens of *M. marginata*, and this species is transferred into the genus Megachile (comb. n.) and placed in synonymy with M. marginata (syn. n.). Megachile sexmaculata Alfken, 1942, M. sexmaculata thracia Tkalců, 1979 and M. (Megachile) pilicrus flavida Zanden, 1998, are placed in synonymy with M. melanogaster (syn. n).

Megachile cyrenaica Schulthess, 1924, M. fumosa Alfken, 1934 and M. fulvocrinita Alfken, 1934 are placed in synonymy with M. sedilloti (syn. n). Megachile insignis Zanden, 1996 is placed in synonymy with M. soikai Benoist, 1961 (syn. n), and M. vicina Morawitz, 1894 [not M. vicina Mocsáry, 1879; Chalicodoma (Pseudomegachile) atropyga Zanden, 1995 was suggested as a replacement name] is placed as a junior synonym of M. giraudi. Megachile semipleta Cockerell, 1921 is placed in synonymy with M. versicolor Smith, 1844. Megachile albocincta Radoszkowski, 1874 is placed in synonymy with M. cyanipennis Guérin-Méneville, 1845.

The subgeneric placement of Megachile rhodoleucura Cockerell, 1937, described from Zimbabwe and known only in the female sex has varied; Pasteels (1965) placed it in Pseudomegachile, while Eardley (2013) recently placed it in synonymy with M. (Eurymella) eurimera Smith, 1853. I examined the holotype of M. rhodoleucura (BMNH) and confirm that it is a member of Pseudomegachile, distinct from M. eurimera and thus *M. rhodoleucura* is reestablished as a valid species here (stat. rev.). The holotype female is sculpturally identical with Megachile riyadhensis (Alqarni, Hannan, Gonzalez and Engel, 2012) and both species may well be conspecific as they only differ in the coloration of the metasomal vestiture (it is fulvous in *M. rhodoleucura* and snow white in *M. riyadhensis*). I do not formally place *M. riyadhensis* as a synonym of *M. rhodoleu*cura as the male of the latter is unknown; however given that many African Megachile reach the Arabian Peninsula I consider likely that both taxa are conspecific. Megachile calloleuca Cockerell, 1931 is newly placed into the subgenus Megachile based on the examination of the holotype (BMNH). Lastly, the examination of paratypes of Megachile basilaris posti Mavromoustakis, 1952 (MSCA) and of a syntype of M. basilaris Morawitz, 1875 (ZIN) indicates that both are not conspecific and *M. posti* is considered as a valid species (stat. n.).

Notes on important morphological characters

Females: Detailed descriptions of important morphological characters can be found elsewhere (Pasteels 1965, Mitchell 1980, Michener 2007) and only a few new or particularly important characters are presented here. The subgenera have mostly been defined on the base of female mandibular characters, especially the conformation of the teeth along the apical margin of the mandible (Michener 2007). Following Michener (2007), the mandibular teeth are numbered from apical-most, or "lowest" tooth (tooth 1), to basal-most, or "upper" tooth (Fig. 1). Often, determining the precise number of teeth is difficult; the upper tooth may be acute, truncate, or more or less divided into two teeth (as in Fig. 1), and even within a given subgenus a continuum may exist between these states. The concave space between teeth is named "interspace"; interspaces are also numbered from apical-most (or lowest) to basal-most (or upper) interspace (Fig. 1). Of central importance for the recognition of the leafcutter subgenera is the presence and location of cutting edges, blade-like edges that are located in the interspaces (Fig. 1). Cutting edges are entirely absent in dauber bees (or group 2 subgen-



Figure 1. Female mandible of *Megachile (Megachile) centuncularis*; the white lines and the numbers indicate the five teeth (numbers on the right) and the four interspaces (numbers on the left); in this species, there is a partial cutting edge in the second interspace and, in front view, no visible cutting edge in the other interspaces. Picture by Andreas Müller (Müller et al. 1997).

era), and mostly present in the leafcutter subgenera (group 1 subgenera). Often, the cutting edges are partial (Fig. 1), thus not filling the entire length of the interspace; in addition, they may be recessed, partially hidden behind the margin of the mandible, and thus invisible or little visible in front view (Fig. 2). When determining whether a cutting edge is present or absent, it is therefore important to rotate the specimen so that the inner margin of the mandible can be seen in lateral view (Fig. 3). However, if a couplet of the key asks whether a cutting edge is visible or invisible *in front view*, such recessed cutting edges are considered invisible. Michener (2007) considered new world taxa such as *Megachile (Megachile) montivaga* Cresson, 1878 (see Sheffield et al. 2011: Fig. 26a), or the subgenus *Chrysosarus* Mitchell, 1943 to lack cutting edges; here species with similar mandibular structure are considered to have cutting edges, although strongly recessed and invisible in front view.

For the separation of the different leafcutter subgenera of Africa, Pasteels (1965) put particular emphasis on the presence or absence of small brushes of orange hairs in the grooves located below and above the outer ridge near the base of tooth 1 in the female mandible (Fig. 2). Species with robust mandibles with tooth 1 particularly broad tend to have reduced brushes of hairs in these grooves, for example *Xanthosarus* and *Eurymella* (see Figs 35, 38, 40, below), while in species of the subgenera *Megachile s. str.*, *Anodonteutricharaea* and most *Eutricharaea*, the mandibular tooth 1 is less developed and these brushes are present (Fig. 2; see also Figs 30–33, 39, 41, below).



Figures 2–3. Female mandible of *Megachile (Eutricharaea) orientalis.* **2** Front view; the white lines indicate the brushes of hairs in the grooves near the base of tooth 1 **3** Lateral view; the cutting edge is continuous and spans the interspaces 2–4, although it is completely recessed behind the mandibular margin and thus not visible in front view.

Another useful character for the separation of the subgenera is the conformation of the two setae on the basal part of the claws (Pasteels 1965, Tkalců 1993), although this character has so far not been included in identification keys. In the key I refer to the setae of the claws of the hind legs, but the condition described is similar on all claws. In group 2 subgenera, the two setae are more or less similar in thickness; the length of the basal seta is equal to approximately a third of the length of the apical seta (Fig. 4); the condition is unclear in some Callomegachile. In most group 1 subgenera (Eutricharaea, Megachile s. str., Xanthosarus), the basal seta is modified to a short, thick process (Fig. 5); this process is less than three times as long as its basal width and visibly thicker than the apical seta. Eurymella (Fig. 6) and especially Anodonteutricharaea (Fig. 7) are distinct among the leafcutter subgenera in that the basal seta is thin and of similar appearance to the apical seta, although considerably shorter; its length is more than four times its basal width. In Creightonella, only one long seta is present (presumably this seta corresponds to the apical seta of other subgenera). This character is not always easy to evaluate, and in old specimens the thin setae may be broken; however, in many cases I find it to be a useful character, especially for the recognition of Anodonteutricharaea.

Males: Michener's key (Michener 2007) to the males for the Palearctic and Oriental subgenera of *Megachile* is problematic because it largely relies on the presence or absence of hairs laterally on S8. Most group 2 subgenera have numerous hairs laterally on S8, while most group 1 subgenera lack such hairs (for exceptions see Michener 2007: 556–557). This morphological trait is not visible when the abdomen is in repose. The key presented here is based on alternative criteria and as a result it does not segregate the dauber from the leafcutter subgenera in a dichotomous way.

Many male *Megachile* bear numerous, conspicuous modifications of their legs; Wittmann and Blochstein (1995) have illustrated these structures and provided a detailed presentation of their possible functions during mating. These structures, which include among others the front coxal spine and the modified front tarsi, are



Figures 4–7. Claw of hind leg of females; the white lines show the basal seta; the seta is considered elongate in **4**, **6** and **7** and modified to a thick process in **5**. **4** *Megachile (Pseudomegachile) ericetorum* **5** *M. (Eutricharaea) deceptoria* **6** *M. (Eurymella) patellimana* **7** *M. (Anodonteutricharaea) thevestensis.*

not presented in detail here (see Mitchell 1980, Wittmann and Blochstein 1995 and Michener 2007 for further details). In the present key to males, the first couplet is based on the presence or absence of a front coxal spine. In the vast majority of the Palearctic species, this character is unambiguous: the tooth is either entirely missing, or clearly present. In some species of the subgenus Megachile [e.g., Megachile ligniseca (Kirby, 1802)], the spine is considered absent in keeping with central European keys (Benoist 1940, Amiet et al. 2004, Scheuchl 2006) although the surface of the coxa is angulate. In M. (Eutricharaea) soikai, the condition is ambiguous because there is a minute tooth hidden in hairs. Pasteels (1965) considered similar species to have a front coxal tooth. I included M. soikai in the first alternative of couplet 1 (front coxa without tooth) because the tooth is nearly impossible to see unless the hairs are removed; however choosing the other alternative for this species would also lead to the correct subgenus. In a few other species [M. lanata (Fabricius, 1775), M. villipes] the tooth is small although much more developed than in M. soikai; such species are included in the second alternative (front coxa with tooth) because the tooth is conspicuous and bears a patch of modified, orange hairs that contrasts with the white hairs of the surface of the front coxa. Another, important diagnostic character is the



Figure 8–9. Inferior projection of male mandible. 8 *Megachile (Eutricharaea) leachella*, inferior projection pointed and projecting posteriorly 9 *M. (Creightonella) albisecta*, inferior projection rounded and directed ventrally.

inferior projection of the mandible (Figs 8–9), which may be present or absent; this projection is sometimes difficult to see, especially if the mandibles are closed; moreover, the projection is often heavily covered by dense vestiture, especially in group 2 subgenera. The shape of this projection is important: in group 1 subgenera (except, for the Palearctic fauna, in *Creightonella*) having such projection, the projection is pointed posteriorly and rests in repose along the gena (Fig. 8), whereas in those group 2 subgenera with inferior projection, as well as in *Creightonella*, the projection is truncate, rounded or quadrate and not pointed posteriorly (Fig. 9). The subgenera *Chalicodoma* and *Anodonteutricharaea*, as well as some species in the subgenera *Pseudomegachile* and *Megachile* lack this inferior projection and the inferior margin is straight, although sometimes swollen medially (e.g. *M. ericetorum* Lepeletier, 1841) or with dense vestiture (e.g. species of *Anodonteutricharaea*).

Lastly, other useful characters to separate the subgenera of Michener's group 1 are found on the metasomal sterna (Figs 10–15). S5 and S6 are commonly hidden in *Megachile* and often bear important diagnostic traits at the specific level; when hidden, these sterna are visibly less sclerotized, punctate and hairy than S4; in this case, the genital opening is closed in repose by the margin of S4 and the apical margin of either T6 or T7 (Fig. 10). In some groups, however, S5 and sometimes S6 are partly exposed and slightly less sclerotized than S4. In the subgenus *Creightonella*, the apical half of S5 is exposed and S6 forms a rounded, weakly sclerotized projection apically (Fig. 11); this projection of S6 covers the concave apical margin of T7 and closes the genital opening in repose. In the *incana* group of *Pseudomegachile*, S5 but not S6 is partly exposed in repose, and in most species of the *montenegrensis* group of *Chalicodoma* (Fig. 15), S6 forms a hyaline, rounded projection that covers the genital opening, approaching the condition found in *Creightonella*. Lastly, the structure of the apical margin of S4 is important to tell apart the subgenera of group 1: in *Anodonteutricharaea*, *Megachile s. str.*, *Amegachile* as well as most *Eurymella* (including the Palearctic species), the apical rim



Figures 10–15. Male metasoma, ventral view. 10 *Megachile (Eutricharaea) giraudi*, metasoma with four exposed sterna, S4 without hyaline rim, T7 small, unmodified 11 *M. (Creightonella) amabilis*, metasoma with six exposed sterna, S6 with rounded, weakly sclerotized projection 12 *M. (Anodonteutricharaea)* sp. *aff. inornata*, metasoma with four exposed sterna, S4 with apical, hyaline rim (note that S5-S8 are visible in this specimen because the metasoma has been stretched) 13 *M. (Megachile) ligniseca*, condition as in Fig. 12 14 *M. (Eurymella) patellimana*, condition as in Fig. 12 15 *M. (Chalicodoma) montenegrensis*, S6 partly exposed, with rounded, weakly sclerotized projection.

of S4 is slightly depressed, hyaline, glabrous and visibly less sclerotized than the disc of S4 (Figs 12–14). In *Eutricharaea*, the hyaline rim is entirely lacking, the apical margin is sclerotized (Fig. 10) and often covered by numerous hairs (not clearly so in Fig. 10).

Key to the Palearctic subgenera of Megachile

Females: scopa present, metasoma with 6 terga, antenna with 12 segments .. 2 1 Males: scopa absent, metasoma with 7 terga (although T7 is often small and little visible, e.g. Fig. 10), antenna with 13 segments11 2 Mandible (Fig. 16) 5- or 6-toothed (upper teeth often small and little visible), apices of all teeth and interspace 2-4 similar in shape and gradually becoming smaller from tooth 1 upwards; interspace 2 with incomplete cutting edge well-visible in front view; interspaces 3 and sometimes 4 with a

small, incomplete cutting edge little visible in front view; surface of mandible

- regularly convex, not forming two plane surfaces, with few ridges but numerous elongate punctures, covered by numerous hairs (Fig. 16). Vertex long, ocelloccipital distance mostly longer than interocular distance [subequal to interocular distance in *Megachile arabica*]. Hind basitarsus comparatively slender, length more than three times its maximal width (as in Fig. 26); claws of hind legs basally with only one elongate seta......Subgenus Creightonella Mandible not as above: tooth 1 often not larger than other teeth; or teeth or interspaces above tooth 1 of different shapes or not becoming gradually smaller (Figs 17-25, 32-41, although see Figs 2, 22); surface of mandible different, not covered by numerous hairs. Length of vertex and shape of hind basitarsus variable, but in forms with cutting edges, vertex shorter and hind basitarsus usually broad (Figs 28-29). Claws of hind legs basally with two setae (Figs 4, 6-7), although basal seta often modified to short, thickened
- Mandible without cutting edges between the teeth (Figs 17-25). First sub-3 marginal cell longer than second. Metasoma more or less parallel-sided, tapering apically only beyond T4. Hind basitarsus comparatively slender, length more than three times (3.3-3.5 x) its maximal width (Fig. 26) [except in the incana group of Pseudomegachile (Fig. 27)]. Basal hair on claws of hind legs not conspicuously thickened, elongate, its length at least a third of the length of apical seta (Fig. 4) [character unclear in some Callomegachile]......4 Mandible with cutting edges in at least one interspace (Fig. 1), although cutting edges sometimes incomplete, not entirely filling the interspace, or recessed and partly hidden under margin of interspace so that they are not visible in front view (Figs 2-3). First submarginal cell subequal in length to second. Metasoma often triangular in dorsal view, its maximal width at level of T2 or T3, and then tapering apically. Hind basitarsus usually comparatively broad, its length less than three times (2.2–2.7) its maximal width (Figs 28–29) [except in a few species of the subgenus Megachile (see Scheuchl 2006: 111)]. Basal hair on claws of hind legs variable, mostly modified to a short, thickened process (Fig. 5)7 Large species, body length above 14 mm. Vestiture predominantly black except snow white on posterior parts of mesosoma and on T1 and T2. Clypeus

4

very short, truncate apically, with truncation forming a nearly vertical, shiny surface (Fig. 17). Mandible elongate, more or less parallel-sided or narrowest preapically, with three blunt teeth (Fig. 17); mandibular ridges shiny, not dulled by microsculpturing (Fig. 17). Hypostomal area with a strong posterior tooth (Fig. 17). Ocelloccipital distance nearly twice the interocellar distance.....Subgenus Maximegachile Body length variable. Vestiture different. Character combination not as above: clypeus modified or not; if modified, then mandible surface dulled by microsculpturing (Fig. 18). Hypostomal area without strong posterior tooth. 5 Clypeus modified, with either a broad, vertical, shiny truncation (Fig. 18), or emarginate apically. Mandible with few shiny ridges, surface dulled by microsculpturing (Fig. 18). Preoccipital carina always present laterally Clypeus with apical margin convex (Fig. 19) or straight (Figs 20-22, 24-25; although see also Fig. 23). Mandible surface variable, often with numerous shiny ridges. Preoccipital carina absent, or weak [e.g. in *M. foersteri*]6 6 Clypeus with apical margin convex and produced over base of labrum, denticulate or at least with 3-4 blunt, impunctate tubercles (Fig. 19). Mandible elongate (Fig. 19), with outer margin nearly straight and apical margin long, with tooth 3 very small or absent, thus with two apical teeth and a nearly straight margin above. Head little developed posteriorly, ocelloccipital distance usually shorter than interocellar distance, rarely subequal to interocellar distance [e.g. in *M. nasidens*].....subgenus Chalicodoma Clypeus with apical margin straight or weakly convex, usually not produced over base of labrum (Figs 20-25); if weakly crenulate and produced medially to small tubercle [M. ericetorum (Fig. 20)], then ocelloccipital distance much longer than interocellar distance; if apical margin sometimes convex and produced over base of labrum, or swollen medially (Fig. 22), then mandible not as above, less elongate, with outer margin regularly rounded and inner margin with four teeth or more (incana and rhodoleucura groups; Fig 22 and Fig. 4 in Algarni et al. 2012). Mandible commonly less elongate, with outer margin rounded (Figs 24-25), although sometimes approaching the condition found in *Chalicodoma* [e. g., *M. ericetorum* (Fig. 20) or *M. lanata*]. Ocelloccipital distance shorter or longer than interocellar distanceSubgenus Pseudomegachile 7 Basal hair on claws of all legs comparatively long, length more than 4 times its basal width, in appearance and color similar to apical hair, although shorter (Fig. 7). Mandible either 4-toothed with upper tooth broad and truncate, approaching the 5-toothed condition (Fig. 30) or 5-toothed (Fig. 31); mandible with a partial cutting edge in second interspace (Fig. 30) (cutting edge often

> small, recessed and difficult to see; Fig. 31), and either a strongly reduced cutting edge or no visible cutting edge in third interspace (Figs 30–31). Scopa usu

ally white to yellowish-white on S2-S4 [light orange in *M. albohirta*] and sterna without apical fasciae beneath the scopa Subgenus Anodonteutricharaea Basal hair on claws of all legs modified to a thicken process, length at most 4 times its basal width (Fig. 5) [except in *Eurymella* (Fig. 6), which has a very different mandible (Fig. 38)]. Shape of mandible variable, with 4 or 5 teeth, position of the cutting edges variable. Color of scopa variable, but if scopa white or yellowish-white (as in most species of the subgenus Eutricharaea) Mandible in front view (Figs 1, 32-34) with a conspicuous, partial cutting edge in second interspace [little visible in *M. genalis*] and no visible cutting edge in third interspace (a partial, recessed cutting edge is present but not visible in front view). Mandible mostly with upper tooth subdivided in two teeth, thus 5-toothed (Figs 1, 32), although sometimes not clearly so (Fig. 33) [except 4-toothed in M. bombycina (Fig. 34)]. Clypeus usually without median, impunctate line; apical half flat or slightly concave in lateral view, with punctation sparse and with shiny interspaces up to 2-3 punctures wide (Fig. 32) [except in M. lapponica, with clypeus densely punctured (Fig. 33), and in M. bombycina, with clypeus modified (Fig. 34)]. Scopa mostly orange-red at least basally, rarely white; sterna without apical fasciae beneath scopa Subgenus Megachile Mandible not as above, either with a complete cutting edge in third interspace (Fig. 35); or all cutting edges recessed and invisible in front view (Figs 2, 36, 39); mandible 4- or 5-toothed. Clypeus different, either densely punctured or with median impunctate line, and without depressed or flat zone in apical third (Figs 35–41). Color of scopa variable; sterna with or without apical fasciae beneath scopa.....9 Scopa usually orange at least on S2-S4, sometimes entirely dark or yellow white on S2-S3 [e.g. in *M. maritima*], rarely entirely yellow-white; sterna always without apical fasciae beneath scopa. Mandible with small, partial cutting edge visible in front view in second interspace (Figs 35–37); third interspace at least as deep as long, mostly with well-visible cutting edge in front view (Fig. 35) [except in M. nigriventris (Fig. 36); unclear in M. willughbiella (Fig. 37)]; mandible robust, tooth one broader than other teeth [unclear in M. nigriventris] Subgenus Xanthosarus Scopa often white on S2-S4 or S2-S5, dark on S6 or on S5 and S6, sometimes entirely dark or orange, but if orange, sterna usually with conspicuous apical fasciae beneath scopa. Mandible with second interspace mostly without visible cutting edge in front view (Figs 38-41); if small cutting edge present in second interspace, then cutting edge usually recessed and hidden behind margin; shape of third interspace variable, mostly longer than deep (Figs 39-41; but see Fig. 38); mandible often less robust10 Mandible robust (Fig. 38), tooth 1 markedly larger than teeth 2-4; mandible apically without tuft of orange hairs near the base of tooth 1; third interspace

8

9

10.

Males:

11	Coxa 1 without tooth or projection, although surface sometimes angulate
	[e.g. in Megachile (Megachile) ligniseca], or tooth minute and little visible
	[apostolica group of Eutricharaea; this group is included under both alterna-
	tives]12
_	Coxa 1 with tooth or projection, projection sometimes short but well vis-
	ible [in M. (Pseudomegachile) lanata, M. (Pseudomegachile) rivadhensis and M.
	(Anodonteutricharaea) villipes]
12	Large species (i.e. body length above 13 mm) with vestiture predominantly
12	black except snow-white on posterior parts of mesosoma on T1 and ba-
	sal part of T2 Preoccipital carina present laterally. Preapical carina of T6
	bilobed without teeth
	Body langth variable. Combination of characters not as described above as
_	body length variable. Combination of characters not as described above, es-
	pecially vestiture. Preoccipital carina absent laterally. Preapical carina of 16
	variable13
13	Small species (i.e. body size 7–9 mm) with mid and hind legs orange-red and
	front tarsi yellow-orange. Mandible with inferior projection. T6 with preapi-
	cal carina denticulate, with area above carina densely covered with white ves-
	titureSubgenus Eutricharaea, apostolica group
-	Combination of characters not as described above; mostly larger species ≥ 10
	mm; if body length less than 10 mm, then preapical carina of T6 rounded,
	vestiture of T6 different. Mandible with or without inferior projection 14
14	Preapical carina of T6 bilobed or rounded, without well-delimitated teeth
	(Fig. 42) Mandible usually with inferior projection (as in Fig. 8) [except in M
	<i>pilicrus</i> and <i>M</i> armenia. First submarginal cell not visibly longer than second
	Subranus Marachila
	Subgenus meguenue

Preapical carina of T6 with at least four well-delimitated teeth, usually with 6-10 teeth. Mandible always without inferior projection. First submarginal T7 produced to a long spine medially (Fig. 43). S5 partly exposed in repose, 15 slightly less sclerotized than S4. Mandible 4-toothed T7 not produced to a long spine medially (Figs 44-45). S5 retracted under S4 in repose, much less sclerotized than S4. Mandible 3-toothed..... Subgenus Chalicodoma, lefebvrei and parietina groups 16 T7 large and exposed, either pointed or triangular in dorsal view with a strong longitudinal carina dorsally (Fig. 46); or rounded, without longitudinal carina but with a spine basally on disc directed ventrally [M. doriae; in this species, disc of T6 with small tooth (Fig. 47)]. Apical margin of S5 and S6 visible in repose, S6 apically convex, margin resting on apical margin of T7 and closing the genital opening (Fig. 11)...... Subgenus Creightonella T7 not as above; if produced to a tooth or a spine, then tooth rounded and without longitudinal carina dorsally [montenegrensis group of Chalicodoma (Figs 15, 48)]; or tooth smaller, compressed laterally [as in numerous Pseudomegachile, for example M. ericetorum (Fig. 51)] and T7 thus not triangular in dorsal view; if T7 rounded or truncate apically (Fig. 45), then disc always without basal spine. S5 and S6 mostly retracted under S4 in repose [except in the montenegrensis group of Chalicodoma (Fig. 15), where the condition of S6 is approaching that seen in *Creightonella*)]17 17 Mandible with inferior process produced posteriorly to a triangular spine resting on hypostomal area in repose (Fig. 8). First submarginal cell not vis-Mandible either without inferior process; or with inferior process truncate, quadrate, not projecting posteriorly, often covered by hairs (as in Fig. 9), 18 T7 large, well-visible, either produced apically to a small tooth medially, or weakly trifid, or broadly truncate. Disc of T6 above carina mostly without light vestiture, surface of integument visible. Front tarsi always white or yellow-orange, often larger than front tibia. Mandible commonly 4-toothed [except in large species such as *M. maritima* and *M. lagopoda*, both of which have a 3-toothed mandible]. S4 apically mostly with hyaline apical margin (as in Figs 12–14)Subgenus Xanthosarus T7 little visible, never produced to a small tooth. Disc of T6 mostly with dense, light vestiture [except sometimes in *M. giraudi*] entirely hiding integument surface. Front tarsi variable. Mandible always 3-toothed. S4 apically without hyaline apical margin (Fig. 10)Subgenus Eutricharaea Front coxal tooth long, at least twice as long as basal width and front coxa 19 with an impunctate, shiny, glabrous area anteriorly to the tooth. T7 medially produced to a tooth (Fig. 15), sometimes trifid and T6 laterally with con-

	spicuous tooth (Fig. 48). Mandible without inferior projection
_	Front coxal tooth not particularly long, <i>or</i> front coxa without impunctate, shiny and glabrous area anteriorly to the spine. T7 variable, if produced to
	median tooth, then 16 laterally without tooth [except with a short tooth in
	M. albohirta and M. saussurei, both with short front coxal tooth]. Mandible
	with or without quadrate inferior projection20
20	T6 with preapical carina narrow, restricted to less than a third of tergal width,
	strongly produced posteriorly (Fig. 49). T6 apically (beneath the preapical
	carina) with two median teeth (Fig. 14). Mandible yellow without inferior
	projection Subgenus Eurymella, patellimana group
_	T6 not as above, if preapical carina denticulate, then carina wider than third
	of tergal width; apical margin of T6 variable. Integument of mandible mostly
	brown, mandible with or without inferior projection21
21	Preoccipital carina present laterally. Preapical carina of T6 bilobed, never
	denticulate. Clypeus often glabrous basally and with dense fringe of hairs api-
	cally. Mandible with quadrate inferior projection, often covered by numer-
	ous hairsSubgenus Callomegachile
_	Preoccipital carina absent laterally or very weak. Preapical carina of T6 most-
	ly denticulate [except in a few Pseudomegachile, e.g. M. lanata]. Vestiture of
	clypeus different, usually entirely covered by dense vestiture. Mandible with
	or without quadrate inferior projection22
22	Mandible always without inferior projection and T6 with a small lateral tooth
	(often hidden under hairs) (Fig. 50). T7 usually small, little visible and unmodi-
	fied (Fig. 50), not produced to a tooth apically [except in <i>M. albohirta</i> , in which
	T7 is small, apically produced to a truncate, median process]. First submarginal
	cell not visibly longer than second. Gonostylus apically broaden and with numer-
	ous hairs on external surface (Fig. 50) Subgenus Anodonteutricharaea
_	Mandible with or without quadrate inferior projection, but if projection ab-
	sent, then T6 without lateral tooth (Fig. 51). T7 either produced to a triangular
	tooth that is compressed laterally [<i>M. ericetorum</i> ; <i>flavipes</i> group (Fig. 51)]; or
	large and exposed and of variable shape [<i>rhodoleucura</i> and <i>cyanipennis</i> groups
	(Fig. 52); <i>M. foersteri</i> (Fig. 53)], rarely small and hidden [<i>M. lanata</i>]. First sub-
	marginal cell longer than second. Gonostylus different, apex with a dense fringe
	of hairs along interior margin (Figs 51-52)Subgenus Pseudomegachile

Species groups, species composition and biology of the Western Palearctic subgenera

Subgenus Anodonteutricharaea

Diagnosis and description. This subgenus is widely distributed in the Old World (Trunz et al. 2016). Of the criteria given here, not all will apply to *Anodonteutricharaea*

outside the Palearctic; characters that appear constant in this subgenus throughout its range are the elongate basal seta on the claws in the female (Fig. 7), which is the most salient diagnostic trait to identify the females of Anodonteutricharaea; and the absence of an inferior projection on the mandible and the characteristic shape of the gonostylus in the male (Fig. 50). Females: Palearctic females of Anodonteutricharaea agree with Eutricharaea in their small to medium size, mostly white or yellowish white scopa (although it is orange in Megachile albohirta). The sterna do not have continuous, apical fasciae beneath the scopa. In contrast to Eutricharaea, the mandible is similar to that of the subgenus Megachile s. str. (Figs 30-31), with a partial cutting edge in the second interspace and no visible cutting edge in the third interspace in the Palearctic species; often in Anodonteutricharaea, the cutting edges are entirely recessed and invisible in front view (Fig. 31). Also as in Megachile s. str., the mandible is 5-toothed, or if 4-toothed, the upper tooth is truncate and weakly divided into two teeth, thus approaching the 5-toothed condition (Fig. 30). In some species, there is a straight, carinate ridge in the middle of the interacetabular interspace; this ridge is placed above the outer ridge (see Gonzalez and Engel 2012: Fig. 5) and extends form the mandibular base to the middle of interspace 1 (Figs 30-31). In most other group 1 subgenera, this ridge is less visible, less carinate or regularly curved. Males: Males of Anodonteutricharaea can be diagnosed by the absence of projection along the inferior margin of the mandible, unlike most other group 1 subgenera; the mandible is either 3- or 4-toothed. The gonostylus is distinct and diagnostic (Fig. 50): it is broadened apically, with numerous hairs on the external surface. In the Palearctic, the few known species are superficially similar to *Eutricharaea* in the light body vestiture, the presense of a front coxal spine (spine short in *M. villipes*), the T6 with disc covered by dense, white tomentum and multidentate preapical carina, and the small, unmodified T7 (except in M. albohirta, where T7 is produced to a short median tooth). In most Palearctic species, the front tarsi are slightly enlarged, yellowish-white or yellowish-brown and have a black macula ventrally on tarsal segments 2 (most species) or 1 and 2 (M. albohirta). Palearctic Anodonteutricharaea are readily distinguished from *Eutricharaea* in the hyaline apical margin of S4 (Fig. 12).

Species composition. The Palearctic species of *Anodonteutricharaea* form a rather homogenous group; how this group relates to the eight species groups recognized by Pasteels (1965) for the African fauna remains to be investigated. The following western Palearctic species belong to this subgenus: *Megachile albohirta, M. inornata, M. thevestensis*, and *M. troodica. M. mandibularis* and *M. villipes* are probably restricted to Central Asia and records of the latter from the western Palearctic (Schulthess 1924, Zanden 1989, Özbek and Zanden 1994) likely refer to other species. I have seen at least three additional, undescribed species in the western Palearctic.

Biology. Very little is known on the biology of this subgenus. Ferton (1920) described nests of *Megachile thevestensis*. The cells were placed individually or in groups of two in existing cavities between rocks or in burrows in the soil; it was unclear whether the female had dug the burrow or used a preexisting burrow. All cells investigated consisted of an external, rigid layer of leaf fragments (not circularly cut as in most other group 1 subgenera) and a layer of petals inside. I have captured *M. villipes* on *Alhagi*

(Fabaceae) in Uzbekistan, while *M. inornata* and a closely related, undescribed species appear oligolectic on Lamiaceae. *M. troodica* also appears to have a distinct or exclusive preference for Lamiaceae (Mavromoustakis 1953), and in *M. thevestensis* and another, undescribed species from Morocco, the hairs on the median parts of the clypeus are short and simple, suggesting pollen collection from nototribic flowers such as Lamiaceae (see comments under the subgenus *Pseudomegachile*).

Subgenus Callomegachile

Diagnosis and description. In the few species present in the Palearctic, the preoccipital carina is always well developed and constitutes a good diagnostic trait. **Females:** Females can be recognized by the mandible without cutting edges and by the dull mandibular surface with comparatively few punctures or ridges [the mandible is also dull in some *Chalicodoma* of the *montenegrensis* group, and to some extend in *Megachile* (*Pseudomegachile*) foersteri Gerstäcker, 1869 (Fig. 23)]. The clypeus is always modified in the species of *Callomegachile* present in the Palearctic, either broadly truncate, with truncation wide, shiny, vertical or overhanging the base of the labrum (Fig. 18). **Males:** Males of the species present in the Palearctic always have a front coxal tooth and a quadrate projection along the inferior margin of the mandible. In many *Callomegachile* (but not in *M. sculpturalis* Smith, 1853), the first segment of the front tarsi forms a ventral concavity. The preapical carina of T6 is entire, without denticulation. The clypeus is mostly glabrous basally and with a dense fringe of hairs apically; in most other Palearctic *Megachile*, the clypeus is entirely covered by hairs.

Species composition. *Megachile sculpturalis*, an Oriental species, has recently been introduced to western Europe (Vereecken and Barbier 2009, Amiet 2012, Quaranta et al. 2014, Westrich et al. 2015); otherwise, only a few species of *Callomegachile* occur on the Arabian Peninsula, including *M. simonyi* Friese, 1903 and *M. cephalotes* Smith, 1853 among others. At least two further species occur on the Arabian Peninsula; they probably belong to previously described African species. As mentioned above, *M. breviceps* likely does not belong to the Palearctic fauna.

Biology. Most species of the subgenus *Callomegachile* investigated so far predominantly use resin to build their nests (Michener 2007), although other materials (wood chips, mud or even leaf fragments) are sometimes used (Piel 1930). *Megachile sculpturalis* nests in existing cavities in wood and uses resin to separate the cells; the nest plug is also built with resin but sometimes covered with a thin layer of mud (Quaranta et al. 2014, Westrich et al. 2015). Whether mud is also used for the cell partitions is unclear. In contrast, *M. cephalotes* appears to build entire cells with mud; the cells are placed in hollow stems (Gupta et al. 2004). Apparently, a "brown-colored detachable membranous layer" (Gupta et al. 2004: 58) lines the inside of the mud walls, but it is unclear what this layer refers to as it exhibits a nipple-shaped projection apically, which seems to refer to the cocoon. The floral choices of the widely polylectic species *M. sculpturalis* have been studied using pollen analyses (Quaranta et al. 2014, Westrich et al. 2015).



Figures 16–23. Female clypeus and mandibles, front view. 16 Megachile (Creightonella) amabilis 17 M. (Maximegachile) maxillosa; the white line indicates the hypostomal tooth 18 M. (Callomegachile) sculpturalis 19 M. (Chalicodoma) hungarica 20 M. (Pseudomegachile) ericetorum 21 M. (Pseudomegachile) incana 22 M. (Pseudomegachile) sp. aff incana 23 M. (Pseudomegachile) foersteri.

Subgenus Chalicodoma

Diagnosis and description. Females: Females can be recognized by the combination of the convex, denticulate apical margin of the clypeus and the elongate mandible with a straight margin above the two apical teeth (Fig. 19) (rarely with minute tooth 3, e.g., in the *montenegrensis* group). Only some species of *Pseudomegachile* have similarly elongate mandibles, for example Megachile ericetorum (Fig. 20) and M. lanata. The former can easily be separated from *Chalicodoma* by the different apical margin of the clypeus (Fig. 20) and the long ocelloccipital distance, which is markedly longer than the interocellar distance; *M. lanata* has a short clypeus with apical margin entire (as in Fig. 24), not denticulate. In some species of the cyanipennis group of Pseudomegachile, notably M. saussurei Radoszkowski, 1874, the apical margin of the mandible is nearly straight, with reduced teeth (Fig. 25), thus approaching the condition found in Chalicodoma. In such species however, the mandible is less elongate, with the outer margin strongly convex. In M. (Pseudomegachile) incana Friese, 1898, the mandible is 5 to 6 toothed (Fig. 21), and in old specimens the teeth may be little visible and the condition thus similar to that seen in *Chalicodoma*; as in *Chalicodoma*, the ocelloccipital distance is shorter than the interocellar distance in *M. incana*. All species of the incana group can easily be diagnosed by the large body size, the light-grey metasomal vestiture without dense tergal fasciae and the comparatively broad hind basitarsus (Fig. 27). Males: Males Chalicodoma fall into three distinct species groups and there are few diagnostic characters common to all. In all species the mandible is comparatively elongate, 3-toothed and without inferior projection, and the preapical carina of T6 is denticulate.

Species groups. Tkalců (1969) and Rebmann (1970) have independently divided the subgenus *Chalicodoma* into the same four groups, to which they gave subgeneric rank. I recognize three groups, not four, because *Megachile hirsuta*, unknown to both Tkalců and Rebmann at that time, renders the distinction between two of their groups difficult in the female sex. Recognizing these groups as subgenera appears little useful for species identification in the Palearctic and I recognize them as species groups.

1. montenegrensis group (Euchalicodoma Tkalců, 1969; Xenochalicodoma Tkalců, 1971; Allomegachile Rebmann, 1970; Katamegachile Rebmann, 1970). Males: Front coxa with large, spatulate tooth. T6 with lateral tooth (Fig. 48) [small in Megachile rufitarsis (Lepeletier, 1841)]. T7 mostly produced to large, rounded, median tooth (Figs 15, 48) (tooth small in *M. rufitarsis*), or trifid. Gonostylus simple, slightly broaden apically (Fig. 48). In this species group, the front tarsi are variously modified. Unusual characters of males of some or all species of this group are the partly exposed S5 (character not visible in Fig. 15), the apically strongly convex margin of S6 (Fig. 15), as in Creightonella, and, in some species, in the lack of hairs laterally on S8, unlike other group 2 subgenera. Females: Surface of mandible mostly dull, with few shiny ridges or punctures, except in *M. rufitarsis*, in which the mandible is as in the parietina group. S6 with depressed apical zone, with strong preapical carina separating the elevated, basal part from the depressed apical zone, except in *M. montenegrensis* Dours, 1873



Figures 24–29. Female clypeus and mandibles, front view. 24. Megachile (Pseudomegachile) seraxensis 25 M. (Pseudomegachile) saussurei 26–29 Female hind basitarsus, lateral view 26 M. (Pseudomegachile) ericetorum 27 M. (Pseudomegachile) incana 28 M. (Eutricharaea) giraudi 29 M. (Eurymella) patellimana.

and *M. hirsuta*, both of which have dull mandibles. In *M. montenegrensis*, the vertex is slightly concave laterally, a unique feature in Palearctic *Chalicodoma* (see Tkalců 1969).

2. *lefebvrei* group (*Allochalicodoma* Tkalců, 1969; *Heteromegachile* Rebmann, 1970). **Males:** Front coxa without tooth. T6 with a small lateral tooth (sometimes reduced to a mere angle, as in Fig. 45). T7 rounded apically, unmodified. Gonostylus tapering apically, thickened preapically and without preapical, projecting lobe

(Fig. 45). **Females:** Surface of the mandible covered with numerous shiny ridges and punctures (Fig. 19), as in the *parietina* group. S6 with depressed apical zone; carina separating the elevated part from the depressed marginal area interrupted medially and only visible laterally. In addition, all females of the *lefebvrei* group have conspicuously modified vestiture on the clypeus (Fig. 19) and the frons: the hairs are short, simple and bent apically (Müller 1996). Such modified hairs are not found in the *montenegrensis* group and only rarely found in the *parietina* group.

3. *parietina* group. Males: Front coxa without tooth. T6 without lateral tooth. T7 rounded or truncate. Gonostylus with preapical lobe (Fig. 44). Females: S6 mostly not divided in two zones (weakly so in some species, such as *Megachile nasidens* Friese, 1898), without preapical carina. Hairs on clypeus mostly branched, except in some rare species [e.g. *M. marina* Friese, 1911 and *M. palaestina* (Tkalců, 1988)].

Species composition. Females of this subgenus are sculpturally uniform and frequently exhibit mimetic color evolution; hidden sternites of males are mostly diagnostic but these structures have only been described for few species (e.g. Tkalců 1969, 1974). Consequently, the taxonomic status of numerous "geographic" forms within *Chalicodoma* remains unclear and a complete species list is not given here. In the West Palearctic, there are at least five species in the *montenegrensis* group [*Megachile hirsuta*, *M. manicata* Giraud, 1861, *M. mauritaniae* (Tkalců, 1992), *M. montenegrensis* and *M. rufitarsis*), two to five species in the *lefebvrei* group [*M. heinii* Kohl, 1906, known only in the female sex; and depending on the species concept adopted one to four additional, parapatric species: *M. albocristata* Smith, 1853, *M. hungarica* Mocsáry, 1877, *M. lefebvrei* (Lepeletier, 1841) and *M. roeweri* (Alfken, 1927)]; and approximately 20 species in the *parietina* group, of which three are undescribed.

Biology. The nesting biology of *Megachile parietina* has been described in detail (reviewed in Westrich 1989 and Müller et al. 1997). This species builds exposed nests made of hard mud in rock crevices, more rarely on twigs (Rebmann 1969, Vereecken et al. 2010). These exposed nests are particularly hard and resistant; Kronenberg and Hefetz (1984) have demonstrated that females of *M. sicula* (Rossi, 1794) add labial gland secretions to the mud; these secretions rapidly harden and render the nest hydrophobic. Accounts of the nesting biology of the few species of the parietina group investigated so far indicate that the cells are build in a similar way: in *M. pyrenaica* Lepeletier, 1841, the cells are often hidden in holes in walls or under stones (Le Goff 2007), or placed in existing holes in steep, hard soil slopes, under overhanging rocks (Müller et al. 1997), or as described by Fabre (1879, 1882) under the roof tiles of old barns; sometimes the nests are exposed on stones as in M. parietina (Le Goff, 2007); in M. rufescens (Pérez, 1879) the nests appear to be mostly placed on twigs (Fabre 1882). M. sicula builds nests both on twigs and on rock surfaces (Kronenberg and Hefetz 1984, Vereecken et al. 2010). Few studies have documented the nesting biology of species of the other species groups: *M. manicata* appears to nest exclusively in existing holes in rocks (Le Goff 2012, Gogala 2014, C. Praz, unpublished data); Le Goff (2012) described one nest containing two cells made of hard mud mixed with pebbles; the nests observed were closed with hard mud. Nests of *M. lefebvrei* have been described in detail by Ferton (1908, 1920); the



Figures 30–37. Female clypeus and mandibles, front view. 30 Megachile (Anodonteutricharaea) albohirta 31 M. (Anodonteutricharaea) thevestensis 32 M. (Megachile) versicolor 33 M. (Megachile) lapponica 34 M. (Megachile) bombycina 35 M. (Xanthosarus) lagopoda 36 M. (Xanthosarus) nigriventris 37 M. (Xanthosarus) willughbiella.

biology of this species slightly deviates from the typical nesting biology seen in the subgenus. Females build 2–4 cells in holes in rocks; these cells have the general appearance of those built by *M. parietina*, thus they consist of mud mixed with "salivary secretions" (Ferton 1908: 545), without pebbles. Once several cells are built, they are covered with a thin (1 mm), concave layer of hardened mud; this layer is located inside the hole of the rock and its outer surface is a few millimeters beneath the external surface of the rock. Subsequently, the female fills the space above the thin mud layer with a mix of pebbles and masticated plant material. According to Ferton, the masticated plant material contains salivary secretions (but no resin), and it hardens quickly. Ferton (1920) reports a nest of *M. lefebvrei* from southern France; the nest structure and the material used were similar but the nest had been built in an empty snail shell.

Many species of *Chalicodoma*, including *Megachile hirsuta*, *M. montenegrensis*, *M. manicata*, *M. parietina*, and *M. pyrenaica* have a distinct or exclusive preference for Fabaceae (Westrich 1989, Müller et al. 1997, Gogala 2014, C. Praz, unpublished data). All species of the *lefebvrei* group are likely polylectic with a preference for Lamiaceae (Müller 1996; C. Praz, unpublished data). The pollen spectrum of the other species remains poorly investigated.

Subgenus Creightonella

Diagnosis and description. The subgenus Creightonella is in many ways intermediate between the leafcutter and the dauber bees. Females: Females can easily be diagnosed by the shape and structure of the mandible (Fig. 16): the mandibular surface is distinct, with numerous, elongate punctures but comparatively few long ridges, and is covered by numerous hairs. The apical margin has 5 or 6 teeth, with tooth 1 broad and larger than the other teeth, and the teeth 2-5 (-6) becoming progressively smaller. There is a conspicuous, partial cutting edge in the second interspace and a small, little visible cutting edge in the third and sometimes fourth. In spite of being a leafcutter, Creightonella does not have the typical tapering metasoma of most other group 1 members and the hind basitarsus is slender (as in Fig. 26). The hind claw has only one elongate seta, a unique condition in Palearctic *Megachile*. Males: Males of *Creightonella* have a strong front coxal tooth and a rounded projection along the inferior margin of the mandible (Fig. 9). The front tarsi are unmodified although in *Megachile albisecta* (Klug, 1817) they are yellowish-brown (Fig. 9) and the second tarsal segment has a dark spot on the ventral side. The preapical carina of T6 is mostly denticulate (weakly so in *M. arabica* Friese, 1901) and laterally the carina extends at right angle towards the base of the tergum. T7 is mostly triangular in dorsal view, with a strong longitudinal carina (Fig. 46), except in *M. doriae*, where T7 is truncate, but with a spine on the basal part of the disc (Fig. 47). The apical margin of S5 is exposed in repose and the apical margin of S6 is convex and rests on the apical margin of T7 in repose (Fig. 11).

Species composition. Most Palearctic species fall into a rather homogenous group of species referred to here as the *albisecta* group (*Metamegachile* Tkalců, 1967), even if

the structure of T7 is rather different in *Megachile doriae*; there are at least four valid species in this group: *M. albisecta*, *M. amabilis* Cockerell, 1933, *M. doriae* and *M. morawitzi* Radoszkowski, 1876; a fifth is undescribed (A. Monfared and C. Praz, in prep). The status of *M. ghigii* Gribodo, 1924, described from Libya, and *M. aurantiaca* Rebmann, 1972 from Iran (a junior homonym of *M. aurantiaca* Friese, 1905) as well as of numerous Central Asian taxa related to *M. albisecta* remains unclear. On the Arabian Peninsula, additional species with Afrotropical affinities occur: Pasteels (1979) placed *M. arabica* in the *aurivilli* group (see Pasteels 1965) and *M. felix* (Pasteels, 1979), known only in the female sex, in the *angulata* group. Mentions of *M. sudanica* Magretti, 1898 from Jordan (Zanden 1989) possibly refer to *M. arabica*, and both species may be conspecific (Pasteels 1965: 26). In addition, I have seen a single specimen putatively from Yemen (BMNH) of an African species with a modified clypeus, possibly either *M. bicornuta* Friese, 1903 or *M. cornigera* Friese, 1904, both in the African *cornigera* group.

Biology. The nesting biology of Megachile albisecta has been described in detail (Ferton 1901). This species nests in burrows in the ground; whether the females dig their own burrows or rent existing cavities as suggested by Ferton is not clear, although a brief description of a nest by Grandi (1961) mentions a nest "excavated in very hard soil" [the Oriental species M. frontalis (Fabricius, 1804) consistently digs its own burrows in hard, heavy soils (Michener and Szent-Ivany 1960, Willmer and Stone 1989]. Reports of nests in dead wood (Benoist 1940) and in stems (Banaszak and Romasenko 2001) are likely identification errors. Unlike the circular leaf discs cut by *M. frontalis* (see Michener and Szent-Ivany 1960: Plate 1), the leaf fragments used by *M. albisecta* are irregular; in *M. frontalis*, the leaf fragments used for the outer layer of the cells are also irregular (Michener and Szent-Ivany 1960: 31 and Plate 3; Willmer and Stone 1989). In M. albisecta the fragments are stuck together by masticated leaf material, and the entire cell rests on a solid plug of masticated leaf pulp mixed with pebbles. The nest plug consists of circular leaf fragments and pebbles cemented together by masticated leaf pulp. Nests of *M. albisecta* do not appear to include resin according to the description by Ferton (1901), although Ferton's subsequent articles (Ferton 1908: 547) suggest that resin was included in the nest. Possibly the leaf pulp is hardened with secretions but not resin. Resin was not found in the nests of *M. frontalis* (Michener and Szent-Ivany 1960; Willmer and Stone 1989) but was reported from the nest of the African M. cornigera (Michener 1968). M. arabica has been observed cutting leaf discs (H. Priesner, cited in Alfken 1934). M. albisecta (and possibly all species of the albisecta group) is oligolectic on Asteraceae, with a preference for Carduoideae (C. Praz, unpublished data).

Subgenus Eurymella

Diagnosis and description. Females: The females of most *Eurymella* have a distinct, robust mandible (Fig. 38), with tooth one markedly larger than the other teeth; the

mandible is 4-toothed in Palearctic and Arabian species and divided into two plane surfaces by the outer ridge; the brushes of orange hairs in the grooves near the base of tooth one are lacking or reduced (Fig. 38). A complete, well-visible cutting edge is present in the third interspace (Fig. 38). Some Eutricharaea (Megachile deceptoria Pérez, 1890 and a few related species; see under the subgenus Eutricharaea) also have a robust mandible, with tooth one comparatively large, and reduced brushes of hairs near the base of tooth one (Fig. 40). In Eurymella, the hind basitarsus is comparatively broad, its length approximately 2.3 times its maximal width (Fig. 29). In Eutricharaea, the hind basitarsus is usually less broad (Fig. 28) (length approximately 2.7 times its maximal width), except in a few species such as M. marginata. In Eurymella the claw of the hind leg bears two thin setae (Fig. 6); the condition is not as clear as in Anodonteutricharaea because the basal seta is short in Eurymella. As in Eutricharaea but unlike most other group 1 subgenera, the sterna have conspicuous apical fasciae beneath the scopa in the Palearctic species. Males: Males of *M. patel*limana Spinola, 1838, the only Palearctic species outside the Arabian Peninsula, are easy to diagnose using the criteria mentioned in the key, especially the uniquely shaped T6 (Fig. 49) and the absence of inferior mandibular tooth (see below for the males of other species from the Arabian Peninsula).

Species composition. This subgenus is diverse in Africa, where it forms numerous, morphologically distinct species groups (Pasteels 1965); very few morphological features characterize all males of *Eurymella*, while the females are more homogeneous. In the Palearctic, *Eurymella* is probably represented by only one distinctive species, *Megachile patellimana*, included in the *patellimana* group (Pasteels 1965). Pasteels (1979) mentions two species of the *eurimera* group (see Pasteels 1965) from the southern parts of the Arabian Peninsula: *M. gibboclypearis* Pasteels, 1979 and "*M. aff. eurimera* Smith, 1854".

Note. Both Arabian species of the *eurimera* group are known only in the female sex, although the male of the widely distributed Afrotropical species *Megachile eurimera* is well known (Pasteels 1965, Eardley 2013). The males of the *eurimera* group differ from those of the *patellimana* group in the pointed, inferior projection of the mandible and the simple T6 with preapical carina not produced posteriorly. In the present key, males of *M. eurimera* would run to couplet 18 (*Eutricharaea* and *Xanthosarus*); they differ from *Eutricharaea* in the strikingly different genitalia (see Pasteels 1965: p. 83), the presence of a wide, hyaline margin apically on S4 (as in Fig. 14), and the apical margin of T6 (beneath the preapical carina) with two teeth (as in Fig. 14). *Xanthosarus* is presumably absent from the Arabian Peninsula.

Biology. Little is known on the biology of *Eurymella*; only a brief account is given by Pasteels (1965: 127) for *Megachile semifulva* Friese, 1922: the nests of this species are placed in burrows in the ground and consist of leaf discs. Gess and Roosenschoon (2017) described nests of *M. patellimana* in the United Arab Emirates. The nests were placed in excavated burrows in compacted sand; it was not clear whether the burrows had been dug by *M. patellimana* or were pre-existing. A female was captured carrying a cut leaf piece, while another was captured carrying a piece of tough green plastic.



Figures 38–41. Female clypeus and mandibles, front view. **38** *Megachile (Eurymella) patellimana* **39** *M. (Eutricharaea) rotundata* **40** *M. (Eutricharaea) deceptoria* **41** *M. (Eutricharaea) giraudi.*

Subgenus Eutricharaea

Diagnosis and description. Females: In females the scopa is mostly white at least basally (often dark apically) and the sterna have distinct apical fasciae beneath the scopa (lacking in Megachile giraudi and M. hohmanni Tkalců, 1993). In a few rare cases, the scopa is orange or entirely black (some populations of *M. melanogaster*, *M.* hohmanni). The upper mandibular tooth is usually truncate (e.g. M. leachella Curtis, 1828), although it is sometimes acute (e.g. *M. deceptoria*; Fig. 40) or conversely clearly divided into two teeth [e.g. M. rotundata (Fabricius, 1787); Fig. 39]. In some species, such as *M. orientalis*, the mandible is clearly 5-toothed (Fig. 2). There is no visible cutting edge in the second interspace (Figs 39-41), in contrast to the subgenera Xanthosarus, Megachile or Anodonteutricharaea (in the latter all cutting edges are often strongly reduced); even in the third interspace, the cutting edge is often small and partly hidden behind the margin in many Eutricharaea. Males: In the Palearctic, males of this subgenus can be recognized by the following criteria: the preapical carina of T6 is mostly denticulate (weakly so in some species such as *M. rotundata*) and the disc of T6 covered with dense, light vestiture entirely hiding cuticula (except in some populations of M. giraudi). T7 is small and little visible. The mandible is 3-toothed, always with triangular inferior projection. In contrast to the subgenera Anodonteutricharaea and

Megachile and to most *Xanthosarus* and *Eurymella*, S4 does not have a hyaline rim apically (Fig. 10). The front tarsi may be modified or not, and the front coxal tooth is present (although minute in the *apostolica* group).

Species groups.

1. *rotundata* **group** (*Neoeutricharaea* Rebmann 1967). **Males:** Gonostylus simple, not bifid apically, s-shaped in lateral view (Fig. 54). Front coxa with tooth. T2 and sometimes T3 with fovea laterally. Apical margin of S4 unmodified, medially without tubercule or spot of dense, golden hairs (Fig. 10). Pretarsal claws of all legs with two similar, thin setae (as on Fig. 4). Front legs modified or not. **Females:** T2 and sometimes T3 with fovea laterally. Ocelloccipital distance often larger than diameter of lateral ocellus. Clypeus apically with comparatively wide, impunctate margin. Scopa usually white, black on S6, sometimes also S5, rarely entirely black.

Note. This group is particularly diverse and additional species groups may be recognized for isolated, divergent species: Megachile giraudi, with a particularly long interspace 3 in the female sex (Fig. 41) and front basitarsus modified, with a long apical projection in the male sex; *M. orientalis*, with the female mandible 5-toothed with cutting edges hidden behind the mandibular margin (Figs 2-3) (the male is a regular member of the *rotundata* group); and *M. hohmanni*, included in a distinct, monotypic subgenus by Tkalců (1993). Another group includes species with robust, 4-toothed mandible (Fig. 40), with tooth one larger than the other teeth and with reduced tufts of hairs apically, approaching the condition seen in *Eurymella*; males of this group are mostly characterized by the strongly convex and medially produced apical margin of T5. In the Palearctic, this group includes *M. communis* Morawitz, 1875, *M. deceptoria*, M. dohrandti Morawitz, 1880, M. sedilloti, M. jakesi Tkalců, 1988, probably M. arachosiana Gonzalez, Engel and Hinojosa-Díaz, 2010 as well as at least one undescribed species. Because all these species do not have particularly distinct gonostylus, I do not recognize separate species groups for them. Of note, the *rotundata* group also occurs in Africa; Pasteels (1965) referred to it as the malangensis group. I have examined the type material of *M. malangensis* Friese, 1904 (ZMHB); this species is a member of *Eu*tricharaea and not of Paracella (=Anodonteutricharaea) as suggested by Eardley (2013).

2. *naevia* group. Males: Similar to males of the *rotundata* group, but gonostylus apically shortly bifid (Fig. 55). Front tarsi modified, yellowish-white. T2 with a weak fovea laterally. **Females:** As in the *rotundata* group, but mandible always red. Apical margin of clypeus straight with comparatively wide impunctate area. Ocelloccipital distance shorter than diameter of lateral ocellus. T2 but not T3 with fovea laterally.

3. *leachella* group. Males: Gonostylus either bifid (Fig. 56) with long (e.g. *Megachile leachella*) or short (e.g. *M. walkeri* Dalla Torre, 1896) preapical process, or simple (e.g. *M. concinna* Smith, 1879), in all cases apically with rounded emargination (Fig. 56). Front coxa with tooth. T2 and T3 without fovea laterally (although the corresponding area on T2 is often finely punctured and covered with brown hairs which contrast with white hairs on rest of the tergum). Apical margin of S4 either with a patch of yellow hairs medially, or a minute tubercle covered with numerous short, white hairs. Pretarsal claw with basal hair short, thickened, as in the female (as in Fig. 5), and api-



Figures 42–49. Apex of male metasoma; 42–46, 48 T5-T7 and apex of genital capsule, dorsal view 47 T5-T7 and apex of genital capsule, lateral view 49 T4-T6, dorsal view 42 *Megachile* (*Megachile*) *melanopyga* 43 *M*. (*Pseudomegachile*) sp. *aff incana* 44 *M*. (*Chalicodoma*) *parietina* 45 *M*. (*Chalicodoma*) *hungarica* 46 *M*. (*Creightonella*) *albisecta* 47 *M*. (*Creightonella*) *doriae* 48 *M*. (*Chalicodoma*) *manicata* 49 *M*. (*Eurymella*) *patellimana*.

cal hair long. Front legs not modified although front tarsi sometimes yellowish brown. **Females:** T2 and T3 without fovea laterally (although the corresponding area on T2 is often finely punctured and covered with brown hairs which contrast with white hairs on rest of the tergum). Ocelloccipital distance commonly equal to the diameter of the lateral ocellus. Clypeus apically with narrow impunctate zone. Scopa white on S1-S5, black on S6, sometimes partly or entirely orange-red, never black on S5.

Note. Megachile ventrisi Engel, 2008, from Saudi Arabia, Yemen (Engel and Schwarz 2011) and at least Kenya (C. Praz and L. Packer, unpublished) belongs to another African and Oriental group in which the male front tarsi are modified (the ventral surface of the first tarsal segment is concave) and the gonostylus simple but differently shaped, without apical emargination. This group was included in the *leachella* group (as the "argentata" group) by Pasteels (1965); it includes the African species known as *M. frontalis* Smith, 1853, which is a junior homonym of *M. frontalis* (Fabricius, 1804); "*M. frontalis* Smith" is a member of *Eutricharaea* and not of *Paracella* (*=Anodonteutricharaea*) as suggested by Eardley (2013).

4. *apostolica* group. Males: As *leachella* group, with the following exceptions: gonostylus bifid apically (as in *Megachile pilidens* Alfken, 1924), but apex conspicuously slender and preapical process long. Front coxa with minute tooth (see comments above). Front tarsi yellowish-white. **Females:** As *leachella* group, with the following exceptions: all legs predominantly orange; terga brown; hairs on ventral side of mid and hind femora modified, short, apically thickened. *M. walkeri* (included in the *leachella* group) also has similarly modified hairs (Engel 2008), but in *M. walkeri* the cuticula of T1 and T2 is orange.

5. *leucomalla* group. Males: Male gonostylus as in *rotundata* group, but bent apex longer (Fig. 57). Front tarsi greatly enlarged, yellowish-white. S2 and S3 (but not S4) medio-apically with dense patch of yellow hairs. T2 and T3 without clearly delimitated fovea. Pretarsal claw of all legs with two similar hairs. **Females:** Body length above 13 mm; punctation of mesonotum coarse and sparse, interspaces shiny and nearly as large as puncture diameters. Apical clypeal margin truncate, premarginal, impunctate zone comparatively narrow. T2 and T3 without clearly delimitated fovea.

Species composition. This is a large and taxonomically complex subgenus in need of revision. The number of unpublished synonymies is large and a list of species is not given here. There is only one species in the *leucomalla* group, *M. leucomalla* Gerstäcker, 1869. I know one Palearctic species in the *apostolica* group, *Megachile soikai*; this species is possibly conspecific with one of the African species related to *M. apostolica* Cockerell, 1937 and listed by Gonzalez et al. (2010: 65). In the *naevia* group, I know two species: *M. naevia* Kohl, 1906 from the Socotra Archipelago and an undescribed species from the Arabian Peninsula, North to Israel. There are more species in the *leachella* group [possibly seven; see Soltani et al. (in press) for a treatment of the taxa allied to *M. concinna*], and a large number of species, a few of which undescribed, in the *rotundata* group, for a possible total of 29 species in the western Palearctic.

Biology. *Megachile rotundata*, a European species introduced into North America for the pollination of alfalfa, has been studied in detail (reviewed in Pitts-Singer and



Figures 50–53. Apex of male metasoma, dorsal view. 50 Megachile (Anodonteutricharaea) sp. aff. inornata 51 M. (Pseudomegachile) ericetorum 52 M. (Pseudomegachile) saussurei 53 M. (Pseudomegachile) foersteri.

Cane 2011). All species of Eutricharaea use leaf discs to build their brood cells, although M. rotundata (and M. giraudi, see below) sometimes use petal fragments and not leaves (Westrich 1989, and references therein). In *M. minutissima* Radoszkowski, 1876, the cell walls are sometimes omitted when the nest is located in cavities of small diameters, so that leaf discs are only used to build the cell partitions (Krombein 1969). The outer nest plug of *M. marginata* consists of a series of leaf discs covered by a layer of mud, possibly mixed with "saliva" (Ferton 1914). Nests of Eutricharaea are mostly built in existing cavities such as stems or beetle burrows (e.g. M. rotundata), under stones or in existing cavities in the ground (e.g. M. pilidens: Müller et al. 1997; M. marginata: Ferton, 1914; M. minutissima: Algarni et al. 2014), or more rarely in burrows dug by the bee in sandy soil (*M. leachella*: Westrich 1989; note that this species may accept trap nests under artificial conditions: Holm and Skou 1972) or in hard soil (M. deceptoria: Benoist 1940, Grandi 1961, Zettel et al. 2005, Mazzucco and Mazzucco 2007). M. giraudi appears to nest specifically in holes in rocks and to use petals for cell construction (Maneval 1939, Banaszak and Romasenko 2001; C. Praz and A. Müller, unpublished). The description of nesting aggregations in the soil for *M. leucomalla* in Central Asia (Marikovsakya 1968; see also Banaszak and Romasenko 2001) likely refers to another species, probably *M. communis*, based on Fig. 1 in Marikovsakya (1968).

The pollen preferences of species included in the subgenus *Eutricharaea* are varied; most species are probably polylectic with a preference for Fabaceae (e.g. *Megachile ro-*
tundata and *M. pilidens*: Westrich 1989; see also O'Neill et al. 2004; *M. minutissima*: Alqarni et al. 2014); Müller and Bansac (2004) have shown that some species have a distinct (e.g. *M. apicalis*) or exclusive preference for Carduoideae (*M. marginata, M. melanogaster* and *M. flabellipes* Pérez, 1895), and in these species a modified pollen collecting device is found under the hind trochanter and femur. Soltani et al. (in press) analyzed the pollen preferences of the taxa allied to *M. concinna*; all taxa were polylectic, although *M. leucostoma* Pérez, 1907 and *M. anatolica* Rebmann, 1969 showed a preference for Plantaginaceae (*Linaria*-type) and Lamiaceae, respectively. Two species have long and conspicuous hairs on the galea, *M. dolosa* Alfken, 1936 and *M. posti*; all known specimens of *M. posti* from Cyprus were collected on *Noaea mucronata* (Forssk.) Asch. & Schweinf. (Chenopodiaceae) (Mavromoustakis 1952). Strikingly similar hairs are found on the galea and first labial palpi of some *Hoplitis* [e.g. *H. karakalensis* (Popov 1936); A. Müller, pers. comm., January 2016]; this pollen collecting apparatus likely constitutes an adaptation for collecting pollen from small flowers of Chenopodiaceae (Müller 2016).

Subgenus Maximegachile Guiglia and Pasteels, 1961

Diagnosis and description. This species-poor, group 2 subgenus is probably represented in the Palearctic by one conspicuous species that is well characterized in the key. In both sexes, *Maximegachile* consists of large, elongate bees with a typical vestiture pattern: hairs are predominantly black except snow white on the propodeum, on T1 and the basal part of T2. No other Palearctic species has such a vestiture pattern. **Females:** In addition, females have an elongate, 3-toothed mandible, a modified clypeus and a strong hypostomal tooth (Fig. 17). **Males:** The males are characterized by the absence of both front coxal spine and inferior mandibular projection, by the bilobed carina of T6 and the strong preoccipital carina (see additional comments to the male morphology below).

Species composition. Two species have been mentioned for the Palearctic region and for the Arabian Peninsula: Pasteels (1979) mentions Megachile maxillosa Guérin-Méneville, 1845 from the Arabian Peninsula and describes M. esseniensis (Pasteels, 1979) from a single male collected in Southern Israel. Based on the examination of numerous specimens of M. maxillosa from Africa, it seems that M. maxillosa occurs as two distinct morphs in the male sex: a large morph (body length approximately 20 mm) with clypeus entirely glabrous and covered by coarse punctures on its disc; and a smaller morph (body length approximately 15 mm) with clypeus covered by dense vestiture at least apically and with finer punctures. A similar conclusion seems to have been reached by Eardley (2012: 26), who mentions that the lower clypeus is "densely pubescent (naked in very large specimens)". I have seen both morphs from the Arabian Peninsula but the limited material that I have seen from Israel were of the small morph, which corresponds to the description of *M. esseniensis*. For now, I thus place *M. esseniensis* as a junior synonym of *M. maxillosa* (syn. n.), in line with the treatment of *M. maxillosa* in Africa, and consequently I recognize only one species in the Palearctic region.



Figures 54–57. Genital capsule, lateral view. 54 Megachile (Eutricharaea) apicalis 55 M. (Eutricharaea) sp. aff. naevia 56 M. (Eutricharaea) leachella 57 M. (Eutricharaea) leucomalla.

Biology. Gess and Roosenschoon (2017) provide a description of the nesting biology of *Megachile maxillosa* in the United Arab Emirates. Nests of this species were found in trap nests. Entire cells were built using a mixture of sand and resin and the completed nests were closed with a plug of sand and resin. According to Gess and Gess (2003), the same species visits plants from various families but shows a preference for the Fabaceae, notably *Crotalaria*, in South Africa and Namibia.

Subgenus Megachile

Diagnosis and description. Females: In females of this subgenus, the mandible always has a conspicuous, partial cutting edge in the second interspace (reduced in *Megachile genalis*, which is easy to diagnose due to the thickened buldge at the base of the mandible: Amiet et al. 2004, Scheuchl 2006), and no visible cutting edge in the third interspace (Figs 32–34). The mandible is mostly 5-toothed with the distance between both upper teeth subequal to the distance between the other teeth (not clearly so in *M. genalis*) (Figs 1, 32); in some species teeth 4 and 5 are poorly separated (Fig. 33). In *M. bombycina*, the mandible is elongate and 4-toothed but the partial cutting edge in the second interspace

is well visible (Fig. 34). In most species, the clypeus is flat or slightly depressed preapically, and there the punctures are coarse and the interspaces wide, shiny (Fig. 32); this condition is not found in *M. lapponica* Thomson, 1872, in which the clypeus is densely punctured (Fig. 33), and in *M. bombycina*, in which the clypeus is modified, short, laterally truncate and medially produced to a blunt triangular process, and with its apical margin forming a wide, smooth and slightly concave area (Fig. 34). In the female sex, many species of *Megachile s. str.* are sculpturally similar to *Anodonteutricharaea*; in the former, the scopa is mostly orange basally and rarely white, while in Anodonteutricharaea the scopa is mostly white to yellowish white; and Anodonteutricharaea can be distinguished by the presence of two unmodified setae on the pretarsal claws; in *Megachile s*. str., the basal seta is modified to a thicken process, as in Eutricharaea or Xanthosarus (as in Fig. 5). Males: Males of the subgenus Megachile s. str. are rather homogenous both in their sculpture and in genitalic structures, and often difficult to identify. All males of the subgenus Megachile s. str. lack a front coxal spine, although in some species (M. ligniseca, M. melanopyga Costa, 1863), the front coxa forms a weak angle. The mandible is always 3-toothed, mostly with inferior projection (lacking in *M. pilicrus* and *M. arme*nia Tkalců, 1992). In most species the disc of T6 is devoid of white or light pubescence (except in *M. pyrenaea* Pérez, 1890, *M. armenia*, *M. pilicrus* and *M. melanopyga*), the preapical carina of T6 is never denticulate, although there is a lateral tooth at the lateral margin of T6 (Fig. 42). T7 is either small or exposed, but mostly unmodified (without tooth apically). The gonostylus is always simple, never bifid apically (Fig. 42).

Species composition. There are at least 14 valid species in the Western Palearctic: *Megachile alpicola* Alfken, 1924, *M. armenia*, *M. bombycina*, *M. calloleuca*, *M. centun-cularis* (Linnaeus, 1758), *M. genalis*, *M. lapponica*, *M. ligniseca*, *M. melanopyga*, *M. melanota* Pérez, 1895, *M. octosignata* Nylander, 1852, *M. pilicrus*, *M. pyrenaea* and *M. versicolor*. I have not been able to locate the type of *M. dacica* Mocsáry, 1879; Schwarz et al. (1996) and Westrich (2011) recognized this species as valid; in contrast, according to identified material in his collection (OLML), B. Tkalců considered *dacica* as a valid subspecies of *M. lapponica*. The status of *M. melanota* is unclear, as it may represent a dark color form of *M. octosignata*.

Biology. All species are leafcutters and build brood cells made of leaf fragments (e.g. Malysheva 1958, Westrich 1989, Ruhnke 2000); no Palearctic species appears to use petals as documented in the Nearctic *Megachile montivaga* (Michener, 2007, and references therein; Orr et al. 2015). The nests are mostly located in existing, above-ground cavities; some species such as *M. centuncularis* are flexible and nest both in above-ground cavities and in the soil (Westrich 1989, and references therein). Nests of *M. pyrenaea* and *M. octosignata* are placed under stones or in the soil (Ferton 1909, Grandi 1961, Westrich 1989), and a nest of *M. melanopyga* was found "loose in the grass" (Friese 1898). *M. genalis* exclusively nests in standing stems, favoring fresh stems, thus from plants of the same year; the female digs an opening and places the brood cells vertically above or below the entrance (Ruhnke 2000, and references therein). According to a brief account by Friese (1898), *M. pilicrus* nests in dry stems of thistles.

Most species of the subgenus *Megachile* are polylectic, often with a preference for Fabaceae and Asteraceae (Westrich 1989). *Megachile lapponica* is an oligolege on *Epilobium* (Westrich 1989, Kühn et al. 2006), while *M. genalis* is possibly oligolectic on Asteraceae (Westrich 1989); *M. pilicrus* is oligolectic on Carduoideae and its hind trochanter and femur are covered by modified, stiff hairs, as observed in some *Eutricharaea* species specialized on these plants (Müller and Bansac 2004).

Subgenus Pseudomegachile

Diagnosis and description. This subgenus is morphologically diverse and in both sexes few diagnostic traits are common to the entire subgenus. The description is given for the each species group. The rather distinct *incana* group has previously been recognized as a distinct subgenus, *Parachalicodoma*, but in Trunz et al.'s phylogeny (Trunz et al. 2016), this group was nested within *Pseudomegachile*, with *Megachile foersteri* being sister to a clade formed by the *cyanipennis* and the *incana* groups. Based on its morphology, the *rhodoleucura* group (not included in Trunz et al. 2016) appears to build a transition between the *incana* and the *cyanipennis* groups. Similarly, the Oriental group of species previously known as *Largella* (considered here to form the *semivestita* group) is rather distinctive, although *M. lanata* is intermediate between the *semivestita* group and other, regular looking *Pseudomegachile*. Thus although *Pseudomegachile* could be split into several subgenera, numerous species are intermediate and the recognition of several subgenera does not seem practical or necessary: the number of species is not particularly large in the Palearctic or in the Oriental region, and having numerous subgenera would not be of much utility.

Species groups.

1. *foersteri* group: Males: Large species (body size above 15 mm) with metasoma densely covered by grey to yellow-brown vestiture. Front coxal spine present. Front tarsi modified, first tarsal segment concave inferiorly, segment 2 and 3 brownish-yellow and with black maculae on ventral surface. Mandible 4-toothed with quadrate inferior projection. Preapical carina of T6 multidentate and T7 produced into a long median tooth (Fig. 53). Females: Large (body size above 17 mm) and robust species with metasoma entirely covered by grey to yellow-brown vestiture. Mandibular surface comparatively dull (Fig. 23); mandible slightly elongate (condition intermediate between that seen in the *cyannipennis* and *ericetorum* groups), with apical margin weakly 4-toothed. Apical margin of clypeus truncate, laterally with a blunt tooth (Fig. 23). Ocelloccipital particularly long, nearly three times longer than the interocellar distance.

2. cyanipennis group (Xenomegachile Rebmann, 1970): Males: Front coxal tooth present. Mandible 4-toothed (teeth sometimes blunt or small), with quadrate inferior projection. Front tarsi slightly enlarged, brownish-yellow to yellowish-white, first segment with one dark spot on ventral surface (except in *Megachile cyanipennis*). Preapical carina of T6 multidentate, laterally mostly without tooth (a small tooth is present in *M. saussurei*). T7 large, well visible from above, produced to a short spine (Fig. 52), or

trifid, or broadly truncate. **Females:** Mandible comparatively short, external margin strongly rounded, apical margin 4-toothed (Fig. 24), although sometimes teeth nearly absent and margin almost straight (Fig. 25); impunctate, premarginal area along apical margin comparatively wide (Fig. 24). Scutellum elevated medially. Ocelloccipital distance shorter than interocellar distance.

3. *rhodoleucura* group: Males: As in *cyanipennis* group, with the following differences: front coxal tooth small; mandible without inferior projection; front tarsi unmodified although first segment with dark spot on ventral surface; T7 with apical margin emarginate medially (Alqarni et al. 2012: Fig 12). Females: As in *cyanipennis* group, but apical clypeal margin apically swollen, projected over base of labrum (Alqarni et al. 2012: Figs 3–4); modified vestiture consisting of simple, short hairs on clypeus, supra-clypeal area and frons; scutellum not elevated medially.

4. *incana* group (*Parachalicodoma* Pasteels, 1966): Males: Medium to large species (body length above 12 mm) with pale metasomal vestiture not forming distinct tergal fasciae. Front coxa without tooth. Front tarsi unmodified. Mandible 4-toothed, without inferior projection. Preapical carina of T6 multidentate, laterally with strong tooth (Fig. 43). T7 produced to rounded or truncate spine (Fig. 43). S5 partly exposed in repose (in all other groups of *Pseudomegachile*, S5 is hidden under S4). Females: Large, robust species (body length above 13 mm) with pale metasomal vestiture not forming distinct tergal fasciae. Mandible 5 to 6 toothed, teeth either blunt (Fig. 21) or acute (Fig. 22); width of impunctate, premarginal area along apical margin intermediate between *cyanipennis* and *ericetorum* groups. Ocelloccipital distance shorter than interocellar distance. Hind basitarsus broad, 2.7 times as long as wide (Fig. 27). Scutellum not elevated medially. In one species the facial vestiture is modified as in the *rhodoleucura* group.

4. ericetorum group: Males: Front coxa with tooth. Mandible 3-toothed, without inferior projection, although inferior margin swollen medially. Front tarsi not particularly modified although partly yellow-brown, second segment ventrally with weak, black spot. Preapical carina of T6 multidentate (Fig. 51). T7 produced to a median tooth that is compressed laterally (Fig. 51). Females: Mandible long and slender, almost as in *Chalicodoma*, weakly 4-toothed, impunctate area along apical margin narrow (Fig. 20). Scutellum not elevated medially. Clypeus flat in profile, medially produced to a small tooth (Fig. 20), laterally weakly denticulate. Ocelloccipital distance longer than interocellar distance.

5. *flavipes* group (*Archimegachile* Alfken, 1933): Males: As in *ericetorum* group, but front tarsal segments 1–3 or 1–4 maculated ventrally, maculations sometimes reduced to thin lines. Females: As in *ericetorum* group, with following differences: clypeus apically without median tooth, or tooth minute; ocelloccipital distance either subequal to or shorter than interocellar distance.

6. *lanata* group: Males: Front coxal spine short; front tarsi unmodified. Mandible weakly 4-toothed, without inferior projection although the inferior margin is swollen medially. Preapical carina of T6 bilobed, not denticulate. T7 small, little visible. **Females:** Mandible as in *ericetorum* group, 4-toothed and comparatively elongate, im-

punctate area along apical margin narrow. Clypeus short, apical margin straight, without medial tooth. Ocelloccipital distance slightly shorter than interocellar distance.

Species composition. There is only one Western Palearctic species each in the *foersteri*, *rhodoleucura*, *ericetorum* and *lanata* groups (*Megachile foersteri*, *M. riyadhensis*, *M. ericetorum* and *M. lanata*; see above for comments on the taxonomic status of *M. riyadhensis*); three species in the *incana* group, of which two are undescribed (Dorchin and Praz, in prep.). At least *M. cinnamomea* Alken, 1926, *M. farinosa* Smith, 1853, *M. flavipes* Spinola, 1838, *M. sanguinipes* Morawitz, 1875 and *M. tecta* Radoszkowski, 1888 are valid species of the *flavipes* group; the status of *M. rubripes* is unclear: both *M. flavipes* and *M. rubripes* are parapatric and sculpturally very similar and have been considered as two subspecies of the same species by some authors (e. g., Özbek and Zanden 1994). At least *M. cyannipennis, M. nigripes* Spinola, 1838, *M. saussurei, M. schnabli* Radoszkowski, 1893 and *M. seraxensis* Radoszkowski, 1893 are valid species (Dorchin and Praz, in prep).

Biology. The nesting biology of Megachile ericetorum has been described in detail (references in Westrich 1989). Ferton (1895) provides a description of the nests, which are located in existing cavities such as existing holes in soil or clay banks, or in reed stems. The cells are arranged linearly and consist of mud; Ferton observed females gathering moist soil close to streams, a behavior not observed in bees of the subgenus Chalicodoma, which add secretions to dry mud to build their nests (see under that subgenus). The outside of the cell is coarse and irregular, while the inner wall is lined with a thin (up to 0.5 mm) layer of resin. The cell is closed with a plug of soil; the cell cap is not lined with resin on the inside of the cell, although resin is found on the outer surface, which constitutes the base of the nest cell. The nest closure consists of a layer of mud covered by a thin layer of resin, with sometimes an additional layer (2 mm) of mud. Rozen and Kamel (2007) described the biology of *M. nigripes*, a member of the saussurei group. The species nests in tunnels dug by the females in "adobe", i. e., hard, dry, mud walls. The cells, oriented almost vertically in the oblique tunnels, are elongate and not arranged linearly. The cell walls probably consist of the excavated mud wall and the inside of the cell is uneven but appears to have been lined with dark coating that is "water retardant but not truly waterproof". The authors conclude that it may consist of "very fine soil particles bound together by partly dried nectar". The nests of species of the *flavipes* group have been briefly described several times (Gutbier 1914, Alfken 1934, Mavromoustakis 1939, Krombein 1969). The most precise account describes the nests of *M. rubripes* in Turkmenistan (Ponomareva 1958). Nests of this species were found in reed stems. Two cells were arranged linearly and made of mud "moistened with water, apparently without using secretions (...); the dry cells instantly disintegrate on submergence in water". As in *M. ericetorum*, the outside of the cell is irregular, but the inside is smooth; in *M. rubripes* resin or secretions were apparently not used to line the inner wall.

Megachile ericetorum is likely oligolectic on Fabaceae (Westrich 1989, Müller et al. 1997), although according to Westrich (1989) Lamiaceae pollen is very occasionally

also used (see also Gogala 2014). Limited evidence based on floral records suggests that *M. foersteri* has a preference for Carduoideae (Asteraceae) (C. Praz, unpublished data). According to Rozen and Kamel (2007), the main host of *M. nigripes* in Egypt is Trifolium alexandrinum L. I observed M. saussurei on Medicago in Uzbekistan and in Iran (see also Popov 1946), M. flavipes and the closely related M. rubripes only on Fabaceae. As indicated by Algarni et al. (2012), many unrelated species of *Pseudomeg*achile have conspicuously modified facial hairs; these modified hairs are always found on the clypeus but may also be found on the supraclypeal area and the frons. In the species associated with Fabaceae listed above, the hairs on the face are plumose at least in fresh specimens, while in species with modified hairs, the hairs are short, simple and often bent downwards apically, or wavy (see Müller 1996). Algarni et al. (2012) listed several species of *Pseudomegachile* with such modification; among the Palearctic species, they cite the following species. M. riyadhensis, which they collected exclusively on Blepharis (Acanthaceae); I examined the pollen present in the scopa of the holotype of M. rhodoleucura (with identical facial vestiture as M. rivadhensis; see comments above) and the pollen also belongs to Acanthaceae. M. farinosa and M. cinnamomea (the condition is not clear in the latter species), both in the *flavipes* group also have modified facial hairs; according to my field observations, M. farinosa has a preference for the flowers of Vitex (Lamiaceae), while M. cinnamomea is likely polylectic. In the saussurei group, Alqarni et al. (2012) cite M. transgrediens Rebmann, 1970 as having modified facial hairs; this mention likely refers to one of two undescribed species from Turkey and Iran with modified hairs (*M. transgrediens* is probably a junior synonym of *M. sau*ssurei; C. Praz, unpublished); these two undescribed species are sculpturally close to M. saussurei, in fact differing from the latter in the female sex mostly by the modified facial vestiture. Host plants of these two species are unknown. M. seraxensis also has modified facial hairs; I collected one female of this species visiting Blepharis. Lastly, I collected in Israel several specimens of an undescribed species of the *incana* group collecting the pollen from *Blepharis*; this species has modified hairs on the clypeus, supraclypeal area and frons, exactly as in *M. rivadhensis*. Another closely related species from the *incana* group from Oman and the UAE has branched hairs on the clypeus; it was observed foraging on Crotalaria (Fabaceae; Sarah Gess, pers. comm., September 2016).

Subgenus Xanthosarus

Diagnosis and description. Females: Most females of *Xanthosarus* have a typical, broad mandible (Fig. 35) with tooth 1 larger than other teeth, without apical brush of hairs in the grooves around the base of tooth 1. In such females there is a well-visible, continuous cutting edge in the third interspace and a partial cutting edge in the second interspace (Fig. 35), the third interspace is deeper than the other interspaces, and the two upper teeth close together or poorly separated, so that the mandible is not clearly 5-toothed. Such females will be easy to identify using the present key. The mandible of *Megachile nigriventris* Schenck, 1868 (Fig. 36) [and to some extend of *M. willughbiella*

(Kirby, 1802): Fig. 37] is different, less robust, with the cutting edges little visible in front view; the upper tooth is broadly truncate and the condition is intermediate between the 4-toothed and the 5-toothed conditions. In all Palearctic species of Xanthosarus, the clypeus is finely and densely punctured, regularly convex (Figs 35-37) unlike the condition found in most females of Megachile s. str. The scopa is mostly orange-red basally, sometimes nearly entirely black (*M. nigriventris*) or yellow-white on sternites 2 and 3 [e.g. *M. maritima* (Kirby, 1802)], rarely entirely yellowish-white. The sterna lack the apical fringe of hairs beneath the scopa, unlike in most *Eutricharaea* or in M. (Eurymella) patellimana. Males: In males of Xanthosarus the front coxal spine is always well developed; often there is a field of modified, short, orange bristles on the surface anteriorly to the spine, but such field may be lacking (e.g. in *M. analis* Nylander, 1852). The front tarsi are always yellow or white, from relatively narrow [e.g. M. analis, M. circumcincta (Kirby, 1802)] to conspicuously enlarged [e.g. M. lagopoda (Linnaeus, 1761), M. maritima]; the first tarsal segment is mostly strongly concave interiorly, except in M. analis. The mandible is either 3-toothed (M. lapogoda, M. maritima) or more commonly 4-toothed; the inferior margin always has a pointed process directed posteriorly; in some large species, this process is particularly large and glabrous, except for some orange hairs apically. The disc of T6 is mostly not covered by white vestiture; the preapical carina of T6 is bilobed or weakly denticulate. The apical margin of T6 often lacks a lateral tooth (a small tooth is sometimes present, e.g. in *M. maritima*). The apex of T7 is usually produced to a small tooth medially, although the tooth is small in some species; in other species T7 is weakly trifid. The gonostylus is variable, either simple or strongly bifid, but this character does not clearly segregate groups.

Species composition. There are at least seven species in the western Palearctic: Megachile analis, M. circumcincta, M. diabolica Friese, 1898, M. lagopoda, M. maritima, M. nigriventris and M. willughbiella. M. fulvimana Eversmann, 1852 has been mentioned from Southeastern Europe (Banaszak and Romasenko 2001); this species is known to me only from Central Asia. M. mguildensis Benoist, 1940, from Algeria and Morocco, apparently closely related to *M. nigriventris*, may either represent a distinct species or merely a color morph of *M. nigriventris*. Özbek and Zanden (1994) further cite *M. metatarsalis* Morawitz, 1894 from Turkey; this species is unknown to me. The status of M. fulvescens Smith, 1853 from Sicily is unclear; it is unlikely to represent a species distinct from those listed above; its description ("the pollen brush is of golden hue towards the base, becoming bright fulvous at the apex") suggests M. maritima. Similarly, the status of M. maacki Radoszkowski, 1874 remains in doubt; Scheuchl (2006) provides a description of the male and the female and differentiates this species from *M. nigriventris*. However, no lectotype has been designated. Of the possible syntypes that I could examine (ISZP), one male agrees with the original description and does not appear specifically distinct from M. nigriventris. Possibly, M. maacki represents an Eastern Palearctic, geographic form of *M. nigriventris. Xanthosarus* appears particularly diverse in the mountains of Central Asia and in Mongolia, where several additional species occur.

Biology. Most species of the sugbenus *Xanthosarus* place their brood cells made of cut leaves in underground burrows or more rarely under stones; the females appear

to dig the burrows themselves (Westrich 1989, and references therein; Hartmann and Arens 1998). *Megachile nigriventris* digs burrows only in decaying wood (Westrich 1989, Dubitzky 2000, Reichholf 2002), while *M. willughbiella* either digs burrows in decaying wood or uses existing cavities such as vacant *Anthophora* cells (Westrich 1989, and references therein; Müller et al. 1997). *Megachile analis* is unusual in that it uses thin bark fragments and not leaves for the construction of the cells (Westrich 1989, and references therein); leaf discs are also used by this species.

Megachile nigriventris is likely oligolectic on Fabaceae (Westrich 1989, Müller et al. 1997) and *M. diabolica* possibly on Campanulaceae (Hartmann and Arens 1998); *M. analis* and *M. willughbiella* are polylectic but show a preference for Fabaceae and Campanulaceae, as well as for the genus *Epilobium* by *M. willughbiella* (Westrich 1989, Müller et al. 1997). *Megachile lagopoda and M. maritima* are likely polylectic with a preference for Fabaceae and Asteraceae.

Additional Arabian subgenera not present in the Palearctic

Amegachile

This subgenus is widespread in Africa and in the Oriental zone. I have seen two specimens from Yemen, one male and one female, presumably from two different species: the female is sculpturally similar to *Megachile fimbriata* Smith, 1853, thus belonging to the *fimbriata* group (Pasteels 1965) while the male is a member of the *bituberculata* group (possibly *M. melanops* Cockerell, 1937), with unmodified front tarsi. Both sexes of the African members of *Amegachile* have been well characterized by Pasteels (1965).

Chelostomoda

This subgenus is distributed in the tropical regions of Southeast Asia, from India to northern Australia; in China and Japan, it enters the East Palearctic region. I have examined one female (possibly *Megachile spissula* Cockerell, 1911; Stephan Risch, pers. comm., May 2014) of this subgenus from Hamburg, Germany (CSE). It is assumed here that this female represents an isolated record, possibly from nests that have been carried overseas, and that populations of this species are not currently established in Europe. For this reason, this subgenus is not included in the key.

Stenomegachile

I have seen one single female from Yemen (BMNH; likely *Megachile chelostomoides* Gribodo, 1894) belonging to this African, group 2 subgenus. This characteristic subgenus has been precisely described elsewhere (Pasteels 1965, Michener 2007).

Discussion

The review of the nesting biology of western Palearctic *Megachile* bees suggests that the morphology of the female mandible, which has largely provided the basis for the subgeneric classification of the genus, appears to be associated with nesting biology. First, the reduction of the cutting edges in some group 1 members appears to be associated with reduced leafcutting activities: in the Palearctic, cutting edges are reduced in some Eutricharaea (Fig. 2) and Anodonteutricharaea, such as Megachile (Anodonteutricharaea) thevestensis (Fig. 31); the latter species is peculiar in using irregularly cut leaf fragments and petals in its nest (Ferton 1911) instead of the circular leaf discs used by most other group 1 subgenera. In the New World, group 1 species in which the cutting edges are reduced use petals or chewed leaves and no leaf discs in their nests [e.g. in some species of the Neotropical subgenera Chrysosarus and Schrottkyapis Mitchell, 1980: Zillikens and Steiner 2004, Martins and Almeida 1994; or in the Nearctic M. (Megachile) montivaga: Orr et al. 2015, and references therein]. Second, the shape of the mandible varies with nesting substrate. Subgenera that are predominantly cavity nesters, such as most members of Eutricharaea and of Megachile s. str., have a less robust mandible with tooth one smaller or subequal to the other teeth. In these species, the apical brushes of hairs near the base of tooth 1 are present (Figs 2, 32-33, 39, 41). Ground-nesting species digging their own burrows (e.g. Xanthosarus, possibly Eurymella and Creightonella) tend to have broad mandibles with tooth one larger than the other teeth; these species also lack or have a reduced brush of hairs in the grooves near the base of tooth 1 (Figs 35, 38). A similarly shaped mandible is found in some species of the subgenus *Eutricharaea*, such as M. deceptoria (Fig. 40); unlike most other species of Eutricharaea, this species probably digs its own burrows (see references above). Lastly, the mandibular structure of *M. ni*griventris (Fig. 36) and M. willughbiella (Fig. 37), both in the subgenus Xanthosarus, differs from the structure seen in other species of the same subgenus (Fig. 35); both species are exceptions in Xanthosarus in that they do not dig their burrows in the soil, but in wood (M. willughbiella also uses existing cavities). The taxonomic lesson to draw from these observations is that the mandibular structure is generally conserved within subgenera as long as the nesting biology is uniform; changes in nesting habits may induce changes in morphology. In nearly all subgenera of *Megachile*, some unusual species are found with strongly modified mandibular morphologies (for example M. genalis and M. bombycina in the subgenus Megachile; M. deceptoria, M. orientalis and M. giraudi in Eutricharaea; M. nigriventris in Xanthosarus; the incana group of species in Pseudomegachile). Such species render the morphological delineation of these subgenera difficult. Conversely, similar nesting habits found in distantly related lineages lead to convergent evolution in the mandibular structure, as observed between M. (Eurymella) patellimana (Fig. 38) and M. (Eutricharaea) deceptoria (Fig. 40), and between M. (Pseudomegachile) ericetorum (Fig. 20) and the species of Chalicodoma (Fig. 19). These convergences in female morphology, as well as the repeated losses and, possibly, reappearance of specialized male structures have contributed to the confusing systematics of the genus Megachile.

Acknowledgements

This study has only been possible thanks to the continuous support of Maximilian Schwarz, to whom I express my deep gratitude. I also thank the curators of the Natural History Museum, London (David Notton), the Muséum national d'histoire naturelle, Paris (Claire Villemant and Agnièle Touret-Alby), the Senckenberg Naturmuseum, Frankfurt (Patricia Peters), the Museum für Naturkunde, Berlin (Frank Koch and Viola Richter), the Institute of Systematic Zoology of the Polish Academy of Sciences, Krakow (Lukasz Przybylowicz) and the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (Yulia Astafurova) for the loan of type material or for hosting the author's visits to their institutions. John Ascher, Fritz Gusenleitner, Margarita Hadjistylli, Michael Kuhlmann, Andreas Müller, Stephan Risch, Stuart Roberts, Christian Schmid-Egger and Jakub Straka have helped to clarify numerous taxonomic questions. All pictures were taken using the Keyence VHX 1000 digital microscope of the Musée d'histoire naturelle de Neuchâtel and the Centre Suisse de Cartographie de la Faune, Neuchâtel. I also thank Gérard Le Goff for numerous discussions on the biology of *Megachile*, Andreas Müller for allowing the use of the SEM picture presented in Fig. 1, Cory Sheffield and the subject editor Jack Neff for numerous constructive comments, and Jessica Litman for her continuous support, for numerous comments on the manuscript and for improving the English.

References

- Alfken JD (1934) Beitrag zur Kenntnis der *Megachile*-Arten von Aegypten. Bulletin de la Société Royale Entomologique d'Egypte 18: 146–163.
- Alqarni AS, Hannan MA, Gonzalez VH, Engel MS (2012) A new species of *Chalicodoma* from Saudi Arabia with modified facial setae (Hymenoptera, Megachilidae). ZooKeys 204: 71–83. https://doi.org/10.3897/zookeys.204.3228
- Alqarni AS, Hannan MA, Gonzalez VH, Engel MS (2014) Nesting biology of the leafcutting bee *Megachile minutissima* (Hymenoptera: Megachilidae) in central Saudi Arabia. Annals of the Entomological Society of America 107: 635–640. https://doi.org/10.1603/AN13165
- Amiet F (2012) Die Blattschneiderbiene *Megachile sculpturalis* Smith, 1853 (Hymenoptera, Apidae) nun auch in der Schweiz. Entomo Helvetica 5: 157–159.
- Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Apidae 4: Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis. Fauna Helvetica 9: 1–274.
- Ascher JS, Pickering J (2016) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed 08.11.2016]
- Astafurova YA, Pesenko YA (2006) Bees of the subfamily Nomiinae (Hymenoptera: Halictidae) in Russia and adjacent countries: an annotated list. Entomological Review 86: 74–84. https://doi.org/10.1134/S0013873806010040

- Baker DB (2004) Type material of Hymenoptera described by O. I. Radoszkowsky in the Natural History Museum, London, and the localities of A. P. Fedtschenko's Reise in Turkestan. Deutsche Entomologische Zeitschrift 51: 231–252. https://doi.org/10.1002/ mmnd.20040510207
- Banaszak J, Romasenko L (2001) Megachilid bees of Europe (Hymenoptera, Apoidea, Megachilidae). Bydgoszcz University, Bydgoszcz, 239 pp.
- Becker W (1917) Violae Asiaticae et Australenses. II. Beihefte zum Botanischen Centralblatt, zweite Abteilung 34: 373–433.
- Benoist R (1940) Remarques sur quelques espèces de mégachiles principalement de la faune française. Annales de la Société Entomologique de France 109: 41–88.
- Casolari C, Casolari MR. (1980) Collezione Imenotterologica di Massimiliano Spinola. Cataloghi I Museo regionale di Scienze Naturali di Torino, Torino, 165 pp.
- Dorn M, Weber D (1988) Die Luzerne-Blattschneiderbiene und ihre Verwandten in Mitteleuropa. Die Neue Brehm Bücherei, Ziemsen, Wittenberg, 110 pp.
- Dubitzky A (2000) Das Nistverhalten der Blattschneiderbiene *Megachile nigriventris*. Beiträge der Hymenopterologen-Tagung in Stuttgart (6.-8.10.2000): 41–43.
- Eardley C (2012) A taxonomic revision of the southern African species of dauber bees in the genus *Megachile* Latreille (Apoidea: Megachilidae). Zootaxa 3460: 1–139.
- Eardley C (2013) A taxonomic revision of the southern African leaf-cutter bees, *Megachile* Latreille sensu stricto and *Heriadopsis* Cockerell (Hymenoptera: Apoidea: Megachilidae). Zootaxa 3601: 1–133. https://doi.org/10.11646/zootaxa.3601.1.1
- Engel MS (2008) A new species of *Megachile (Eutricharaea)* from Western Saudi Arabia related to *Megachile walkeri* (Hymenoptera: Megachilidae). Acta Entomologica Slovenica 16: 151–156.
- Engel MS, Schwarz M (2011) New records and the male of *Megachile ventrisi* Engel 2008 (Hymenoptera: Megachilidae). Entomofauna 32: 121–128.
- Fabre JH (1879) Souvenirs entomologiques. Études sur l'instinct et les moeurs des insectes. Delagrave, Paris, 327 pp.
- Fabre JH (1882) Nouveaux souvenirs entomologiques. Études sur l'instinct et les moeurs des insectes. Delagrave, Paris, 355 pp.
- Ferton C (1895) Nouvelles observations sur l'instinct des hyménoptères gastrilégides de la Provence. Actes de la Société Linnéenne de Bordeaux 48: 241–249.
- Ferton C (1901) Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs avec la description de quelques espèces. Annales de la société entomologique de France 70: 83–149.
- Ferton C (1908) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (4ème série) avec la description de quelques espèces. Annales de la Société Entomologique de France 77: 535–586.
- Ferton C (1909) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (5ème série) avec la description d'une espèce nouvelle. Annales de la Société Entomologique de France 78: 401–422.
- Ferton C (1914) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (8ème série) avec la description de quelques espèces nouvelles. Annales de la Société Entomologique de France 83: 81–119.

- Ferton C (1920) Notes détachées sur l'instinct des hyménoptères mellifères et ravisseurs (9ème série) avec la description de deux espèces nouvelles. Annales de la Société Entomologique de France 89: 329–375.
- Friese H (1898) Die Bienen Europa's (Apidae europaeae). Theil V. Solitäre Apiden: Genus *Lithurgus*. Genus *Megachile (Chalicodoma)*. Friedländer, Berlin, 228 pp.
- Friese H (1911) Apidae I, Megachilinae. Das Tierreich. Friedländer, Berlin, 440 pp.
- Gess SK, Gess FW (2003) A catalogue of flower visiting records for aculeate wasps and bees in the semi-arid to arid areas of southern Africa. Albany Museum, Grahamstown, 529 pp.
- Gess SK, Roosenchoon PA (2017) Notes on the nesting of three species of Megachilinae in the Dubai Desert Conservation Reserve, UAE. Journal of Hymenoptera Research 54: 43–56. https://doi.org/10.3897/jhr.54.11290
- Gogala A (2014) Megachilid bees of Slovenia (Hymenoptera: Apoidea: Megachilidae). Scopolia 80: 1–195.
- Gonzalez VH, Engel MS (2012) African and Southeast Asian *Chalicodoma* (Hymenoptera: Megachilidae): New subgenus, new species, and notes on the composition of *Pseudomegachile* and *Largella*. Annales Zoologici 62: 599–617. https://doi.org/10.3161/000345412X659669
- Gonzalez VH, Engel MS, Hinojosa-Díaz IA (2010) A new species of *Megachile* from Pakistan, with taxonomic notes on the subgenus *Eutricharaea* (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 83: 58–67. https://doi.org/10.2317/JKES0905.16.1
- Grandi G (1961) Studi di un entomologo sugli imenotteri superiori. Bollettino dell'Istituto di Entomologia dell'Università di Bologna 25, 659 pp.
- Gupta RK, Naval RK, Charan SK, Rajpurohit A (2004) Nesting biology of *Megachile* (*Callomegachile*) *cephalotes* Smith, a solitary bee that nests in castor sticks (Hymenoptera, Megachilidae). Mellifera 4: 53–64.
- Gutbier A (1914) Ueber einige Hymenopterennester aus Turkestan. Zeitschrift für wissenschaftliche Insektenbiologie 10: 339–345.
- Hartmann P, Arens W (1998) Beitrag zur Kenntnis der Biologie und Verbreitung der Megachile diabolica Friese 1898 mit Erstbeschreibung des Männchens. Linzer Biologische Beiträge 30: 349–364.
- Holm SVN, Skou JP (1972) Studies on trapping, nesting, and rearing of some *Magachile* [sic] species (Hymenoptera, Megachilidae) and on their parasites in Denmark. Entomologica Scandinavica 3: 169–180. https://doi.org/10.1163/187631272X00274
- Krombein KV (1969) Life history notes on some Egyptian solitary wasps and bees and their associates (Hymenoptera: Aculeata). Smithsonian Contributions to Zoology 19: 1–18. https://doi.org/10.5479/si.00810282.19
- Kronenberg S, Hefetz A (1984) Role of labial glands in nesting behaviour of *Chalicodoma sicula* (Hymenoptera; Megachilidae). Physiological Entomology 9: 175–179. https://doi.org/10.1111/j.1365-3032.1984.tb00696.x
- Kuhlmann M et al. [co-authors as listed in "Contributors"] (2016) Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila). http://westpalbees.myspecies.info [accessed 08.11.2016]
- Kühn J, Hamm A, Schindler M, Wittman D (2006) Ressourcenaufteilung zwischen der oligolektischen Blattschneiderbiene *Megachile lapponica* L. (Hymenoptera, Apiformes) und

anderen Blütenbesuchern am schmalblättrigen Weidenröschen (*Epilobium angustifolium*, Onagraceae). Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 15: 389–392.

- Latreille PA (1805) Histoire naturelle, générale et particulière des crustacés et des insectes. Vol. 14. Dufart, Paris, 432 pp.
- Le Goff G (2007) La nidification de *Megachile* (*Chalicodoma*) *pyrenaica* Lepeletier dans la province de Granada (Espagne) (Hymenoptera Apoidea Megachilidae). Lambillionea 107: 277–281.
- Le Goff G (2012) Nidification dans des cavités pierreuses de deux Megachilidae de Grèce (Epire): *Hoplitis (Hoplitis) fabrei* van der Zanden, 1987 et *Megachile (Chalicodoma) manicata* Giraud, 1861 (Hymenoptera, Megachilidae, Osmiini et Megachilini). Osmia 5: 3–4.
- Malysheva MS (1958) Leaf-cutting bees of the genus *Megachile* Latr. (Hymenoptera, Megachilidae) injurious to young forest stands and shelter belts in the USSR. Entomological review 37: 268–276.
- Maneval H (1939) Notes sur les Hyménoptères (6^c Série). Annales de la Société Entomologique de France 108: 103–108.
- Marikovskaya TP (1968) New data on the biology of some species of social bees (Hymenoptera, Megachilidae) from southeast Kazakhstan. Entomological review 47: 487–491.
- Martins RP, Almeida DAO (1994) Is the bee, *Megachile assumptionis* (Hymenoptera: Megachilidae), a cavity-nesting specialist? Journal of Insect Behavior 7: 759–765. https://doi. org/10.1007/BF01997444
- Mavromoustakis GA (1939) On the bees of the genera *Osmia* and *Megachile* from Cyprus (Apoidea), I. The Annals and Magazine of Natural History Series 11, 4: 154–160.
- Mavromoustakis GA (1952) On the bees (Hymenoptera, Apoidea) of Cyprus, Part III. The Annals and Magazine of Natural History Series 12, 5: 814–843. https://doi. org/10.1080/00222935208654357
- Mavromoustakis GA (1953) On the bees (Hymenoptera, Apoidea) of Cyprus, Part IV. The Annals and Magazine of Natural History Series 12, 6: 769–781. https://doi.org/10.1080/002229-35308654482
- Mazzucco K, Mazzucco R (2007) Wege der Mikroevolution und Artbildung bei Bienen (Apoidea, Hymenoptera): Populationsgenetische und empirische Aspekte. Denisia 20, zugleich Kataloge der oberösterreichischen Landesmuseen Neue Serie 66: 617–685.
- Michener CD (1965) A classification of the bees of the Australian and South Pacific regions. Bulletin of the American Museum of Natural History 130: 1–362.
- Michener CD (1968) Nest of some African Megachilid bees, with description of a new *Hoplitis* (Hymenoptera, Apoidea). Journal of the Entomological Society of Southern Africa 31: 337–359.
- Michener CD (1997) Genus-group names of bees and supplemental family group names. Scientific Papers, Natural History Museum, University of Kansas no. 1: 1–81.
- Michener CD (2007) The Bees of the World, second edition. Johns Hopkins University Press, Baltimore, Maryland, 953 pp.
- Michener CD, Szent-Ivany JJH (1960) Observations on the biology of a leafcutter bee "*Megachile frontalis*," in New Guinea. Papua and New Guinea Agricultural Journal 13: 22–35.
- Mitchell TB (1980) A generic revision of the Megachiline bees of the Western Hemisphere. Contribution from the Department of Entomology, North Carolina State University, Raleigh, North Carolina, 95 pp.

- Müller A (1996) Convergent evolution of morphological specializations in Central European bee and honey wasp species as an adaptation to the uptake of pollen from nototribic flowers (Hymenoptera, Apoidea and Masaridae). Biological Journal of the Linnean Society 57: 235–252. https://doi.org/10.1111/j.1095-8312.1996.tb00311.x
- Müller A (2016) Palaearctic osmiine bees systematics and biology of a fascinating group of solitary bees. ETH Zürich. http://blogs.ethz.ch/osmiini [accessed 08.11.2016]
- Müller A, Bansac N (2004) A specialized pollen-harvesting device in western palaearctic bees of the genus *Megachile* (Hymenoptera, Apoidea, Megachilidae). Apidologie 35: 329–337. https://doi.org/10.1051/apido:2004020
- Müller A, Amiet F, Krebs A (1997) Bienen. Mitteleuropäische Gattungen, Lebensweise, Beobachtung. Naturbuch Verlag, Augsburg, 384 pp.
- Nieto A, Roberts SPM, Kemp J, Rasmont P, Kuhlmann M, García Criado M, Biesmeijer JC, Bogusch P, Dathe HH, De la Rúa P, De Meulemeester T, Dehon M, Dewulf A, Ortiz-Sánchez FJ, Lhomme P, Pauly A, Potts SG, Praz C, Quaranta M, Radchenko VG, Scheuchl E, Smit J, Straka J, Terzo M, Tomozii B, Window J, Michez D (2014) European Red List of bees. Luxembourg: Publication Office of the European Union, 84 pp. Https:// doi.org/10.2779/77003
- O'Neill KM, O'Neill RP, Blodgett S, Fultz J (2004) Composition of pollen loads of *Megachile rotundata* in relation to flower diversity (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 77: 619–625. https://doi.org/10.2317/E-24.1
- Ornosa C, Ortiz-Sánchez FJ, Torres F (2007) Catálogo de los Megachilidae del Mediterráneo Occidental (Hymenoptera, Apoidea). II. Lithurgini y Megachilini. Graellsia 63: 111–134. https://doi.org/10.3989/graellsia.2007.v63.i1.85
- Orr MC, Portman ZM, Griswold TL (2015) Megachile (Megachile) montivaga (Hymenoptera: Megachilidae) nesting in live thistle (Asteraceae: Cirsium). Journal of Melittology 48: 1–6. https://doi.org/10.17161/jom.v0i48.4847
- Özbek H, Zanden G van der (1994) A preliminary review of the Megachilidae of Turkey, Part IV. Megachilini and Lithurgini (Hymenoptera: Apoidea). Turkish Journal of Entomology 18: 157–174.
- Pasteels JJ (1965) Révision des Megachilidae (Hymenoptera Apoidea) de l'Afrique Noire, 1. Les genres Creightoniella [sic], Chalicodoma et Megachile (s. str.). Musée Royal de l'Afrique Centrale, Annales Série 8, Sciences Zoologiques 137, Tervuren, Belgium, 579 pp.
- Pasteels JJ (1966) Megachilidae (genres: *Creightoniella* [sic], *Megachile* et *Chalicodoma* peu connues ou nouvelles des régions paléarctique et africaine. Bulletin et annales de la société royale d'entomologie de Belgique 102: 1–19.
- Pasteels JJ (1979) Notes sur de Megachilidae (Hymenoptera, Apoidea) d'Arabie et des régions désertiques limitrophes. 1. Quelques espèces à affinité africaine. Bulletin et annales de la Société royale belge d'entomologie 115: 250–257.
- Piel O (1930) Nidification de Megachile monticola Smith, chez Xylocopa rufipes Sm. f, pictifrons Sm. m. Notes d'Entomologie Chinoise 5: 1–8.
- Pitts-Singer TL, Cane JH (2011) The alfalfa leafcutting bee, *Megachile rotundata*: The world's most intensively managed solitary bee. Annual Review of Entomology 56: 221–37. https:// doi.org/10.1146/annurev-ento-120709-144836

- Ponomareva AA (1958) Nesting habits of certain species of higher bees (Hymenoptera, Apoidea) in southwestern Turkmenistan. Entomological review 37: 535–546.
- Popov VB (1946) Notes on the nomenclature of the bees (Hymenoptera, Apoidea). Proceedings of the Royal Entomological Society of London B 15: 106–109. https://doi.org/10.1111/j.1365-3113.1946.tb00834.x
- Quaranta M, Sommaruga A, Balzarini P, Felicioli A (2014) A new species for the bee fauna of Italy: *Megachile sculpturalis* continues its colonization of Europe. Bulletin of Insectology 67: 287–293.
- Rebmann O (1969) Zur Nestbauweise von Megachile (Chalicodoma) parietina Fourcroy (Hym., Apidae). Entomologische Zeitschrift 79: 138–139.
- Rebmann O (1970) 6. Beitrag zur Kenntnis der Gattung Megachile Latr. (Hym., Apidae). Über paläarktische Subgenera von Megachile. II. Zur Systematik der "Chalicodoma" Arten. Nachrichtenblatt der Bayerischen Entomologen 19: 37–47.
- Reichholf JH (2002) Ein ungewöhnlicher Nistplatz der Schwarzbäuchigen Blattschneiderbiene Megachile nigriventris am unteren Inn. Mitteilungen der zoologischen Gesellschaft braunau 8: 199–201.
- Rozen JG, Kamel SM (2007) Investigations on the biologies and immature stages of the cleptoparasitic bee genera *Radoszkowskiana* and *Coelioxys* and their *Megachile* hosts (Hymenoptera: Apoidea: Megachilidae: Megachilini). American Museum Novitates 3573: 1–43. https://doi.org/10.1206/0003-0082(2007)3573[1:IOTBAI]2.0.CO;2
- Ruhnke H (2000) Zur Nistbiologie der Megachile genalis Mor (Hymenoptera: Apidae). Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 12: 513–516.
- Scheuchl E (2006) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band II: Megachilidae - Melittidae. Second, revised edition. Apollo Books, Stenstrup, Denmark, 192 pp.
- Schletterer A (1889) Monographie der Bienen-Gattungen *Chelostoma* LATR. und *Heriades* SPIN. Zoologisches Jahrbuch für Systematik 4: 591–691.
- Schulthess A von [de] (1924) Contribution à la connaissance de la faune des hyménoptères de l'Afrique du Nord. Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord 15: 293–320.
- Schwarz M, Gusenleitner F, Westrich P, Dathe HH (1996) Katalog der Bienen Österreichs, Deutschlands und der Schweiz (Hymenoptera, Apidae). Entomofauna Supplement 8, Ansfelden, 398 pp.
- Sheffield CS, Ratti C, Packer L, Griswold T (2011) Leafcutter and Mason Bees of the Genus Megachile Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian Journal of Arthropod Identification 18: 1–107. https://doi.org/10.3752/cjai.2011.18
- Soltani G, Bénon D, Alvarez N, Praz C (2017) When different contact zones tell different stories: putative ring species in the *Megachile concinna* complex (Hymenoptera, Megachilidae). Biological Journal of the Linnean Society in press.
- Spinola M (1806) Insectorum Liguriæ Species Novæ aut Rariores, quas in agro Ligustico nuper detexit, descripsit, et iconibus illustravit. Vol. 1. Genuæ, xvii+159 pp.

- Spinola M (1808) Insectorum Liguriae Species novae aut rariores quas in agro ligustico nuper deterit. Vol. 2. Genuæ, 262 pp.
- Tkalců B (1969) Beiträge zur Kenntnis der Fauna Afganistans *Chalicodoma* Lep., Megachilidae, Apoidea, Hym. Acta Musei Moraviae 54 (suppl.): 347–384.
- Tkalců B (1974) Ergebnisse der Albanien-Expedition 1961 des 'Deutschen Entomologischen Institutes'. 89. Beitrag, Hymenoptera: Apoidea V (Megachilidae). Beiträge zur Entomologie 24: 323–348.
- Tkalců B (1993) Neue Taxa der Bienen von den Kanarischen Inseln. In: Hohmann H, LaRoche F, Ortega G, Barquín J (Eds) Bienen, Wespen und Ameisen der Kanarischen Inseln, Band II. Veröffentlichungen aus dem Übersee-Museum Bremen, Naturwissenschaften 12: 791–858.
- Trunz V, Packer L, Vieu J, Arrigo N, Praz CJ (2016) Comprehensive phylogeny, biogeography and new classification of the diverse bee tribe Megachilini: Can we use DNA barcodes in phylogenies of large genera? Molecular Phylogenetics and Evolution 103: 245–259. https://doi.org/10.1016/j.ympev.2016.07.004
- Ungricht S, Müller A, Dorn S (2008) A taxonomic catalogue of the Palaearctic bees of the tribe Osmiini (Hymenoptera: Apoidea: Megachilidae). Zootaxa 1865: 1–253.
- Vereecken N, Barbier E (2009) Premières données sur la présence de l'abeille asiatique Megachile (Callomegachile) sculpturalis SMITH (Hymenoptera, Megachilidae) en Europe. Osmia 3: 4–6. Available at: http://oabeilles.net/wordpress/osmia/osmia-numeros-entiers.
- Vereecken N, Niolu P, Dufrêne E, Le Goff G (2010) Observations sur les nids de deux chalicodomes et leurs occupants en Sardaigne (Italie). Osmia 4: 15–19. http://oabeilles.net/ wordpress/osmia/osmia-numeros-entiers
- Volkovitsh MG, Kalashian MY (2003) A new species of Sphenoptera (subgenus Chrysoblemma) from Iran with taxonomic notes on some Palaearctic species of Sphenoptera from subgenera Chrysoblemma, Hoplistura and Tropeopeltis (Coleoptera: Buprestidae). Zoosystematica Rossica, 11: 331–342.
- Westrich P (1989) Die Wildbienen Baden-Württembergs. Ulmer, Stuttgart, 972 pp.
- Westrich P (2011) Bienen (Hymenoptera, Apidae) als Blütenbesucher von Odontites viscosus und Odontites luteus (Scrophulariaceae). Eucera 6: 3–18. http://www.wildbienen.info/ downloads/eucera-6–2011.pdf
- Westrich P, Knapp A, Berney I (2015) Megachile sculpturalis Smith 1853 (Hymenoptera, Apidae), a new species for the bee fauna of Germany, now north of the Alps. Eucera 9: 3–10. Available at: http://www.wildbienen.info/eucera/index.php
- Willmer PG, Stone GN (1989) Incidence of entomophilous pollination of lowland coffee (*Coffea canephora*); the role of leaf cutter bees in Papua New Guinea. Entomologia Experimentalis et Applicata 50: 113–124. https://doi.org/10.1111/j.1570-7458.1989.tb02380.x
- Wittmann D, Blochtein B (1995) Why males of leafcutter bees hold the females' antennae with their front legs during mating. Apidologie 26: 181–196. https://doi.org/10.1051/ apido:19950302
- Zanden G van der (1989) Neue oder wenig bekannte Arten und Unterarten der palaearktischen Megachiliden (Insecta, Hymenoptera, Apoidea: Megachilidae). Entomologische Abhandlungen, Staatliches Museum für Tierkunde Dresden 53: 71–86.

- Zettel H, Schödl S, Wiesbauer H (2005). Zur Kenntnis der Wildbienen (Hymenoptera: Apidae) in Wien, Niederösterreich und dem Burgenland (Österreich) - 2. Beiträge zur Entomofaunistik 6: 107–126.
- Zillikens A, Steiner J (2004) Nest architecture, life cycle and cleptoparasite of the Neotropical leafcutting bee *Megachile (Chrysosarus) pseudanthidioides* Moure (Hymenoptera: Megachilidae). Journal of the Kansas Entomological Society 7: 193–202. https://doi.org/10.2317/0310.29.1

Supplementary material I

Additional notes on the new synonymies

Authors: Christophe J. Praz

Data type: species data

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

RESEARCH ARTICLE



On the identity of the adventive species of *Eufriesea* Cockerell in the USA: systematics and potential distribution of the coerulescens species group (Hymenoptera, Apidae)

Victor H. Gonzalez¹, Terry Griswold², Marianna Simões³

I Undergraduate Biology Program and Division of Entomology, Natural History Museum, Haworth Hall, 1200 Sunnyside Ave., University of Kansas, Lawrence, KS, 66045, USA 2 USDA-ARS Pollinating Insects Research Unit, Utah State University, Logan, Utah 84322-5310, USA 3 Division of Entomology, Natural History Museum, Haworth Hall, 1200 Sunnyside Ave., University of Kansas, Lawrence, KS, 66045, USA

Corresponding author: Victor H. Gonzalez (victorgonzab@gmail.com)

Academic editor: M. Ohl	Received 10 February 2017 Accepted 8 March 2017 Published 28 April 2017
,	tp://zoobank.org/5DA0672A-D578-41C5-ADAB-BD6528D9ED5D

Citation: Gonzalez VH, Griswold T, Simões M (2017) On the identity of the adventive species of *Eufriesea* Cockerell in the USA: systematics and potential distribution of the *coerulescens* species group (Hymenoptera, Apidae). Journal of Hymenoptera Research 55: 55–105. https://doi.org/10.3897/jhr.55.12209

Abstract

In the summer of 2010, two male specimens of the neotropical orchid bee genus *Eufriesea* Cockerell were collected in the Guadalupe Mountains of western Texas and southeastern New Mexico, USA. We tentatively identified them as *E. coerulescens* (Lepeletier de Saint Fargeau) because of the uncertainty surrounding the limits of this taxon and hypothesized that they were members of a persistent bee population, rather than long-distance transient vagrants. The goals of this paper are to clarify the identity of these specimens, assess the species limits of *E. coerulescens*, and to evaluate suitability of habitats in the USA for this adventive species. Herein, we revise the species in the *coerulescens* group using morphological features of both sexes and confirm that the specimens of *Eufriesea* from the USA are *E. coerulescens*. We recognize the following six species in the *coerulescens* group: *E. coerulescens*, and three new species from Mexico (*E. barthelli* Gonzalez & Griswold, **sp. n.**, *E. engeli* Gonzalez & Griswold, **sp. n.**, and *E. oliveri* Gonzalez & Griswold, **sp. n.**). To facilitate the identification of these taxa, we present a fully illustrated account of the species, comparative diagnoses, descriptions, and an updated key to all Mexican species of *Eufriesea*. Our analyses using species distribution modelling show an absence of suitable habitat for *E. coerulescens* in western Texas and southeastern New Mexico, thus favoring the long-distance dispersal

Copyright Victor H. Gonzalez et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

hypothesis. The analyses also suggest high suitability of habitats across the Caribbean and some areas in Florida, as well as in other regions in Mexico and Central America. We discuss the implications of these results and compare them with the predicted distribution available for the other two known adventive orchid bee species in the USA.

Keywords

Anthophila, Apoidea, Mexico, orchid bees, pollinators

Introduction

This paper is the result of investigations into the identity of two male specimens of the neotropical orchid bee genus *Eufriesea* Cockerell (Apidae: Euglossini) collected in the southern United States, and an exploration of whether this represents suitable habitat. Orchid bees are primarily lowland to mid-elevation neotropical bees, but they are occasionally collected outside of their native altitudinal and latitudinal ranges. Most of these records consist of a single or a few individuals, and they are often the product of accidental long-distance dispersal rather than extensions of the natural range of the species. In the Andes, except for the monotypic genus *Aglae* Lepeletier de Saint Fargeau & Serville, specimens of one or two species of the remaining four genera of Euglossini have been collected at elevations above 2500 m (Gonzalez and Engel 2004, Gonzalez et al. 2014, Perger 2015). In the USA, in addition to *Eufriesea*, two other orchid bee species have been documented: *Euglossa dilemma* Bembé & Eltz [as *E. viridissima* (Friese)] in southern Florida and *Eulaema polychroma* (Mocsáry) in southern Arizona and southernmost Texas (Minckley and Reyes 1996, Búrquez 1997, Skov and Wiley 2005, Griswold et al. 2015).

Extralimital records of bees may be the result of large body size and a capacity for long distance flight, allowing individuals to reach higher elevations or latitudes while searching for food. In other cases, bees are accidentally transported by storms or bee nests are transported by humans when moving lumber or plant materials (Minckley and Reyes 1996, Gonzalez and Engel 2004, Michener 2007).

Adventive species may fail to become established if suitable habitats or adequate resources are not available. Using species distribution modelling (SDM), Hinojosa-Díaz et al. (2009) estimated the suitability of habitats in the USA for *E. dilemma* and *E. polychroma*. They found a high suitability of habitat in southern Florida for *E. dilemma*, the area of its accidental introduction and current establishment (Pemberton and Wheeler 2006). In contrast, they found low to complete absence of suitable habitat in southernmost Texas and southern Arizona for *E. polychroma*, thus supporting the idea of a long-distance dispersal event, as Minckley and Reyes (1996) inferred based on the heavily worn wings of the captured specimen. Unlike the specimen of *E. polychroma*, the two males of *Eufriesea* collected in the USA displayed no signs of major wing damage, and thus Griswold et al. (2015) suggested that these specimens might be members of a persistent bee population, rather than long-distance transient vagrants. If this were correct, a SDM would predict highly suitable habitat for this species of *Eufriesea* in the southern USA, as in the case of *E. dilemma*.

The identity of the two male specimens of *Eufriesea* collected in the USA during the summer of 2010 in the Guadalupe Mountains of Texas and New Mexico has proved challenging. Griswold et al. (2015) tentatively identified them as E. coerulescens (Lepeletier de Saint Fargeau), a rarely collected bee from Mexico whose species limits and true geographical distribution are unclear. The name E. coerulescens has been applied to specimens of both sexes with a short tongue (not exceeding the third sternum in repose) and concolorous tagmata, ranging from metallic green or blue to violet. However, while addressing the identity of the USA specimens, Griswold et al. (2015) noted a number of morphological variations including tongue length among the male and female specimens standing in collections under E. coerulescens sensu Kimsey (1982), which not only questioned its species limits, but also suggested the existence of undescribed species. Although literature records suggest that *E. coerulescens* is widely distributed in Mexico, possibly occurring south as far as Honduras and Guatemala, records from the last two countries and others from Central America listed by Kimsey (1982), Roubik and Hanson (2004), and Moure et al. (2007) remain unconfirmed (Griswold et al. 2015).

Kimsey (1982) separated *E. coerulescens*, along with the Mesoamerican *E. anisochlo*ra (Kimsey) and the South American species *E. fragrocara* (Kimsey) and *E. brasiliano*rum (Friese), in the species group "XII" "or caerulescens group [sic]". However, recent morphological and molecular studies (Faria 2009, Ramírez et al. 2010) have shown that most of Kimsey's species groups, including the coerulescens group, are not monophyletic. In the analysis of Ramírez et al. (2010), *E. coerulescens* and *E. micheneri* Ayala & Engel resulted as sister species whereas *E. anisochlora* and *E. fragrocara* appeared in a clade with species of the groups XI and VI. Thus, herein we consider *E. coerules*cens and *E. micheneri* as the only members of the coerulescens group. These results are not surprising because, as noted by Kimsey (1982), the proposed species groups were meant as a tool in species identification and sometimes included species that did not fit all the characters listed for each group. For example, Kimsey (1982) indicated sexually dimorphic coloration as a diagnostic feature of the coerulescens group, but it does not occur in *E. micheneri* nor in *E. simillima* (Moure & Michener), a species regarded as a synonym of *E. coerulescens* by Kimsey (1982).

Herein, we revise the species in the *coerulescens* group to assess the species limits of *E. coerulescens* and to clarify the identity of the specimens of *Eufriesea* from the USA. In addition to *E. coerulescens* and *E. micheneri*, we recognize four other species in the *coerulescens* group (one species revalidated from synonym and three described as new). We also confirm that the two male specimens of *Eufriesea* from the USA are *E. coerulescens* and, based on the SDM, suggest that they are likely transient, long-distance vagrants because of the predicted absence of suitable habitat in western Texas and southeastern New Mexico.

Material and methods

Morphology and species descriptions. Morphological terminology follows that of Kimsey (1982) and Michener (2007). Species descriptions are based on the primary type, except for the comparative comments on E. micheneri, which were based on the paratypes available to us. Descriptions emphasize structural characters that are reliable for species identification, such as width of the posterior felty patch of the male mesotibia, presence or absence of setae on the area between the medial margin of this patch and the anterior margin of tibia (Figs 1–6), shape of the subapical projection above the male metatibial spurs (Figs 7-19), punctation of the mesoscutellum and terga (Figs 20–23), and presence of setae on the dorsal lobe of the gonostylus of the male genitalia (Figs 24–26). In the female, punctation and pubescence of the mesoscutellum (Figs 27, 28), terga, and tegula (Figs 29, 30), shape of the posterodistal margin and width of the distal emargination of metatibia (Figs 31-33), as well as width of the metabasitarsus, have proven to be reliable in species recognition. The following common characters are omitted from the descriptions: Male mesotibia with anterior felty patch triangular, about half length of posterior patch, midbasally with sparse (integument largely visible among setae), short setae, otherwise covered with dense, longer setae obscuring integument. Male metatibia outer surface coarsely, contiguously punctate basally, punctures smaller, fainter, widely scattered on apical one-third. Female metatibia about twice as long as broad, with posterodistal angle broadly rounded. Female metabasitarsus about half of tibial length, with posterodistal margin projected in acute angle. The abbreviations S and T are used for metasomal sternum and tergum, respectively.

Measurements were taken with an ocular micrometer on an Olympus SZX-12 stereomicroscope. Intertegular distance was measured as the shortest distance between the inner margins of tegulae. Forewing length was measured from the posterior margin of tegula to the tip of the wing. We measured the maximum width and length of the posterior patch of the mesotibia and compared the subapical width of this patch with the maximum width of the distance between its medial margin and the anterior margin of the tibia. Photomicrographs were prepared using a Canon 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and were assembled with the CombineZM[™] software package.

Institutional acronyms used herein are: AMNH, American Museum of Natural History, New York, USA (J. Rozen); BBSL, USDA-ARS, Pollinating Insects Research Unit, Utah State University, Logan, Utah, USA (H. Ikerd); ECOSUR, Colección de Insectos, El Colegio de la Frontera Sur, Division Agroecológica, Tapachula, Chiapas, Mexico (R. Vandame, P. Sagot); EMEC, Essig Museum of Entomology, University of California, Berkeley, USA (C. Barr, R.L. Zuparko); FSCA, Florida State Collection of Arthropods, Florida State University, Gainesville, Florida, USA (C. White-hill); MNHN, Museo National D'Histoire Naturelle, Paris, France (A. Touret-Alby); SEMC, Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA (Z. Falin, J. Thomas, M.S. Engel); UNAM, Museo de Zoología Alfonso L. Herrera, Facultad de Ciencias, Universidad Nacional Autónoma de México, México (M.A. Luis, O. Yañez).

Species distribution modelling. We obtained occurrence data from the labels on specimens we examined. We georeferenced each collecting locality using the Global Gazetteer (http://www.fallingrain.com) and Google Earth (Google, Mountain View, CA, USA). We assembled 46 occurrence records to characterize the distribution of the *coerulescens* group, 24 of which are of *E. coerulescens*.

We obtained environmental data from WorldClim (version 1.3, http://www. world-clim.org; Hijmans et al. 2005), which contains climate data (i.e., monthly precipitation, and monthly mean, minimum, and maximum temperatures) at a spatial resolution of 0.1° (ca. 10 × 10 km resolution) that is obtained by interpolation among climate-station records from 1950 to 2000. These data are used to derive biologically meaningful bioclimatic variables representing annual trends, seasonality, and extreme conditions. We excluded 4 of the 19 variables available in WorldClim (mean temperature of wettest quarter, mean temperature of driest quarter, and precipitation of warmest and coldest quarters) due to anomalies and odd discontinuities between neighboring pixels. To reduce dimensionality and collinearity, we conducted a principal component analysis to the matrix of environmental variables using the "*princomp*" routine in R (v. 3.2.2 Core Team, 2014). This transformation rotates all extracted measures in a new space to capture the most variance, in decreasing order. In each case, models were estimated with the first four principal components of the environmental variables, which accounted for 95% of overall variance in the environmental dataset.

We used Maximum Entropy (MaxEnt 3.3.3.k; Phillips et al. 2006) implemented in the R package 'dismo' to estimate the potential distribution. Such an algorithm is considered one of the most reliable methods, especially with few biased samples of occurrence points (Hernandez et al. 2006, Pearson et al. 2007, Wisz et al. 2008). Calibration was done via 10 bootstrap replications, which creates replicates from the original data set by resampling with replacement (Warren and Turreli 2009). Model performance was evaluated using a partial ROC (receiver operating characteristic) area under the curve (AUC, Peterson et al. 2008). Partial ROC is based on the traditional approach, but it considers the extent of coverage of the commission error axis by model predictions. Also, it gives priority to omission error over commission in evaluating model robustness (Peterson et al. 2008). Models were evaluated by calibrating them with a random 50% of occurrences, and comparing the threshold-independent area under the curve (AUC) to null expectations. To compare partial ROC to AUC ratios of each model with null expectations, the dataset was bootstrapped, and probabilities were obtained by direct count, with AUC ratios calculated using a Visual Basic script developed by Narayani Barve (University of Kansas), based on 100 iterations and an E=10% omission threshold.

The background area used to run the model is of paramount importance, as its geographic extension can determinately influence the results of ecological niche modeling analyses (Barve et al. 2011). Therefore, we used two different extensions of background area as calibration datasets, one to run the models for the group and another one just for *E. coerulescens*, representing their respective area of known distribution. Model results were processed and visualized using the GIS software ArcView and ArcGIS 10.4.



Figures 1–3. Male mesotibia showing anterior (ap) and posterior (pp) felty patches. The presence or absence of setae in the area between the medial margin of the posterior patch and the anterior margin of tibia (aa) distally, is an important feature in species identification. I *E. coerulescens* (Mexico: Nuevo León; ECO-TAP-E-104040) **2** *E. oliveri* (holotype) **3** *E. simillima* (holotype).



Figures 4–6. Male mesotibia. **4** *E. barthelli* (holotype) **5** *E. engeli* (paratype, KUNHM-ENT 0504531) **6** *E. micheneri* (paratype. Mexico: Jalisco, Mascota, KUNHM-ENT 1121713).

Results

Systematics

Coerulescens species group

Diagnosis. Species of this group can be recognized by the combination of the following features: head, mesosoma, and metasoma concolorous; body integument metallic blue, purple, or green; tongue in repose not surpassing S2; male labrum sharply pointed in lateral view; male mesotibial brush absent; male gonostylus with dorsal lobe longer than ventral lobe; and male mesotibia with anterior felty patch triangular, about half length of posterior patch.

Included species. *E. barthelli* Gonzalez & Griswold, sp. n., *E. coerulescens* (Lepeletier de Saint Fargeau), *E. engeli* Gonzalez & Griswold, sp. n., *E. micheneri* Ayala & Engel, *E. oliveri* Gonzalez & Griswold, sp. n., and *E. simillima* (Moure & Michener). These six species are presently known only from Mexico (except for *E. coerulescens*) and can be arranged into two subgroups based on the shape of the subapical projection of the concavity on the anterior margin of the male metatibia and the pubescence and shape of the dorsal lobe of the male gonostylus (Table 1). In *E. coerulescens, E. oliveri* sp. n., and *E. simillima* the subapical projection on the metatibia is positioned posteriorly on the concavity and spine-like when seen in anterior as well as lateral view (Figs 8–13) and the dorsal lobe of the gonostylus is largely asetose, not distinctly broad apically (Fig. 25). In the remaining species the subapical projection consists of a carina that is positioned dorsally and only appears spine-like in lateral view (Figs 14–19) and the dorsal lobe is distinctly setose and apically broad (Fig. 26).

Table	I. Summary	of currently	included	species in	the	coerulescens	group	of <i>Eufriesea</i>	with inform	nation
on som	e morpholog	ical features.	. Plus (+)	and dash	(-)	symbols in	dicate J	presence and	l absence, 1	respec-
tively, c	of a particular	feature, ? = 1	unknown.							

	Features						
Spacias	Sexual color	Subapical	Subapical Glossa length		d Gonostylus		
Species	dimorphism	projection of	8	Ŷ	(dorsal lobe)		
		🕈 metatibia					
<i>E. coerulescens</i> Lepeletier de Saint Fargeau	+	spine-like	mesotrochanter	metatrochanter	Narrow, asetose		
<i>E. oliveri</i> Gonzalez & Griswold, sp. n.	+	spine-like	S2	S2	Narrow, asetose		
<i>E. simillima</i> (Moure & Michener)	_	spine-like	metatrochanter	metatrochanter	Narrow, asetose		
<i>E. barthelli</i> Gonzalez & Griswold, sp. n.	+	carinate	S2	S2	Broad, setose		
<i>E. engeli</i> Gonzalez & Griswold, sp. n.	?	carinate	S2	?	Broad, setose		
<i>E. micheneri</i> Ayala & Engel	_	carinate	S2	S1	Broad, setose		



Figures 7–13. Outer view of the male hind leg (**7**) and detail of the subapical projection (indicated by an arrow) above the tibial spurs in anterior (**8**, **10**, **12**) and lateral views (**9**, **11**, **13**) Red box in Fig. 7 indicates detailed area in subsequent figures **7–9** *E. coerulescens* (Mexico: Nuevo León, ECO-TAP-E-104040) **10**, **11** *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069134) **12**, **13** *E. simillima* (paratype. Mexico: Chihuahua, KUNHM-ENT 0504566).



Figures 14–19. Detail of the subapical projection (indicated by an arrow) above the spurs of the male metatibia in anterior (**14**, **16**, **18**) and lateral views (**15**, **17**, **19**). **14**, **15** *E. barthelli* (paratype. Mexico: Jalisco, Ajijic, KUNHM-ENT 0504535); **16**, **17** *E. engeli* (paratype, KUNHM-ENT 0504531) **18**, **19** *E. micheneri* (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712).

Key to Mexican Species of Eufriesea

(Modified from Ayala and Engel 2008)

Male

1	Head, mesosoma, and metasoma concolorous, usually metallic blue or dark
	green (Figs 36, 37, 53, 56, 68, 69, 85, 86, 101, 102, 113, 114)
_	T1 dark and T2. T5 with vellow or golden shining pubescence, sometimes
	with blue or purple iridescence)
2(1)	Anterior margin of metatibia in inner view with distinct spine-like subapical
2(1)	projection above inner spur in anterior view (Figs 7–13); genitalia with dorsal
	lobe of gonostylus spatulate, not distinctly broad apically, largely asetose (Figs
	24, 25) 3
_	Anterior margin of metatibia in inner view without a distinct spine-like sub-
	apical projection above inner spur, but upper margin of distinctly depressed
	area projected medially, thus often appearing spine-like in profile (Figs 14-
	19); genitalia with dorsal lobe of gonostylus apically broad, distinctly setose
	on outer surface (Fig. 26)5
3(2)	Glossa reaching S2 in repose; T2 with punctures on disc separated by at most
	half a puncture width (Fig. 23), impunctate distal margin very narrow, at
	most as wide as a puncture width E. oliveri Gonzalez & Griswold, sp. n.
_	Glossa shorter, not surpassing metatrochanter; T2 with punctures sparser on
	disc, separated by at least half a puncture width (Figs 22, 72), impunctate
	distal margin usually broader, at least as wide as a puncture width
4(3)	Glossa reaching metatrochanter; anterior margin of metatibia in inner view,
	above tibial spurs, not bordered laterally by an elevated ridge and thus not $(1, (12, 12, 12))$
	forming a distinct pocket, subapical projection acute in profile (Figs 12, 13);
	outer surface of mesotibia with area between the anterior margin and poste-
	rior feity patch largely bare distanty (Fig. 5); disc of cippeus weakly convex,
	some and metasome dark purple (Figs 67, 69) (Western slope of the Cordil
	lera of Chihuahua)
_	Glossa shorter, reaching mesotrochanter; anterior margin of metatibia in in-
	ner view, above tibial spurs, laterally bordered by an elevated ridge, forming a
	distinct pocket, subapical projection stout in profile (Figs 8, 9); outer surface
	of mesotibia with area between the anterior margin and posterior felty patch
	pubescent throughout (Fig. 1); disc of clypeus with longitudinal median de-
	pression bounded laterally by weak longitudinal ridge (Fig. 35); mesepisternum
	blue, dorsum of mesosoma and metasoma largely green sometimes with weak
	purple highlights (Figs 36, 37) <i>E. coerulescens</i> (Lepeletier de Saint Fargeau)

66

5(2)T2 with punctures separated by at least a puncture width on disc (Fig. 117); metabasitarsus with posterodistal margin projecting in an acute angle (Fig. 115), inner surface near base strongly protuberant (Figs 18, 19); metatrochanter distinctly projecting ventrally, thus appearing somewhat triangular in ventral view (Fig. 116); outer surface of mesotibia with area between the anterior margin and posterior felty patch largely asetose on apical half, with scattered setae along patch (Fig. 6)..... E. micheneri Ayala & Engel T2 with punctures contiguous or separated by at most a puncture width on disc (Figs 89, 105); metabasitarsus with posterodistal margin broadly rounded (Figs 87, 103), inner surface near base weakly protuberant (Figs 14-17); metatrochanter not distinctly projecting ventrally; outer surface of mesotibia with area between the anterior margin and posterior felty patch pubescent throughout except on apical third (Figs 4, 5)6 6(5) Posterior felty patch of mesotibia subapically broader than distance between its medial margin and anterior margin of tibia (Fig. 5) (southern Mexico).... E. engeli Gonzalez & Griswold, sp. n. Posterior felty patch of mesotibia subapically about as wide as distance between its medial margin and anterior margin of tibia (Fig. 4) (central Mexico)..... 7(1)Glossa short, not reaching S2.....10 Vertex and anterior half of mesoscutum with pale pubescence (southern 8(7)Mexico) *E. pallida* (Kimsey) Vertex with black pubescence, contrasting with brown or pale brown setae on 9(8) Forewing medial cell not darker than remainder of wing; S8 produced into a single, elongate apical point in lateral view (Mexico to northern Costa Rica).... Forewing medial cell darker than remainder of wing; S8 produced into two apical points in lateral view (Mexico to Brazil).. E. surinamensis (Linnaeus) Clypeus with strong sublateral ridges; surface of metatibia black, without me-10(7)Clypeus without sublateral ridges; metatibia with exterior surface reddish brown, remainder of tibia black (Mexico to western Panama)..... Clypeus without medial ridge, area between sublateral ridges concave and 11(10)impunctate; mesotibia with setal brush poorly developed (Mexico to southeastern Brazil) E. concava (Friese) Clypeus with medially punctate, with ridge or welt; mesotibia with setal brush well developed (Mexico to southeastern Brazil) E. mussitans (Fabricius)



Figures 20–26. Dorsal views of male mesoscutellum (**20**, **21**) and second metasomal tergum (**22**, **23**), and lateral views of the genital capsule (**24**) and dorsal (**gsd**) and ventral lobes (**gsv**) of the gonostylus (**25**, **26**). Red box in Fig. 24 indicates detailed area in subsequent figures. **20** *E. micheneri* (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712) **21**, **23–25** *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069134, -35) **22** *E. coerulescens* (lectotype) **26** *E. engeli* (paratype, KUNHM-ENT 0504531).

Female

(Female of *E. engeli* unknown)

1	Body concolorous, metasoma without contrasting anterior to posterior in- tegument or pubescence (Figs 46–48, 54, 57, 79–81, 96–98, 124–126)2
_	Body with strongly contrasting colors of the integument and pubescence, pubescence of metasoma with at least T1 dark and posterior terga light 6
2(1)	Glossa long, reaching S2 or beyond, two or more times as long as compound eve length
	Classe short, not reaching S2 langth loss than twice compound are langth (
-	M 11 C 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
3(2)	groove distinct, with row of dense pubescence (Fig. 27)
	<i>E. barthelli</i> Gonzalez & Griswold, sp. n.
_	Mesoscutellum with coarser, noncontiguous punctures submedially; medial
	longitudinal groove weak, lacking distinct row of dense pubescence (Fig.
	28) E. oliveri Gonzalez & Griswold, sp. n.
4(2)	Metasoma with dark brown to black setae; labrum with distinct median tu-
	bercle basally, sublateral carinae absent (Western slope of the Cordillera of
	Chihuahua)
_	Metasoma with apical terga and sterna with white setae at least laterally; labrum
	with strong, elevated median line and often with distinct sublateral carinae5
5(4)	Mesoscutum and mesoscutellum with pubescence not partially obscuring
. ,	integument (Fig. 47); mesoscutellum with fine, dense punctures (Fig. 49);
	tegula densely punctate, punctures separated by a puncture width or less
	(Fig. 29); metatibia with emargination on distal margin broad, about 0.7–0.8
	times width of posterodistal projection; metabasitarsus 1.7–1.8 times longer
	than broad (Fig. 31); glossa extending to metatrochanter (pine-oak forests
	of the Sierra Madre Oriental; eastern Mexico from Coahuila to Hidalgo and
	Querétaro)
_	Mesoscutum and mesoscutellum with denser pubescence partially obscur-
	ing integument (Fig. 126); mesoscutellum with coarser, sparser punctures
	(Fig. 127); tegula more sparsely punctate, punctures separated by at least
	a puncture width (Fig. 30); metatibia with emargination on distal margin
	narrow, about half width of posterodistal projection; metabasitarsus longer,
	about twice as long as broad (Fig. 32); glossa extending to S1 (west-central
	Mexico)
6(1)	Integument of all terga dark, blue or purple greenish (Mexico to western
. /	Panama)
_	Posterior terga light, bright golden to light vellowish green, often with red-
	dish tinges7



Figures 27–33. Dorsal views of female mesoscutellum (27, 28) and tegula (29, 30), and outer view of hind leg (31–33). 27 *E. barthelli* (paratype. Mexico: Morelos, Tepoztlán, UNAM 01827) 28, 33 *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069136) 29, 31 *E. coerulescens* (Mexico: San Luis Potosí, ECO-TAP-E-104700; Querétaro, ECO-TAP-E-104753) 30, 32 *E. micheneri* (paratype. Mexico: Jalisco, Mascota, KUNHM-ENT 1121708). Arrows in Fig. 27 indicate the distinct medial longitudinal groove with row of dense pubescence.

7(6)	Clypeus with strong, narrow medial ridge, without sublateral ridges; galea
	long, in repose reaching S2 or beyond, two or more times as long as com-
	pound eye length
_	Clypeus with sublateral ridges; galea short, in repose not reaching S2, length
	less than twice compound eye length9
8(7)	Forewing medial cell darker than remainder of wing; mesoscutellum and
	mesoscutum posteromedially doubly punctate with scattered large punctures
	among fine ones (Mexico to Brazil)E. surinamensis (Linnaeus)
_	Forewing medial cell not darker than remainder of wing; mesoscutellum and
	mesoscutum posteromedially not distinctly doubly punctate, puncture size
	somewhat variable but not extreme (Mexico to northern Costa Rica)
	E. mexicana (Mocsáry)
9(7)	Clypeus with sublateral ridges, without medial ridge, area between sublateral
	ridges concave, impunctate and polished (Mexico to southeastern Brazil)
	<i>E. concava</i> (Friese)
_	Clypeus with sublateral and weak medial ridges (Mexico to southeastern Bra-
	zil)

Genus Eufriesea Cockerell, 1908

70

Eufriesea coerulescens (Lepeletier de Saint Fargeau, 1841)

Male, Figs 1, 7-9, 22, 34-45; Female, Figs 29, 31, 46-50

Euglossa coerulescens Lepeletier de Saint Fargeau, 1841: 11 (Lectotype: MNHN; ³, Mexico); Moure, 1967: 407 (lectotype designation)

Diagnosis. The male of this species shares with that of *E. oliveri* and *E. simillima* the subapical projection of the anterior margin of the male metatibia, which is formed by the medial portion of the ridge that borders the depressed area and thus located above the inner spur, and the dorsal lobe of the gonostylus, which is apically about as broad as its base and largely bare on its outer surface. It can be separated from *E. simillima* by the length of the glossa (reaching mesotrochanter in *E. coerulescens* vs. reaching metatrochanter in *E. simillima*), presence of a longitudinal median depression on clypeus (absent in *E. simillima*), outer surface of mesotibia with area between the medial margin of the posterior felty patch and the anterior margin of tibia pubescent throughout except for small area apically (half bare apically in *E. simillima*), and by the body color (largely metallic green in the male of *E. coerulescens* vs. dark blue with violet hues in both sexes of *E. simillima*). In addition, both species are geographically separated: *E. simillima* is restricted to the western slope of the Cordillera of Chihuahua whereas *E. coerulescens* is more widely distributed, occurring along the Sierra Madre Oriental and eastern Mexico. From *E. oliveri*, which shares the same body coloration, it can be separated by the length

of the glossa (reaching S2 in *E. oliveri*), punctation of T2 (punctures on disc separated by at least half a puncture width in *E. coerulescens*, closer in *E. oliveri*), and posterior felty patch of mesotibia, which is broader medially than apically (about the same width across its length in *E. oliveri*). The female can be recognized by the following combination of features: glossa extending to metatrochanter; dorsum of mesosoma with pubescence not obscuring integument; metasoma with apical terga and sterna with white setae at least laterally; T2 with sparse, coarse punctures; mesoscutellum with fine, dense punctures; and metabasitarsus short, 1.7–1.8 times longer than broad. In *E. simillima* the pubescence of metasoma is black, T2 is more finely punctate, and metabasitarsus is longer (2.2 times longer than broad). In *E. micheneri* the pubescence on the dorsum of mesosoma is denser, partially obscuring the integument, the mesoscutellum is more coarsely and sparsely punctate, and the metabasitarsus is about twice as long as broad.

Redescription. Lectotype, δ : Head width 5.9 mm; intertegular distance 4.9 mm; body length 17.8 mm; forewing length 14.6 mm. Glossa in repose reaching mesotrochanter. Anterior margin of metatibia in inner view with elevated ridge bordering depressed, smooth and hairless area above tibial spurs, medial portion above inner spur projecting into a spine; metabasitarsus about twice as long as broad, inner surface near base weakly protuberant in frontal view, posterior margin gently convex, posterodistal margin angled. Dorsal lobe of gonostylus apically about as broad as its base, largely bare on its outer surface.

Mandible black on apical two-thirds, basally blue with weak green hues as on labrum; face green with weak golden hues; vertex and gena blue with weak green and purple hues; antenna black. Mesosoma (excluding legs) predominantly green except mesoscutellum blue, with weak golden hues on mesoscutum anteriorly, weak blue hues on axilla laterally, mesepisternum ventrally, and propodeum basal and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and metatibia basally. Wing membrane darkly infuscate, veins dark brown to black. T1–T4 green except distal margins blue to purple; T5–T7 blue with purple marginal zones; sterna mainly green except S6 dark brown, with blue to purple hues on apical sterna.

Head mainly with off-white setae, with gray to black setae on vertex. Mesosoma with black setae except whitish setae on outer surface of mesobasitarsus and off-white on anterior half of mesoscutum, lateral face of mesepisternum anteriorly, and small patch laterally on propodeum. Metasoma with off-white to light brown setae, longer and denser on apical terga and sterna.

Clypeus with longitudinal medial depression, bounded laterally by weak longitudinal ridge. T2 with punctures on disc separated by at least half a puncture width, impunctate distal margin at least as wide as two times a puncture width.

 \bigcirc : Head width 5.7–6.0 mm; intertegular distance 4.9–5.0 mm; body length 14.6–16.9 mm; forewing length 13.1–13.8 mm. Metatibia with emargination on distal margin 0.7–0.8 times width of posterodistal angle; metabasitarsus 1.7–1.8 times longer than broad.

Blue-green with purple hues on mandible, labrum, clypeus, vertex, gena, mesoscutellum, legs, discs of sterna, and marginal zones of terga.



Figures 34–39. Male lectotype of *E. coerulescens*. 34 Facial view 35 Detail of clypeus with arrows indicating weak sublateral ridges that form a median longitudinal depression 36 Dorsal habitus 37 Lateral habitus 38 right and left forewings 39 Dorsal view of mesoscutellum.

Pubescence black, except off-white on sides of T3, T4–T6 entirely, sides of S3, entire S4 and S5. Mesoscutellum with poorly defined row of dense pubescence on median longitudinal groove.

Clypeus sometimes with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, dense punctures. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.
lupe Mountains National Park, Pine Springs, N31.8955 W104.8271, 20 Jul 2010, J.D. Herndon, A. Druk, H. Ikerd , pantrap, GUMO27853 (BBSL); 13, New Mexico, Eddy County: Longview Spring, 0.7km E, N32.1007 W104.6317, 1551m, 22 Jul 2010, J.D. Herndon, Cirsium sp., CAVE20415 (BBSL); Mexico: 29, Chihuahua, General Trias, August 20, 1991, J. Rozen/N. Pember, SM0307820, -21, KUNHM-ENT (SEMC); 12, **Coahuila**, Cuesta la Muralla, ix-12-76/ J.A. Chemsak, J. Powell, A.&M Michelbacher collectors/ EMEC1069129 (EMEC); 8♀, **Durango**, Dgo., Mex., 6200ft. Aug. 14, 1947 / D. Rockefeller, Exp. Gertsch / SM0504556,-59-65 KUNHM-ENT (SEMC); 13, idem (FSCA); 19, idem / BBSL849648 (BBSL); 19, idem / D. Rockefeller, Exp. Spieth / SM0504557, KUNHM-ENT (SEMC); 1 2, *idem* / D. Rockefeller, Exp. Cazier / SM0504558, KUNHM-ENT (SEMC); 12, ECO-TAP-E-105054, Mex., Hgo. [Hidalgo], La Misión, Puerto de Piedra, 1678 m, 21,05076N, 99,11475W, 19/8/2013, 09:10, Col. Jorge Mérida; 3^Q, Mexico: Hidalgo, 24km NW Cardonal (Barranco del Tulanlango), 1590m / 13 July 1990, R.L. Minckley, ex., Cassia / SM0504551-53, KUNHM-ENT (SEMC); 1^Q, Mexico: Hidalgo, 3.5km W Canyon of Tolantongo / NE of Ixmiquilipan, 1590 m, 13 July 1990, I. Yarom, on Cassia?/ SM0504576, KUNHM-ENT (SEMC); 3° , Mexico: Hidalgo, Grutas Tolantongo, 30km NW Cardonal, 1230m, 13 July 1990. W.J. Bell #2 / SM0504521–22,-75, KUNHM-ENT (SEMC); 1 , Mexico: Hidalgo, 31 km S Jacala, 1050m, 12 July 1990, W.J. Bell #2/ SM0504579, KUNHM-ENT (SEMC); 1^Q, Mexico: Hidalgo, Santorun, Atotonlico el Grande, 13 Sept. 1997, L. Godinez, #736, ex. Senecio salignus / SM0504580, KUNHM-ENT (SEMC); 13, ECO-TAP-E-104040, NL [Nuevo León], Aranberri, P. de Anteojitos, 2041 m, 24,21185N, 99,88922W, 8/8/2013, 09:05, Col. Jorge Mérida (ECOSUR); 2♀, ECO-TAP-E-104736, -53, Mex., Qro. [Querétaro], La Loma, 1830 m, 21,36714N, 99,76277W, 16/8/2013, 10:35, Col. Jorge Mérida, Erika Esquivel; 1^Q, Mexico: Querétaro, 27km W San Luis Potosi, 1270 m, 8 July 1990, W.J. Bell #1 / SM0504577, KUNHM-ENT (SEMC); 2♀, idem, 26.5 km W San Luis Potosi / borde ron Hwy. 120, 1270 m, 9 July 1990, R.L. Minckley / SM0504523,-70, KUNHM-ENT (SEMC); 19, ECO-TAP-E-104700, Mex., SLP [San Luis Potosí], Alaquines, Las Huertas, 1384 m, 22,04671N, 99,53239W, 15/8/2013, 11:30, Col. Erika Esquivel; 4^o, *idem*, ECO-TAP-E-104661, S.J. de Corito, 1353m, 22,00349N, 99,49312W, 8:25, Col. Jorge Mérida; 2[♀], ECO-TAP-E-104939, Mex., SLP, Xilitla, La Soledad, 1356 m, 21,33348N, 99,08237W, 18/8/2013, 10:40, Col. Jorge Mérida, Erika Esquivel; 19, idem, ECO-TAP-E-104965, Buenavista, 1648 m, 21,33774N, 99,10539W; 19, 17 mi. W, Xilitla, S.L.P., Mex., vii-22-54,4700 ft/Univ. Kans. Mex. Expedition/ SM05045, KUNHM-ENT (SEMC); 1^Q, Mexico, San Luis Potosi, 17 mi E Cd. Maiz, 3200', 23 July 196, U.Kans. Mex. Exped. / SM0504569, KUNHM-ENT (SEMC); 1[♀], *idem*, 15 mi. E Cd. Maiz, 3700' / SM0504528, KUN-HM-ENT (SEMC); 2° , *idem*, 5 mi. E Ciudad del Maiz, S.L.P., Mex. 4700 feet, viii-22, 23-1954/ SM0504554, -55, KUNHM-ENT (SEMC); 1 Q, Mex: San Luis Potosi, 15 mi. W, Xilitla, 1350m, viii-15-1977, E.I.Schlinger/ on plant #8, Cassia sp. / EMEC1069131 (EMEC); 1^Q, Villagran, Tamaulipas, Mex, ix-8-1966, D.H. Janzen, Thevetia/AMNH_ BEE 00164041 (AMNH); 1^Q, Mex: Tamaulipas, 15 mi. SW Cd. Victoria, 5000', ix-



Figures 40–45. Male terminalia of *E. coerulescens* (Mexico: Nuevo León, ECO-TAP-E-104040). **40** Seventh metasomal sternum in ventral view **41, 42** Eighth metasomal sternum in ventral and lateral views **43–45** Genital capsule in dorsal, ventral, and lateral views.

19-76/ J.A. Chemsak, J. Powell, A.&M Michelbacher collectors/ EMEC1069128, -30 (EMEC).

Distribution. (Fig. 128) Mexico: Chihuahua, Coahuila, Durango, Hidalgo, Nuevo León, Querétaro, San Luis Potosí, Tamaulipas. USA (accidental?, see results and discussion): Texas, New Mexico.

Floral records. Females have been collected on flowers of *Cassia* sp. (Fabaceae), *Solanum* sp. (Solanaceae), *Senecio salignus* (Kunth) H.E. Robins. & Brett (Asteraceae), and *Thevetia* sp. (Apocynaceae). One of the two males captured in the US was visiting flowers of *Cirsium* sp. (Asteraceae).



Figures 46–50. Female of *E. coerulescens* (Mexico: San Luis Potosí, ECO-TAP-E-104161; Querétaro, ECO-TAP-E-104753 [Fig. 46]). 46 Facial view 47 Dorsal habitus 48 Lateral habitus 49 Dorsal view of mesoscutellum 50 Second metasomal tergum.

Comments. The male lectotype is in poor condition (Figs 34–39). Both forewings are detached from the specimen and the left leg, right antenna and most of the left flagellum are missing. In addition, the left mesepisternum, right sides of S1, S2, S5, S6, T5–T7, and part of genital capsule appeared to have been eaten by dermestid beetles. Because the right mesotibia is very close to the body and the genitalia is partly destroyed, the following measurements and photographs were taken from the specimen collected in Nuevo León, Mexico: mesotibia with area between medial margin of

posterior patch and anterior margin of tibia setose throughout except by small apical area; posterior patch about four times longer than broad, subapically broader than distance between its medial margin and anterior margin of tibia. Hidden sterna and genitalia as in Figs 40–45.

Female specimens vary considerably in the presence of green hues, from nearly absent to very distinct on face, mesoscutum and terga. The identity of the male from "Durango, Dgo., Mex., 6200ft. Aug. 14, 1947 / D. Rockefeller, Exp. Gertsch" is questionable, made more difficult because the two hind legs that are glued to the body are from different species; this male lacks the blue mesepisternum considered diagnostic for *E. coerulescens*.

Eufriesea oliveri Gonzalez & Griswold, sp. n.

http://zoobank.org/049C4796-6175-4614-B502-C96DADD79DF0 Male, Figs 2, 10, 11, 21, 23–25, 51, 53, 55, 56, 58–62; Female, Figs 28, 33, 52, 54, 57, 63

Diagnosis. Both sexes of this species are most similar to *E. coerulescens*, from which it can be separated easily by the longer glossa and more densely punctate disc of T2. The female of *E. oliveri* can be recognized from that of *E. barthelli* by the mesoscutellum coarsely and non-contiguously punctate submedially, with a weak medial groove lacking a distinct row of setae (finely, contiguously punctate with stronger medial groove having a distinct row of setae in *E. barthelli*), and by the T2, which is more densely punctate on disc, with punctures separate by at most a puncture width (punctures separated by 1.0–2.0 times a puncture width in *E. barthelli*).

Description. Holotype, \eth : As described for *E. coerulescens* except as follows: Head width 5.7 mm; intertegular distance 4.6 mm; body length 15.4 mm; forewing length 13.5 mm. Glossa in repose reaching S2; metabasitarsus with posterodistal margin more rounded, not as acute as in *E. coerulescens*. Hidden sterna and genitalia as in Figs 58–62.

Vertex and gena green with weak blue and purple hues. Mesosoma (excluding legs) predominantly green except mesoscutellum green with weak blue and golden hues; metatibia basally mostly green with golden hues; wing membrane infuscate, lighter than in *E. coerulescens*. Metasoma green with distal margins of terga and sterna (excluding S6) weakly blue to purple.

Head with whitish setae, with scattered gray to black setae on vertex. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose on basal half, distal half asetose; posterior patch 5.7 times longer than broad, subapically narrower than distance between its medial margin and anterior margin of tibia.

T2 with punctures on disc separated by at most half a puncture width, impunctate distal margin very narrow, at most as wide as a puncture width.

 \bigcirc : Head width 6.3 mm; intertegular distance 4.9 mm; body length 18.4 mm; forewing length 13.5 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus twice as long as broad.



Figures 51–57. Male holotype (except paratype in Fig. 55, EMEC 1069134) and female paratype (Mexico: Guerrero, EMEC 1069136) of *E. oliveri*. **51, 52** Facial view **53, 54** Lateral habitus **55** Outer view of hind leg **56, 57** Dorsal habitus **51, 53, 55, 56** Male **52, 54, 57** Female.

Blue with purple hues on mandible basally, labrum, frons, vertex, gena, dorsum of mesosoma, mesepisternum, propodeum, legs, discs of sterna, and marginal zones of terga.

Pubescence black, except off-white on sides of T2, T3–T6, sides of S2 and S3, entire S4 and S5, and S6 basally. Mesoscutellum without row of dense setae on weak medial longitudinal groove.

Clypeus with median longitudinal ridge continuing onto supraclypeal area; labrum with distinct median and sublateral carinae. Mesoscutellum with coarse, non-contiguous punctures submedially. T2 with punctures sparser than in the male, separated by a puncture width or less.

Holotype. \mathcal{E} , Mexico: Guerrero, 3 km N Chilpancingo, VI-4-12-91, JA Chemsak / EMEC 1069133 (barcode label). Deposited in EMEC.

Paratypes. $(n = 9 \[3mm], 2 \]$) Two males and two females with the same data as the holotype but with barcode label numbers 1069132, 1069134–1069136 (EMEC); C. [Clowesia] thylaciochila, La Joya, Morelos, Mex [Mexico], Ernesto Aguirre, 3-22-1977 (FSCA); remaining paratypes deposited in the UNAM with the following label data: 2 $\[3mm]$, Morelos] La Joya, 1450 m.s.n.m / # 10442; 1 $\[3mm]$, Mich. [Michoacán], La Zauda, 1100 m.s.n.m / #10443; 1 $\[3mm]$, Arrollo las Damas, Mex., Guerrero, Tetipac. 8-vi-1986, 1800 m. Luis A. / # 10446; 1 $\[3mm]$, *idem*, Llorente J. / #10445; 1 $\[3mm]$, Km 19.5, Autopista Mexico-Cuautla, Tepoztlán; Morelos. 16/06/1996. I. Hinojosa HD-737, 14:10 H, 1350 m, 18°56'17"N, 99°02'18"W, selva baja caducifolia, atraida por esencia (mezcla) / # 00366.

Additional material. (n = 53, 12, not designated as paratypes) 3, Mexico: Morelos, 4 mi SW Yautepec, 2 July 1961, 3800', C.D. Michener/ on flowers of Cassia sp./ KUNHM-ENT 504573, 504526, 504529 (KU); 1♀, Cañon de Lobos, Mor. [Morelos], 16-xi-83, R y G. Ayala / #10447 (UNAM); 13, Ocuilan, @ Stanhopea hernandezii, 2001, M.A. Soto (FSCA); 39, Mex [Mexico], Oaxaca, Tehuantepec, 56 mi N.W., vii-27-63/W.A. Foster collectors/ AMNH_BEE 00265723 (AMNH); 2^Q, Mexico, Puebla, 12 mi NW Tehuitzingo, 4050 ft, 29 June 1961, U. Kans. Mex. Exped. / KUNHM-ENT 504524, 504572 (KU); Mexico, Jalisco, Estacion de Biologia Chamela, 5-viii-86 / M. Sánchez/ / KUNHM-ENT 730197; 1^Q, *idem*, 10/14 Jul 1989, T. Griswold/ BBSL861169 (BBSL); 1^Q, idem, 4-vii-1984/ R. Ayala/ #10448 (UNAM); 13, Tzararacua, near Uruapan, Mich. [Michoacán], Mexico, 28 June 68 [1968], N.H. Williams, Eugenol, 276 (FSCA); 13, Mexico, Mich. [Michoacán], Tzararacua, nr. Uruapan, 29 VI 1968, N.H. Williams, 276, Eugenol (FSCA); 1⁽²⁾, Mexico, Mich. [Michoacán], Tzararacua, nr. Uruapan, 6 VII 1968, N.H. Williams, 276, Eugenol (FSCA); C. [Clowesia] glaucoglossa, La Huacana, Mich. [Michoacán], Mex [Mexico], Ernesto Aguirre, 3-22-1977 (FSCA).

Etymology. This species is named after Oliver Mitchell Betancourt, son of the first author (March 11, 2015), who daily brings love and joy.

Distribution. (Fig. 128) Mexico: Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla.



Figures 58–62. Male terminalia of *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069134). **58** Seventh metasomal sternum in ventral view **59, 60** Eighth metasomal sternum in ventral and lateral views **61, 62** Genital capsule in dorsal and ventral views.

Floral records. Females have been collected on flowers of *Cassia* sp. (Fabaceae). Males have been collected on *Clowesia glaucoglossa* (Rchb.f.) Dodson, *C. thylaciochila* (Lem.) Dodson, and *Stanhopea hernandezii* (Kunth) Schltr. (Orchidaceae).

Comments. The two female paratypes as well as some female specimens from Morelos and Oaxaca have a distinctly large impunctate area just anterior to the median ocellus, but in specimens from Jalisco and Puebla this area is very reduced to nearly absent. Also, in some female specimens from these two states and Oaxaca, the punctures on the disc of T2 are sparser (1.0–2.0 times a puncture width) than in the female paratypes, and the sublateral carinae of the labrum are weak.



Figures 63–66. Female second metasomal tergum. 63 *E. oliveri* (paratype. Mexico: Guerrero, EMEC 1069136) 64 *E. simillima* (paratype. Mexico, Maguarichi, KUNHM-ENT 1091973) 65 *E. barthelli* (paratype. Mexico: Morelos, Tepoztlán, UNAM 01827) 66 *E. micheneri* (paratype. Mexico: Jalisco, Mascota, KUNHM-ENT 1121708).

Eufriesea simillima (Moure & Michener, 1965) stat. n.

Male, Figs 3, 12, 13, 67-78; Female, Figs 64, 79-83

Euplusia simillima Moure & Michener in Moure, 1965: 275 (Holotype: SEMC; ³, Mexico: Chihuahua, Maguarichi)

Diagnosis. Both sexes of this species can be easily recognized by their body color, which is predominantly dark purple, thus resembling *E. micheneri*. However, they can be easily separated from that species by the shorter glossa (not surpassing metatrochanter in *E. simillima* and reaching S1 in *E. micheneri*), shape of the subapical projection on the anterior surface of the male metatibia, male gonostylus, and metasoma with dark brown to black pubescence (apical terga and sterna with white setae at least laterally in *E. micheneri*). (See comparative diagnosis for *E. micheneri*)

Redescription. Holotype, 3: As described for *E. coerulescens* except as follows: Head width 6.0 mm; intertegular distance 4.9 mm; body length 15.4 mm; forewing length 14.3 mm. Glossa in repose reaching metatrochanter. Anterior margin of metatibia in inner view, above tibial spurs, not bordered laterally by an elevated ridge and thus not forming a distinct pocket, subapical projection above inner spur acute in profile; metabasitarsus about 2.2 times longer than broad. Hidden sterna and genitalia as in Figs 73–78.

Mandible black on apical two-thirds, basally purple as on labrum; face largely green, remainder of body purple with weak bluish-green hues on tegula and mesoscutum.



Figures 67–72. Male holotype of *E. simillima* (except paratype in Fig. 70; Mexico: Chihuahua, Barranca del Cobre, KUNHM-ENT 0504566). 67 Facial view 68 Dorsal habitus 69 Lateral habitus 70 Outer view of hind leg; 71 Dorsal view of mesoscutellum 72 Second metasomal tergum.

Gena with gray to black setae as on vertex. Mesosoma with black setae except whitish setae on outer surface of mesobasitarsus and off-white on anterior half of mesoscutum. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose on apical third; posterior patch 4.5 times longer than broad, subapically about as broad as distance between its medial margin and anterior margin of tibia.

 \bigcirc : Head width 6.2 mm; intertegular distance 5.2 mm; body length 14.6 mm; forewing length 13.5 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus 2.2 times longer than broad.

Coloration as in male but face blue with weak green hues, mesoscutum and tegula lacking green hues.

Pubescence black including on legs and metasoma.



Figures 73–78. Male terminalia of *E. simillima* (paratype. Mexico: Chihuahua, Barranca del Cobre, KUNHM-ENT 0504566). **73** Seventh metasomal sternum in ventral view **74, 75** Eighth metasomal sternum in ventral and lateral views **76–78** Genital capsule in dorsal, ventral, and lateral views.

Clypeus sometimes with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, contiguous punctures submedially, median longitudinal groove weak, lacking distinct row of dense pubescence. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.

Distribution. (Fig. 128) This species is known only from the western slope of the Cordillera of Chihuahua, Mexico.

Comments. This species is reinstated from synonymy with *E. coerulescens*. As indicated in the key to species and the diagnosis, both sexes of this species are morphologically distinct as well as geographically separated from *E. coerulescens*. Moure (1965: 275)



Figures 79–83. Female paratype of *E. simillima* (Mexico: Maguarichi, KUNHM-ENT 1091973). 79 Facial view 80 Dorsal habitus 81 Lateral habitus 82 Outer view of hind leg 83 Dorsal view of mesoscutellum.

indicated that the length of the interocellar distance is greater than the ocellocular distance in the male of *E. coerulescens* whereas such a distance was subequal in the male of *E. simillima*; however, such a difference was not observed in the lectotype of *E. coerulescens*, thus suggesting that Moure's observation may have not been based on the type specimen. We were only able to examine the holotype and paratypes from Maguarichi and Barranca del Cobre, Chihuahua, all deposited in SEMC and FSCA.

Eufriesea barthelli Gonzalez & Griswold, sp. n.

http://zoobank.org/65E0C67C-D1CF-4F66-8CD5-F82F1971769D Male, Figs 4, 14, 15, 84–95; Female, Figs 27, 65, 96–99

Diagnosis. This species shares with *E. micheneri* and *E. engeli* the subapical projection of the anterior margin of the male metatibia, which is formed by the upper ridge that borders the depressed area, and the dorsal lobe of the gonostylus, which is apically



Figures 84–89. Male holotype of *E. barthelli* (except paratype in Fig. 87, KUNHM-ENT 0504535).
84 Facial view 85 Dorsal habitus 86 Lateral habitus 87 Outer view of hind leg 88 Dorsal view of mesos-cutellum 89 Second metasomal tergum.

broad and covered by setae on its outer surface. It is most similar to *E. engeli* from southern Mexico. It can be separated from that species by the posterior felty patch of the mesotibia, which is subapically about as wide as the distance between its medial margin and the anterior margin of the tibia (broader in *E. engeli*), the finer and slightly sparser punctures on disc of T2, and its geographical distribution (*E. barthelli* occurs in central Mexico). The female of *E. barthelli* is similar to that of *E. oliveri* in



Figures 90–95. Male terminalia of *E. barthelli* (paratype. Mexico: Jalisco, Ajijic, KUNHM-ENT 0504535). 90 Seventh metasomal sternum in ventral view 91, 92 Eighth metasomal sternum in ventral and lateral views 93–95 Genital capsule in dorsal, ventral, and lateral views.

the long glossa, reaching at least to S2. However, they can be separated primarily by the punctation of the mesoscutellum. In *E. barthelli* it is finely, contiguously punctate throughout, with a distinct medial longitudinal groove that bears a row of dense setae. In *E. oliveri*, the mesoscutellum is coarsely, non-contiguously punctate, and with a weak medial longitudinal groove lacking a distinct row of dense pubescence.

Description. Holotype, 3: Head width 6.0 mm; intertegular distance 5.0 mm; body length 18.9 mm; forewing length 15.0 mm. Glossa in repose reaching S2. Anterior margin of metatibia in inner view with elevated ridge bordering depressed, smooth and hairless area above tibial spurs, upper margin of ridge medially projected, appear-



Figures 96–99. Female paratype of *E. barthelli* (Mexico: Morelos, Tepoztlán, UNAM 01827). 96 Facial view 97 Dorsal habitus 98 Lateral habitus 99 Outer view of hind leg.

ing as a spine in profile; metabasitarsus about twice as long as broad, inner surface near base weakly protuberant in frontal view, posterior margin gently convex, posterodistal margin broadly rounded. Hidden sterna and genitalia as in Figs 90–95; dorsal lobe of gonostylus broader apically than basally, distinctly setose on outer surface.

Mandible black on apical two-thirds, basally blue; labrum blue with weak green hues; remainder areas of head green with weak golden hues on face and bluish hues around ocelli and gena; antenna black. Mesosoma excluding legs predominantly green, with weak golden hues on mesoscutum anteriorly, disc of tegula and mesepisternum dorsally; weak bluish hues on axilla laterally, mesoscutellum, and propodeum basal and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and most of metatibia. Wing membrane infuscate, veins dark brown to black. T1–T4

green except distal margins blue to purple; T5–T7 blue-purple; sterna mainly green with weak blue-purple hues except S6 dark brown, with blue-purple hues barely visible basolaterally.

Head mainly with off-white setae, with gray to black setae on vertex. Mesosoma with gray to black setae except: whitish setae on posterior margin of meso- and metatibiae, outer surfaces of mesobasitarsus and metatibia; off-white on anterior half of meso-oscutum, and lateral face of mesepisternum. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia setose except on apical one-fourth; posterior patch 4.5 times longer than broad, subapically about as wide as distance between its medial margin and anterior margin of tibia. Metasoma with off-white to light brown setae, longer and denser on apical terga and sterna.

Clypeus without longitudinal medial depression. T2 with fine punctures on disc separated by at most a puncture width, distal margin narrow, about twice a puncture width.

 \bigcirc : Head width 6.3–6.5 mm; body length 16.5–17.8 mm; forewing length 15.0 mm. Metatibia with emargination on distal margin about half width of posterodistal angle; metabasitarsus twice as long as broad.

Blue with purple hues on mandible basally, labrum, dorsum of mesosoma, mesepisternum ventrally, propodeum, legs, discs of sterna, and marginal zones of terga.

Pubescence black, except off-white on sides of T2, T3–T6, S1–S5, and S6 basally. Pubescence denser on mesosoma, not obscuring integument.

Clypeus with median longitudinal ridge continuing onto supraclypeal area; labrum with basal, longitudinally elongate tubercle, sublateral carinae sometimes weak. Mesoscutellum with fine, contiguous punctures submedially, median longitudinal groove well defined, with distinct row of dense pubescence. T2 with punctures on disc sparser than in the male, separated by at least a puncture width, impunctate distal margin wide, at least three or four times a puncture width.

Holotype. ♂, Chalchijapa, Santa Maria, Chimalapa; Oaxaca, 28-v-1995. J.L. Salina, 100 m, Selva Alta Perennifolia, al vuelo JL-265. Red Ornitológica 09:00 h// Museo de Zoología, Hymenoptera 11086. Deposited in UNAM.

Paratypes. (n = 53, 29), Mexico: 13, km. 12, Autopista México-Cuautla, Tepoztlán; Morelos. 30/06/1996, I. Hinojosa, HD-755. 14:20 H, 1650 m. 18°58'24"N, 99°04'57"W, Cultivo de temporal, s/*Podranea ricasoliana | #* 02290 (UNAM); *idem*, 13, 13/07/1996, O. Yáñez, OY-752, 13:30 H / # 02310 (UNAM); *idem*, 19, 10/11/1996, H. Hinojosa, HD-1334, 12:55 H, s/*Tithonia tubaeiformis | #* 02709 (UNAM); *idem*, 19, 08/10/1995, O. Yáñez, OY-169, 12:10 H, atraída por esencia (mezcla) / # 01827 (UNAM); 13, mts. N. Ajijic, JAL [Jalisco]., MEX. to 5300', 23 July, 1964, WLNutting & sons, scrub forest // BBSL849647 (BBSL); 13, *idem* (FSCA); 13, Canyon N. Ajijic, JAL. MEX. to 5400', 22 July 1964, WLNutting & sons, scrub forest / SM0504535, KUNHM-ENT (SEMC).

Additional material. (n = 6, not designated as paratypes) 1, ECO-TAP-E-95712, Mex., Jal., [Jalisco], Tamazula, Agua Zarca, 1829 m, 19.82484N, 103.27449W, 31/10/2012, 10:00, Col. Jorge Mérida (ECOSUR); 1, Mexico: Jalisco, 13km SE La Manzanilla, La Loma Alla, 31-x-1990, C.M. Estrada #69 / SM0730193, KUNHM-ENT (SEMC); 1 \bigcirc , Museum Paris, Mexique, Etat de Jalisco, L.Diguet, 1900 (MNHN); 1 \bigcirc , Ahuacatlan, Nay. [**Nayarit**], Mex., vii-18-22-51 / H.E. Evans, collector / SM0504525, KUNHM-ENT (SEMC); 1 \bigcirc , 3mi W. Jacona, Mich [**Michoacan**], vii-18-53, 5300ft/ Univ. Kans. Mex. Expedition / SM0504527, KUNHM-ENT (SEMC); 1 \bigcirc , Mexico, **Morelos**, 4 mi. SW Yautepec, 2 July 1961, 3800', C.D. Michener, on flowers of *Cassia* sp. (FSCA).

Variation. The blue-purple coloration is strong in both males from Morelos and one of the males from Jalisco. In particular, one of the males from Morelos (UNAM, #02290) has extensive blue hues on all tagmata.

Etymology. This species is dedicated to our friend and colleague Dr. John Barthell (University of Central Oklahoma) for his contributions to be ecology and efforts to promote undergraduate research on bees.

Distribution. Central Mexico: Jalisco, Michoacán, Morelos, Nayarit, Oaxaca.

Eufriesea engeli Gonzalez & Griswold, sp. n.

http://zoobank.org/0339D195-AC0A-4F3B-8F74-28C033F2AFA6 Male, Figs 5, 16, 17, 26, 100–111

Diagnosis. This species is known only from the male sex. It along with *E. micheneri* and E. barthelli belong to a group of species that differs from other concolorous metallic blue to dark green Mexican Eufriesea by the anterior margin of metatibia in inner view without a distinct spine-like subapical projection above inner spur, but upper margin of distinctly depressed area projected medially, thus often appearing spine-like in profile (Figs 14–19) and the genitalia with dorsal lobe of gonostylus apically broad, distinctly setose on outer surface (Fig. 26). It can be separated from *E. micheneri* by the metabasitarsus broadly rounded posterodistally (angled in *E. micheneri*), T2 with punctures separated by at most a puncture width on disc (punctures separated by 1-2 times a puncture width in *E. micheneri*), and by the body color (largely metallic green in the male of *E. engeli* vs. dark blue with violet hues in both sexes of *E. micheneri*). From E. barthelli it can be separated by the posterior felty patch of mesotibia, which is subapically broader than the distance between its medial margin and anterior margin of tibia (narrower in E. barthelli), punctation of T2 (punctures coarser and nearly contiguous in *E. engeli*, finer and slightly sparser in *E. barthelli*), and its geographical distribution (E. engeli occurs in southern Mexico whereas E. barthelli in central Mexico).

Description. Holotype, 3: As described for *E. barthelli* except as follows: Head width 5.9 mm; body length 16.7 mm; intertegular distance 4.6 mm; forewing length 14.4 mm. Glossa in repose reaching S2. Hidden sterna and genitalia as in Figs 106–111.

Gena mostly green. Mesosoma excluding legs predominantly green, with weak golden hues on mesoscutum anteriorly, disc of tegula and mesepisternum dorsally; weak bluish hues on axilla laterally, mesepisternum ventrally, and propodeum basal



Figures 100–105. Male holotype of *E. engeli* (except paratype in Fig. 103, KUNHM-ENT 0504531). 100 Facial view 101 Dorsal habitus 102 Lateral habitus 103 Outer view of hind leg 104 Dorsal view of mesoscutellum 105 Second metasomal tergum.

and laterally. Legs mostly blue-purple except green on pro- and mesotibiae anteriorly and metatibia basally. T1–T4 green except distal margins blue to purple; T5–T7 blue



Figures 106–111. Male terminalia of *E. engeli* (paratype, KUNHM-ENT 0504531). 106 Seventh metasomal sternum in ventral view 107, 108 Eighth metasomal sternum in ventral and lateral views 109–111 Genital capsule in dorsal, ventral, and lateral views.

with purple marginal zones; sterna mainly green except S6 dark brown, with blue to purple hues on apical sterna.

Mesosoma with mostly off-white setae except gray to black setae on pronotum, posterior half of mesoscutum, mesoscutellum, mesepisternum ventrally, metepisternum, and propodeum. Legs with off-white setae, except gray to dark brown setae on inner surfaces of tibiae, basitarsi, and tarsi of all legs. Mesotibia with posterior patch subapically broader than distance between its medial margin and anterior margin of tibia.

Disc of T2 with coarser and denser punctures on disc than in *E. barthelli*, punctures separated by less than a puncture width to nearly contiguous.

Female. Unknown.

Holotype. \mathcal{J} , Mexico: Chiapas, Sumidero Cnyn. [Canyon] Nat. [National] Pk. [Park]. vi-12-1991., B. Ratcliffe, J. Ashe, M. Jameson colls. // SM0504516, KUN-HM-ENT. Deposited in SEMC.

Paratypes. Eight males with the same data as the holotype and also deposited in SEMC, but with the following barcode label numbers: SM0504513–15, -17, -18, -20, -31, and 0748219.

Additional material. ($n = 73^\circ$, not designated as paratypes) 13°, Mexico: Chiapas, L.[Lago] Montebello, 20 v 1970, 1410, R.L. Dressler (FSCA); 53°, Tuxtla Gutierrez, Chiapas, Mexico, C. Dodson, 7-21-1968, No. 310, Cineole (FSCA); 13°, Mexico: Chis [Chiapas], Tuxtla Gutierrez, Cineole, C.H. Dodson, 310, 19-23 VII 1968 (FSCA).

Etymology. This species is dedicated to our friend and colleague Dr. Michael S. Engel (University of Kansas), in recognition of his significant contributions to systematic melittology.

Distribution. (Fig. 128) This species is known only from Chiapas, southern Mexico, but can be expected to be found in Guatemala since Lago Montebello is on the border with Guatemala.

Comments. In some paratypes the golden hues are more conspicuous on the face and mesoscutum and the subapical projection of the anterior surface of the metatibia is more acutely projected than the holotype. The tongue has been pulled out in all specimens, including the holotype, and thus it appears to surpass the apex of metasoma. The tongue length provided in the description is based on measuring the galea alone and confirmed by the Lago Montebello specimen where the tongue is in repose.

Eufriesea micheneri Ayala & Engel, 2008

Male, Figs 6, 18, 19, 20, 112–123; Female, Figs 30, 32, 66, 124–127

Eufriesea micheneri Ayala & Engel, 2008: 228 (Holotype: UNAM; ♂, Mexico: Jalisco, Mascota)

Diagnosis. Superficially this species resembles *E. simillima* in that both sexes are primarily blue with purple hues. In addition to their geographical separation (*E. simillima* occurs in the Sierra Madre de Occidental whereas *E. micheneri* occupies western parts of the Transverse Volcanic Belt), it can be separated by the length of the tongue (reaching S2 in *E. micheneri* and only the metatrochanter in *E. simillima*), the subapical projection of the anterior margin of the male metatibia (formed by the upper portion of the ridge that borders the depressed area in *E. micheneri* and by the medial portion of the ridge, and thus located above the inner spur, in *E. simillima*), and by the dorsal lobe of gonostylus (apically about as broad as its base and largely bare on its outer surface in *E. simillima* and apically broad and setose on outer surface in *E. micheneri*). From *E. barthelli* and *E. engeli* it can be separated by T2 with sparser punctures on disc (contiguous or separated by at most a puncture width in *E. barthelli* and *E. engeli*),



Figures 112–117. Male paratype of *E. micheneri* (Mexico: Jalisco, Mascota, KUNHM-ENT 1121713). **112** Facial view **113** Lateral habitus **114** Dorsal habitus; **115** Outer view of hind leg **116** Ventral view of metatrochanter with arrow pointing to distinct projection **117** Second metasomal tergum.

metabasitarsus with posterodistal margin angled (broadly rounded in *E. barthelli* and *E. engeli*) and pubescence of mesotibia, between the medial margin of posterior felty



Figures 118–123. Male terminalia of *E. micheneri* (paratype. Mexico: Jalisco, Talpa, KUNHM-ENT 1121712). **118** Seventh metasomal sternum in ventral view **119, 120** Eighth metasomal sternum in ventral and lateral views **121–123** Genital capsule in dorsal, ventral, and lateral views.

patch and anterior margin of tibia (presence on basal half in *E. micheneri* and basal two-thirds in *E. barthelli* and *E. engeli*).

Morphology. ∂, As described for *E. engeli* except as follows: Head width 6.3 mm; body length 17.8 mm; forewing length 16.3 mm. Metabasitarsus with inner surface near base strongly protuberant in frontal view, posterodistal margin angled. Hidden sterna and genitalia as in Figs 118–123.

Mandible black with green, blue, and purple hues on basal third as on labrum; face green with golden and blue hues; vertex and gena blue with purple hues. Mesoand metasoma blue with green hues on anterior two-thirds of mesoscutum and disc of



Figures 124–127. Female paratype of *E. Micheneri* (Mexico: Jalisco, Mascota, KUNHM-ENT 1121708). 124 Facial view 125 Lateral habitus 126 Dorsal habitus 127 Dorsal view of mesoscutellum.

tegula, weak purple hues on remainder areas of mesosoma and marginal zones of terga and sterna.

Face with off-white setae, vertex and gena with gray to black setae. Mesosoma with gray to black setae except on outer surfaces of mesobasitarsi and distitarsi. Mesotibia with area between medial margin of posterior patch and anterior margin of tibia bare on distal half; posterior patch subapically about as broad as distance between its medial margin and anterior margin of tibia. Metasoma with gray setae on terga, white or off-white on S3–S5.

Disc of T2 with finer and sparser punctures than on *E. barthelli*, punctures separated by at least a puncture width.

Q: Head width 6.0 mm; body length 17.5 mm; forewing length 14.7 mm. Coloration as in the female of *E. barthelli* but with stronger purple hues. Pubescence black, with whitish on sides of T4 and T5 and discs of S4 and S5 in some specimens. Mesos-



Figure 128. Collection localities for species of *Eufriesea* of the *coerulescens* group.

cutellum with poorly defined row of dense pubescence on median longitudinal groove. T2 with finer, sparser punctures than on *E. barthelli*.

Distribution. (Fig. 128) Mexico: Durango, Jalisco, Michoacán, Nayarit. This species appears to be restricted to mid elevation oak and pine forests in the western parts of the Transverse Volcanic Belt.

Material examined. In addition to the paratypes deposited in SEMC (five males and one female from Mascota, Jaslico, and one male from Santa Tereresa, Nayarit), we also examined the following two females deposited in ECOSUR: 1♀, ECO-TAP-E-118160, Méx., Dgo. [**Durango**], San Dimas, 1760 m, 24,53210N, 105,81339W, 2/10/2013, 10:00, Col. Liliana Tlapaya; 1♀, ECO-TAP-E-102831, Mex., Mich. [**Michoacán**], Morelia, J. del Monte, 2172 m, 19,63395N, 101,14644W, 4/7/2013, 10:05, Col. Oscar Martínez López.

Floral records. Females have been collected on flowers of Salvia sp. (Lamiaceae).



Figure 129. Potential distribution for all species of *Eufriesea* of the *coerulescens* group combined (top map) and for *E. coerulescens* alone (bottom map) with collection localities.

Comments. Some of the specimens listed under this species by Ayala and Engel (2008) in the section "additional material examined" correspond to *E. barthelli*. These two species partially overlap in distribution.

Known and potential distribution

All examined specimens of the *coerulescens* species group are from Mexico, except for the two males of *E. coerulescens* collected in the USA, over 420 km north of the northernmost known locality for this species (Chihuahua, General Trias). Except for *E. coerulescens*, which occurs along pine-oak forests of the Sierra Madre Oriental from Coahuila to Hidalgo, as well as in Durango and Chihuahua, all species of the *coerulescens* group appear to be geographically localized (Fig. 128). *Eufriesea olivieri* and *E. barthelli* appear to be restricted to the Sierra Madre del Sur, *E. simillima* to the northern Sierra Madre de Occidental, *E. micheneri* to western areas of the Transverse Volcanic Belt, and *E. engeli* to deciduous rain forests in southern Mexico.

The potential distribution maps obtained for *E. coerulescens* as well as for all occurrence records of all species combined were largely similar in their general predictions (Fig. 129). Model evaluation showed high scores of performance for both models (*coerulescens* species group: AUC \bar{x} = 0.828, 0.787–0.854; ROC \bar{x} = 1.262, 1.009–1.918. *Eufriesea coerulescens*: AUC \bar{x} = 0.908, 0.874–0.954; ROC \bar{x} = 1.553, 0.964–1.916). In both models, the two localities in the USA where *E. coerulescens* was collected show a complete absence of habitat suitability. However, high suitability of habitats (>0.3) in the USA for *E. coerulescens* occurs in some locations in Florida while inclusion of all species in the group expands suitable habitat to much of the southeastern USA. The models also suggest high suitability of habitats across the Caribbean as well as in other regions in Mexico and Central America.

Discussion

Herein we circumscribe the species in the *coerulescens* group and confirm that the two male specimens of *Eufriesea* from the USA are *E. coerulescens*. We also provide a fully illustrated account of the species, comparative diagnoses, and an updated key to the Mexican species of *Eufriesea* to facilitate their identification. Both sexes of the three new species described here are superficially almost identical to either E. coerulescens or E. micheneri, and were discovered while examining specimens standing under these names. They can reliably be distinguished by differences in the length of the glossa, punctation of the male second tergum and female mesoscutellum, and the shape of the posterior felty patch of the male mesotibia. The dark female specimens from Islas Marias of Nayarit State, located 112 km from the coast, mentioned by Ayala and Engel (2008), might also correspond to another undescribed species. However, these specimens were not available for study. Kimsey (1982) was aware of variations among the specimens she examined and determined as E. coerulescens, but considering the small number of specimens available, she appropriately regarded them as variants. For example, in addition to mentioning the differences in the integumental coloration, she also pointed out differences in the length and width as well as the distance between the apical lobes of the male S7 of E. coerulescens (e.g., Figs 40 and 90). Such differences among the material she examined correspond to the species newly defined herein.

Species distribution modeling (SDM) based on observed occurrences are good tools for predicting the potential distribution of exotic species including bees (e.g., Hi-nojosa-Díaz et al. 2005, 2009, Gonzalez et al. 2010, Silva et al. 2014). Incorporating biotic interactions in these models, such as plant-bee relationships, is expected to have a major influence on the modeled distribution. However, host plant associations are not always available or reliable for bees, and available studies suggest that they do not

significantly improve the algorithm's ability to predict the distribution (e.g., Silva et al. 2014). A few plant records are available for the species of the *coerulescens* group, but most are determined to the genus level and do not distinguish between bees collecting pollen versus nectar. Thus, these records may not represent pollen host associations.

Our models had high AUC and ROC values, which indicate high performance and quality. According to our analyses, the males of *E. coerulescens* collected in the Guadalupe Mountains of western Texas and southeastern New Mexico, USA, are likely long-distance transient vagrants, as suggested by the complete absence of predicted suitable habitat for stable populations of this species to persist in that area. The model using the occurrence records of *E. coerulescens* alone (Fig. 129) predicts habitat suitability (0.169–0.298) in some areas in western Texas and across the state of Coahuila with a similar value to that of the northernmost known locality for this species (Chihuahua, General Trias). Such areas ought to be sampled to determine if populations of the species exist there. The same should be done in western Chihuahua and southeastern Sonora, where conditions appear to be suitable for this species. The model also predicts some areas of southern New Mexico, Arizona, and Florida with high values of habitat suitability, which suggests that the species has the potential to occupy these areas if it eventually reaches there (Fig. 129).

Our model also indicates high habitat suitability (>0.425) for *E. coerulescens* in western and southern Mexico, as well as in Guatemala, El Salvador, Honduras, Nicaragua, northwestern Costa Rica, and part of Panama. This suggests the possibility of a broader overlap in its distribution with the other species of the group in Mexico than currently known and opens up the possibility that some of the literature records for this species from Central America might be correct. Interestingly, our analyses also show the presence of suitable habitats for *E. coerulescens* in the Caribbean, similar to the potential distribution models developed for the other two adventive species of orchid bees in the USA (Hinojosa-Díaz et al. 2009). Except for one species of *Euglossa* from Jamaica, orchid bees are otherwise absent from the modern melittological fauna of the Caribbean, although two fossil species (one of *Euglossa* and one of *Eufriesea*) have been recorded from the island of Hispaniola (Engel 1999).

Acknowledgements

We thank David Roubik for comments and suggestions that helped us improved this work, and the curators, collection managers, and staff personnel of the collections from which we borrowed specimens. Agnièle Touret-Alby (Muséum National d'Historie Naturelle, France) kindly arranged the loan of the type of *Eufriesea coerulescens*. This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

References

- Ayala R, Engel M (2008) A new species of *Eufriesea* from Jalisco, México, with a key to Mexican species of the genus (Hymenoptera: Apidae). Beiträge zur Entomologie 58: 227–237.
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J, Villalobos F (2011) The crucial role of the accessible area in ecological niche modelling and species distribution modelling. Ecological Modelling 222: 1810–1819 https://doi. org/10.1016/j.ecolmodel.2011.02.011
- Búrquez A (1997) Distributional limits of euglossine and meliponine bees (Hymenoptera: Apidae) in northwestern Mexico. Pan-Pacific Entomologist 73(2): 137–140.
- Cockerell TDA (1908) Notes on the bee-genus *Exaerete*. Psyche 15: 41–42. https://doi. org/10.1155/1908/10750
- Engel MS (1999) The first fossil of *Euglossa* and phylogeny of the orchid bees (Hymenoptera: Apidae; Euglossini). American Museum Novitates 3272: 1–14.
- Faria Jr LRR (2009) Sobre as abelhas das orquídeas (Hymenoptera, Euglossina): reavaliação das relações entre os géneros da subtribo, filogenia de *Eufriesea* Cockerell e análise da estrutura das interações entre machos de Euglossina e plantas fornecedoras de compostos aromáticos. PhD Dissertation, Universidade Federal do Paraná, Curitiba, 330 pp.
- Gonzalez VH, Engel MS (2004) The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. Entomologische Abhandlungen 62: 65–75.
- Gonzalez VH, Koch JB, Griswold T (2010) Anthidium vigintiduopunctatum Friese (Hymenoptera: Megachilidae): the elusive "dwarf bee" of the Galápagos Archipelago? Biological Invasions 12(8): 2381–2383. https://doi.org/10.1007/s10530-009-9651-9
- Gonzalez VH, Velez-Ruiz RI, Engel MS (2014) A new paracolletine bee from Colombia (Hymenoptera: Colletidae), with an updated checklist of the tropical Andean bee fauna. Journal of Melittology 43: 1–26. https://doi.org/10.17161/jom.v0i43.4812
- Griswold T, Herndon JD, Gonzalez VH (2015) First record of the orchid bee genus *Eufriesea* Cockerell (Hymenoptera: Apidae: Euglossini) in the United States. Zootaxa 3957: 342–346. https://doi.org/10.11646/zootaxa.3957.3.7
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29(5): 773–785. https://doi.org/10.1111/j.0906-7590.2006.04700.x
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25(15): 1965–1978. https://doi.org/10.1002/joc.1276
- Hinojosa-Díaz IA, Feria-Arroyo TP, Engel MS (2009) Potential distribution of orchid bees outside their native range: The cases of *Eulaema polychroma* (Mocsáry) and *Euglossa viridissima* Friese in the USA (Hymenoptera: Apidae). Diversity and Distributions 15: 421–428. https://doi.org/10.1111/j.1472-4642.2008.00549.x
- Hinojosa-Díaz IA, Yáñez-Ordóñez O, Chen G, Peterson AT, Engel MS (2005) The North American invasion of the giant resin bee (Hymenoptera: Megachilidae). Journal of Hymenoptera Research 14(1): 69–77.

- Kimsey L (1982) Systematics of bees of the genus *Eufriesea* (Hymenoptera, Apidae). University of California Publications in Entomology 95: 1–125.
- Lepeletier de Saint-Fargeau ALM (1841) Histoire Naturelle des Insectes. Vol. 2. Hyménoptères. Roret, Paris, 680 pp.
- Michener CD (2007) The Bees of the World [2nd Edition]. Johns Hopkins University Press, Baltimore, 953 pp.
- Minckley R, Reyes S (1996) Capture of the orchid bee, *Eulaema polychroma* (Friese) (Apidae: Euglossini) in Arizona, with notes on northern distributions of other Mesoamerican bees. Journal of the Kansas Entomological Society 69(1): 102–104.
- Moure JS (1965) Some new species of Euglossinae bees (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 38: 266–277.
- Moure JS (1967) A check-list of the known euglossine bees (Hymenoptera, Apidae). Atas do Simpósio Sôbre a Biota Amazônica, Zoologia 5: 395–415.
- Moure JS, Melo GAR, Faria Jr LRR (2007) Euglossini Latreille, 1802. In: Moure JS, Urban D, Melo GAR (Eds) Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. On-line version. http:// www.moure.cria.org.br/catalogue [accessed 20 March 2017]
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson TA (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34(1): 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x
- Pemberton RW, Wheeler GS (2006) Orchid bees don't need orchids: evidence from the naturalization of an orchid bee in Florida. Ecology 87: 1995–2001. https://doi.org/10.1890/0012-9658(2006)87[1995:OBDNOE]2.0.CO;2
- Perger R (2015) The highest known euglossine bee community from a garden in the Bolivian Andes (Hymenoptera, Apidae, Euglossini). Journal of Hymenoptera Research 45: 65–73. https://doi.org/10.3897/JHR.45.5003
- Peterson AT, Papeş M, Eaton M (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and MaxEnt. Ecography 30: 550–560. https:// doi.org/10.1111/j.0906-7590.2007.05102.x
- Peterson AT, Papeş M, Soberón M (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213(1): 63–72. https:// doi.org/10.1016/j.ecolmodel.2007.11.008
- Phillips SJ, Anderson RP, Schapire RP (2006) Maximum entropy modelling of species geographic distributions. Ecological Modelling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026
- Ramírez SR, Roubik DW, Skov C, Pierce NE (2010) Phylogeny, diversification patterns and historical biogeography of euglossine orchid bees (Hymenoptera: Apidae). Biological Journal of the Linnean Society 100: 552–572. https://doi.org/10.1111/j.1095-8312.2010.01440.x
- Roubik DW, Hanson PE (2004) Abejas de Orquídeas de la América Tropical: Biología y Guía de Campo. Instituto Nacional de Biodiversidad, Santa Domingo de Heredia, Costa Rica, 370 pp.

- Silva DP, Gonzalez VH, Melo GAR, Lucia M, Alvarez LJ, De Marco P (2014) Seeking the flowers for the bees: Integrating biotic interactions into niche models to assess the distribution of the exotic bee species *Lithurgus huberi* in South America. Ecological Modelling 273: 200–209. https://doi.org/10.1016/j.ecolmodel.2013.11.016
- Skov C, Wiley J (2005) Establishment of the Neotropical orchid bee *Euglossa viridissima* (Hymenoptera: Apidae) in southern Florida. Florida Entomologist 88: 225–227. https://doi.org/10.1653/0015-4040(2005)088[0225:EOTNOB]2.0.CO;2
- Warren DL, Turelli M (2009) ENMTools User Manual v1.0. http://www.danwarren.net
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. Diversity and Distributions 14(5): 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

RESEARCH ARTICLE



An unusual new species of Hedychridium Abeille from Africa

Lynn S. Kimsey¹, Robert S. Copeland²

1 Bohart Museum of Entomology, University of California, Davis, California 95616, USA **2** International Centre of Insect Physiology and Ecology, Nairobi, Kenya, and Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Corresponding author: Lynn S. Kimsey (lskimsey@ucdavis.edu)

Academic editor: M. Ohl Received 8 February 2017 Accepted 27 February 2017 Publishe	ed 28 April 2017
http://zoobank.org/99D93520-E8A2-482E-9858-81A94F0E9790	

Citation: Kimsey LS, Copeland RS (2017) An unusual new species of *Hedychridium* Abeille from Africa. Journal of Hymenoptera Research 55: 103–108. https://doi.org/10.3897/jhr.55.12191

Abstract

The species *Hedychridium buffingtoni* Kimsey & Copeland, **sp. n**. is described from two male specimens collected in Kasaala, Kenya. They are distinguished from other species of *Hedychridium* by the strongly transversely carinate metasomal terga II and III, edentate apical rim of tergum III, strongly lobed propodeal tooth, ecarinate frons and darkly pigmented cuspis.

Keywords

Africa, Kenya, eastern Sahel, Kasaala, Acrotoma, Buyssonia

Introduction

Hedychridium Abeille de Perrin, 1878 is the second most speciose genus of Chrysididae, after *Chrysis* Linnaeus, 1767. In Africa a number of *Hedychridium* species exhibit a diversity of unusual modifications including a transverse carina on the frons, ridged metasomal terga, dentate apical metasomal terga, and lobate propodeal teeth. Many of these oddly modified species were at one time placed in the genera *Acrotoma* Mocsáry, 1902 and *Buyssonia* Mocsáry, 1902. *Acrotoma* proved to be a junior homonym of the gastropod genus *Acrotoma* Boettger, 1881. Kimsey and Bohart (1991) synonymized *Acrotoma* Mocsáry and *Buyssonia* Mocsáry under the genus *Hedychridium*. Only 45 species of *Hedychridium* have been described from continental subSaharan Africa (see Madl and Rosa 2012), and the vast majority of the described species are from southern Africa, 18 of which were described by Kimsey (1988). Given the diversity of habitats and potential hosts this seems to be a substantial underestimate of the actual species diversity of the genus in Africa.

The new species described below belongs to the *H. dybowskii* group of Kimsey and Bohart (1991). It exhibits extreme modifications of some of the more unusual features seen in African species, particularly modifications of the metasomal terga.

Materials and methods

The type specimens are deposited in the National Museums of Kenya in Nairobi. Terminology follows Kimsey and Bohart (1991). Images were taken with a Leica MC 190 HD camera, mounted on a Leica MZ75 stereomicroscope, using the Leica Application Suite version 4.8.0 and image stacking software Zerene Stacker 64 bit version 1.04.

Taxonomy

Hedychridium buffingtoni Kimsey & Copeland, sp. n. http://zoobank.org/748558CD-40A1-46FA-917D-F9D927D5E86F Figs 1–7

Diagnosis. This species is characterized by the lack of a transverse frontal carina, strongly lobate propodeal tooth, sharply angulate mesopleuron, expanded and ventrally carinate forefemur, metasomal tergum II with an elevated medial carina, elevated U-shaped subbasal welt, a subapical transverse, punctate ridge, metasomal tergum III with a subapical ridge and edentate apical rim. It resembles *H. arnoldi* (Edney, 1940) based on the very short malar space. It belongs to the. *H. dybowskii* group of species, but can be distinguished from other members of the group, which includes *H. arnoldi*, *H. braunsii* (Mocsáry, 1902) and *H. dybowskii* du Buysson, 1898 by the edentate apical rim of metasomal tergum III and the lack of a transverse frontal carina on the face. The darkly pigmented cuspis of the male genitalia is unusual in *Hedychridium*.

Male description. Body (Figs 5–7): length 3.5–4.0 mm. Head (Fig. 1): frons without transverse frontal carina, with large, contiguous punctures, changing abruptly in scapal basin to tiny punctures separated by 0.5–1.0 puncture diameters, basin covered by decumbent silvery setae, with medial, asetose band of fine, transverse carinae occupying medial fourth; distance between midocellus and antennal sockets equal to narrowest interocular distance; subantennal distance 1 midocellus diameter long; malar space 0.1 midocellar diameter; antenna (Fig. 2), flagellomeres I, II 1.3x as long as broad; flagellomeres III and IV as long as broad. Mesosoma: pronotal punctures large, separated by 0.2–0.5 puncture diameter, intervening areas finely shagreened; scutum



Figures 1–7. *Hedychridium buffingtoni* Kimsey & Copeland, sp. n. I Front view of face 2 Lateral view of antenna 3 Oblique lateral view of propodeal tooth. 4 Ventral view of male genital capsule 5 Lateral view of body 6 Dorsal view of metasoma 7 Dorsal view of body.

with punctures separated by 0.5–1.0 puncture diameters, punctures smaller and more widely separated between notauli, finely shagreened in between; scutellum with large punctures separated by 0.2–0.5 puncture diameters, finely shagreened in between; mesopleuron sharply angulate with well-developed omaulus, scrobal sulcus and verticaulus, posterior surface finely rugose; metanotum angulate in lateral view; forefemur subbasally expanded and flattened, with ventral carina; propodeal tooth with large ventral lobe (Fig. 3); hindfemur with slightly depressed elongate dark brown triangular patch on inner surface; forewing Rs about one-third as long as R1; medial vein broadly

curved reaching M+Cu at oblique angle. Metasoma: tergum II with well-developed longitudinal medial ridge, basal third with transverse U-shaped, punctate ridge or welt opening basally, with subapical, transverse, punctate ridge or swelling becoming narrowly V-shaped medially; tergum III without medial ridge or apical dentition, with transverse, punctate subapical ridge, apical margin translucent brown. Color: body overall dark metallic blue, becoming purplish on scutellum between notauli; legs metallic blue, except tarsi yellowish; wing veins dark brown, membrane untinted; tegula brown, external metasomal sterna metallic blue. Male genitalia (Fig. 4); cuspis darkly pigmented, blackish; digitus broadest subapically; paramere apically rounded, with short, marginal setae.

Female. unknown.

Type material. Holotype male; Kenya: Eastern Prov., Kasaala area, 733 m, 2.07836°S, 38.22517°E, Malaise trap, 5–19 July 2015, R. Copeland, No. 0693–0722 [image numbers], (National Museums of Kenya, Nairobi). Paratype male: same data as holotype, except 8–22 Oct. 2015, No. 3083–3103 [image numbers] (National Museums of Kenya, Nairobi).

Etymology. This species is named for our friend Matt Buffington, expert microhymenopterist with whom RSC has had the pleasure of working both in Kenya and in the United States.

Remarks. This is a very unusual looking Hedychridium due to the strongly triridged metasomal tergum II. In addition, it is unusual for a species to be collected in both the dry (Fig. 9) and wet (Fig. 10) seasons in a site, but this one was. The holotype and paratype were collected in a Malaise trap in the Kasaala area of eastern Kenya (Figs 8-10). This area falls within the easternmost extension of the Sahel which extends southward through most of eastern Kenya and into northeastern Tanzania (Coe et al. 1999). According to Pratt et al. (1966) it belongs in ecological zones IV/V, semiarid to arid habitats with only "marginal agricultural potential", and where natural vegetation includes dry woodland and bushland, usually characterized by the presence Acacia and Commiphora species, and often shrubby. These zones correspond to Thornthwaite's (1948) moisture indices of -20 to -40 and -40 to -60 for semi-arid and arid climates, respectively. Rainfall data is not available for the Kasaala area but the region is known for its hot climate and marginal rainfall. Maize is often planted, but because it is associated with a high percentage of crop failure, it is usually cultivated together with sorghum (Sorghum bicolor (L.) Moench), finger millet (Eleusine coracana Gaertn.) and pearl millet (Pennisetum glaucum (L.)R.Br.), grains suitable for areas with low rainfall and relatively high evaporation rates, and with the similarly drought-resistant legume, pigeon pea (Cajanus cajan (L.) Millsp.). The area in which the Malaise trap was set has remnant and disturbed plots of mixed woodland/bushland and wooded grassland (Pratt et al. 1966), with considerable farmland separating these plots. Vegetation is dominated by deciduous, often thorny, plants, providing a stark contrast when viewed during dry or wet periods (Figs 9–10).



Figure 8–10. 8 Map of collecting site in Kasaala, Kenya **9–10** Malaise trap where *Hedychridium buffingtoni* Kimsey & Copeland was collected in the dry season (**9**) and wet season (**10**).

Acknowledgements

We thank Mr. Mulu Musingila for his work in maintaining the Kasaala Malaise trap in excellent condition and for letting RSC place the trap on his property. RSC thanks the director general of ICIPE for her continuing support of our programme on insect diversity.

References

- Coe M, Volleson K, Abdallah R, Mboya EI (1999) Vegetation and habitats of Mkomazi. In: Coe M, McWilliam N, Stone G, Parker M (Eds) Mkomazi: the ecology, biodiversity and conservation of a Tanzanian savanna. Royal Geographic Society (with the Institute of British Geographers), London, 117–144.
- Kimsey LS (1988) *Hedychridium* of the Afrotropical Region. Journal of the Entomological Society of Southern Africa 51(2): 193–205.

- Kimsey LS, Bohart RM (1990 (1991)) The Chrysidid Wasps of the World. Oxford University Press, ix+652 pp.
- Madl M, Rosa P (2012) A catalog of the Chrysididae of the Ethiopian Region, excluding Malagasy Subregion. Linzer Biologische Beiträge 44(1): 5–169.
- Pratt DJ, Greenway PJ, Gwynne MD (1966) A Classification of East African Rangeland, with an Appendix on Terminology. Journal of Applied Ecology 3(2): 369–382. https://doi. org/10.2307/2401259
- Thornthwaite CW (1948) An approach toward a rational classification of climate. Geographical Review 38(1): 55–94. https://doi.org/10.2307/210739
RESEARCH ARTICLE



Morphology and ultrastructure of the Dufour gland of Myzinum sp. (Tiphiidae)

Johan Billen¹, Cíntia Eleonora Lopes Justino², Fernando Henrique Carnimeo², Fernando Barbosa Noll²

l Zoological Institute, KU Leuven, Naamsestraat 59, B-3000 Leuven, Belgium **2** Universidade Estadual Paulista, Depto. Zoologia e Botânica, Cristóvão Colombo, 2265, 15054-000, São José do Rio Preto, SP, Brazil

Corresponding author: Johan Billen (Johan.Billen@kuleuven.be)

Academic editor: M. Ohl	Received 23 December 2016 Accepted 3 March 2017 Published 28 April 2017

Citation: Billen J, Justino CEL, Carnimeo FH, Noll FB (2017) Morphology and ultrastructure of the Dufour gland of *Myzinum* sp. (Tiphiidae). Journal of Hymenoptera Research 55: 109–119. https://doi.org/10.3897/jhr.55.11618

Abstract

The Dufour gland of two *Myzinum* females was studied with light and electron microscopy, and is formed by a large sac lined with a monolayered secretory epithelium. The epithelium displays a crenellate appearance, which is the result of the peculiar shape of the secretory cells, that have a cupola-like central portion and a more flattened appearance in the contact region with other cells. The ultrastructural organization is indicative for the elaboration of a non-proteinaceous secretion. The gland opens ventrally to the sting base, but does not open through the sting, as does the venom gland duct. The sting itself is dorsally curved, which may be a functional adaptation to facilitate stinging large beetle larvae from above, as these are the common hosts for tiphiid wasps.

Keywords

Morphology, ultrastructure, Dufour gland, curved sting, Myzinum, Tiphiidae

Introduction

Social insects no doubt are the champions of having the most elaborate exocrine system among the hexapods, with 149 known glands (Billen and Šobotník 2015). As only 20 of these occur in termites, it is clear that this impressive gland variety is especially prominent in the social Hymenoptera, with 84 glands in ants, 53 in bees and bumblebees,

and 49 in wasps (Billen and Šobotník 2015). Much less studied is the exocrine system of solitary Hymenoptera, with almost nothing known of the glands in the Tiphiidae. Tiphiidae comprises seven subfamilies, of which the Myzininae are distributed around the world and are one of the most diverse groups of Tiphiidae (Kimsey 1991). The genus Myzinum Latreille is still largely unknown regarding its biology and taxonomy (Kimsey 2009, Spence and Hodges 2010). The species in this genus present a strong sexual dimorphism (Kimsey 1991), with fully winged males that are easy to recognize by their last hook-like metasomal segment. Females can be winged, brachypterous, or wingless (Pate 1947, Kimsey 1991). They are stronger than the males and their antennae are curved (see Fig. 1D). Tiphiidae are parasitoid wasps of beetle larvae in general and Myzininae species probably parasitize Scarabaeidae and Cicindelidae (Pate 1947, Brown 1985, Kimsey 1991). Males are pollinators and are commonly collected flying in groups. However, females are harder to collect because they are found alone, usually on flowers (Kimsey 2009). Thus, the limited knowledge of internal body structure in this parasitoid wasp family is also due to the low chance of finding females alive, as live material is needed for proper tissue fixation for microscopical analysis. In addition, proper species identification of Myzinum wasps is difficult because males and females are very rarely collected together. Kimsey (2009) proposed a key for Myzinum in North America, but as this key comments that the North American fauna is different from South America, we do not have tools to identify the species used in the present work. All those characteristics make it difficult to study these wasps and literature is very scarce.

As a modification of the accessory glands of the reproductive system, the Dufour gland is one of the standard glands of female Hymenoptera. Both in solitary and social species, several functions have been attributed to the gland, ranging from provisioning of larval food and nesting material to several pheromonal functions (reviewed in Hefetz 1987, Abdalla and Cruz-Landim 2001a, Mitra 2013). Because of the very scarce information about *Myzinum* biology, we can only speculate about the function of their Dufour gland. Literature shows that its secretion can be associated with host marking in solitary wasps (Mitra 2013). Parasitoid wasps mark their hosts to avoid superparasitism and guarantee the fitness of their offspring. Odor marks may be used in host discrimination (Sheehan et al. 1993) and could be associated with Dufour gland secretion. An analysis of the Dufour gland morphology and chemistry in four species of bethylid and pteromalid ectoparasitoid wasps confirms its opening into the oviduct and supports its involvement in the elaboration of a lipidic secretion (Howard and Baker 2003).

Several studies have been done on the anatomy and ultrastructure of the Dufour gland, mainly in the social Hymenoptera (Billen 1986 for ants, Abdalla et al. 1999 for bumblebees, Abdalla and Cruz-Landim 2001b for bees, Billen 2006 and Fortunato and Turillazzi 2012 for wasps). In ants, the appearance of the epithelial gland cells shows subfamily-specific characteristics (Billen 1986). In Tiphiidae, however, no information on this gland is available until now (Robertson 1968, Mitra 2013). As we had the luck to collect two live *Myzinum* females, we here report on the morphology and ultrastructure of their Dufour gland, which brings the first information on this gland in tiphiid wasps.

Material and methods

We collected two live Myzinum females at the Estação Ecológica do Noroeste Paulista (EENP), São José do Rio Preto, SP, Brazil (20°50'43.6"S 49°26'05.5"W). Because of the complex taxonomy in this genus, we refer to them as Myzinum sp.1 and sp.2, of which sp.1 is characterized by a black and yellow thorax, whereas sp.2 has an almost entirely black thorax (Fig. 1). Myzinum sp.1 is similar in its color pattern to M. macu*lata*, which is also a common species in insect collections. Reference specimens of both species can be found in the entomological collection at the Departamento de Zoologia e Botânica at the UNESP-campus in São José do Rio Preto, SP (Brasil). From the sp.1 female, the Dufour gland was carefully dissected, so that optimal fixation quality for microscopy could be obtained. From the sp.2 female, we fixed the posterior abdomen part to have material of Dufour's gland in situ with its surrounding tissues. Both the dissected gland and the abdomen part were fixed in cold 2% glutaraldehyde, buffered at pH 7.3 with 50 mM Na-cacodylate and 150 mM saccharose. Tissues were postfixed in 2% osmium tetroxide in the same buffer. After dehydration in a graded acetone series, they were embedded in Araldite and sectioned with a Leica EM UC6 microtome. Semithin 1 µm sections of both females were stained with methylene blue and thionin and viewed in an Olympus BX-51 microscope, double stained 70 nm thin sections of the gland of the sp.1 female were examined in a Zeiss EM900 electron microscope. To illustrate the sting shape, two pinned collection specimens of *Myzinum* sp. 1 were treated with 10% KOH during 1.5 hours, and then further dissected under insect Ringer solution.

Results

The Dufour gland is a wide elongated sac that opens ventrally of the sting base. The main portion of the gland is formed by a monolayered epithelium with a thickness of approximately 10 μ m (Fig. 2A). At its lumen side, it is lined with a cuticular intima around 1 μ m, while isolated muscle strands occur at the basal side (Fig. 2B). The epithelium has a crenellate appearance, which is the result of the peculiar shape of the secretory cells. Each cell has a cupola-like central portion, in which the round nucleus with a diameter of 5 μ m is apically situated (Fig. 2B). More laterally, cell height is considerably less, and reaches a thickness of hardly 2 μ m. The resulting cell shape is schematically illustrated in Figure 2C.

Electron microscopy shows how intercellular junctions occur at the thin lateral cell parts (Fig. 3A, C). The apical cell membrane is differentiated into microvilli with a length around 1 μ m (Fig. 3B), although they are less developed and shorter in the lateral portions of the cell (Fig. 3C–E). The cytoplasm contains scattered mitochondria, and probably a diffuse network of smooth endoplasmic reticulum, of which tubular extensions can be found inside the apical microvilli (Fig. 3C). The basal cell membrane shows some deep basal invaginations that penetrate up to 3 μ m into the gland cell



Figure 1. A, B Profile and frontal view of female of *Myzinum* sp.1. C, D Profile and frontal view of female of *Myzinum* sp.2.

(Fig. 3C). The lateral cell contacts show a pattern with folded and interdigitating cell membranes, with desmosomes in the apical region, followed by septate junctions, and undifferentiated parallel membranes in the basal part (Fig. 3D, E). Intercellular spaces may be wedged in between the two neighbouring cell membranes (Fig. 3D). On one occasion, we observed an intercellular bridge, that appeared as a barrel-shaped tube between the two cells. The connecting structure has a smooth electron-dense lining and has a diameter of $0.4 \mu m$ and a length of $0.6 \mu m$ (Fig. 3E).

A remarkable observation in our *Myzinum* females was the dorsally curved sting (Fig. 4A–C), that results in the sting shaft being parallel with the posterior tergites, rather than having a more 'horizontal' orientation parallel with the posterior sternites, as is the usual case. In its posterior part, the reservoir sac abruptly narrows into a thin slit-like duct that opens ventrally of the sting base (see black arrows in Fig. 5A,B), whereas the venom gland duct enters the sting, and thus will discharge its secretion through the sting (see white arrows in Fig. 5A, B). The slit-like duct has a length of almost 200 μ m and a width around 80 μ m, and is provided with a massive muscular supply at both the dorsal and ventral side (Fig. 5A–C). The muscle fibres cannot attach directly onto the rigid duct cuticle, as the gland epithelium forms an intermediate layer (Fig. 5D). The pulling forces of the myofilaments are transmitted to parallel bundles of microtubules that occur in the epithelial cells. These microtubules run perpendicularly to the inner cuticular surface, to which they adhere. The contact region between myofilaments and microtubules is characterized by a tortuous shape and numerous hemidesmosomes (Fig. 5D, E).



Figure 2. A Semithin section through the Dufour gland reservoir sac (DGr) and duct region (DGd) in *Myzinum* sp.1. The arrowheads indicate the transition between the reservoir and duct region **B** Detail of crenellate epithelial lining of reservoir sac with strands of surrounding muscle fibres (MF) **C** Schematical view of cupola-like shape of gland cell. bi: basal invaginations, ct: cuticle, lcj: lateral cell junction, mv: microvilli, N: nucleus.

Discussion

Our observations revealed that the epithelial gland cells have a peculiar shape with a cupola-like central part. This cell shape does not correspond to any of the 8 types that have been described in ants (Billen 1986), but does show some resemblance to the epithelial appearance in vespid wasps (see figure 2A in Billen 2006). The presence of smooth endoplasmic reticulum, including its extension into the apical microvilli,



Figure 3. Electron micrographs of Dufour gland secretory cells in *Myzinum* sp.1. **A** Low magnification survey of crenellate epithelium, arrowheads indicate cell junctions **B** Cupola-like apical part of gland cell with nucleus (N) **C** Low lateral part of gland cell with apical microvilli (mv) and basal invaginations (bi). Arrowheads indicate extensions of smooth endoplasmic reticulum (SER) into microvilli **D** Detail of intercellular junction with apical desmosome (d), followed by septate junction (sj). Note intercellular space (is) wedged in between neighbouring cell walls. **E**. Occurrence of intercellular bridge (ib). ct: cuticle, M: mitochondria.



Figure 4. A Partially dissected gaster of a collection specimen of *Myzinum* sp.1, showing the dorsally curved sting (arrow) **B** Overview of sting (*Myzinum* sp.1) **C** Longitudinal semithin section through the posterior abdomen part of *Myzinum* sp.2 female, showing upward curved sting (st). DGr: Dufour gland reservoir, HG: hindgut.

is in line with the general ultrastructural appearance of Dufour's gland in other Hymenoptera (Billen 1986, 2006, Abdalla and Cruz-Landim 2001a). This cytoplasmic characteristic supports the elaboration of a non-proteinaceous secretion, which therefore can also be postulated to be the case in Tiphiidae. This is also in agreement with the lipidic secretion that has been found in Dufour's gland of four bethylid and pteromalid ectoparasitoid wasps (Howard and Baker 2003). The occurrence of apical microvilli and basal invaginations represent an increase of the cell surface, and can be understood by giving the epithelial cells an efficient uptake of precursor molecules from the hemolymph basally, and an efficient discharge of secretory products apically. An interesting observation was the occurrence of an intercellular bridge, as such structures usually do not occur in somatic tissues of adult insects. Intercellular bridges, on the other hand, are common in the germarium of ovarioles, where they occur as 1.2 μ m wide connecting channels between neighbouring cystocytes, that allow transport of large amounts of material to the future oocyte (Billen 1985).

At the general anatomical level, the Dufour gland reservoir is surrounded by a loose network of muscle fibres, that upon contraction push the secretion towards the duct region. In this duct region, a conspicuous muscular supply with dorsal and ventral muscles attaching onto the slit-like duct is very prominent. This muscular arrangement is similar to that described in ants (Billen 1986) and wasps (Billen 2006), and will result in active opening of the duct by muscular contraction, while passive closing is the result of the thickened cuticle returning to its rest position when muscles stop contracting. At the cell level, the muscular forces onto the rigid duct cuticle have to be transmitted through the epithelium layer. This is achieved by the occurrence of bundles of parallel microtubules in the epidermal cells and hemidesmosomes that form a strong mechanical system ensuring efficient transmission of pulling forces. This set-up corresponds to the typical myo-epidermal junction, that was first described in Diptera



Figure 5. A Longitudinal semithin section through sting base region in *Myzinum* sp.2, showing Dufour gland opening ventrally of the sting base (black arrow), whereas the venom gland duct opens through the sting (white arrow) **B** Enlargement from A showing sting base region **C** Cross semithin section through Dufour gland duct in *Myzinum* sp.1, showing slit-like duct with attachment of dorsal and ventral muscle fibres (MF) **D** and **E** Electron micrographs of muscular attachments onto Dufour gland duct of *Myzinum* sp.1. Myofilaments of muscle fibres (MF) transmit their pulling force onto bundles of microtubules (MT) in the duct cells via hemidesmosomes (hd). bi: basal invaginations, DGd: Dufour gland duct, DGr: Dufour gland reservoir sac. G: ganglion, lv: lancet valves, N: nucleus, st: sting, VGd: venom gland duct.

(Auber 1963), and that is also found in the duct region of Dufour's gland (Billen 1982, 1986, 2006).

As in mutillids (Hermann 1968), the sting in *Myzinum* shows a dorsally curved sting, which so far has never been reported for tiphiid wasps. Both Mutillidae and Tiphiidae are parasitoids of larvae of other insects. Mutillidae are commonly described to be parasitoids of social insects, however, Brothers et al. (2000) provided new records for Mutillidae hosts, including beetle larvae that are generally described as hosts for Tiphiidae. These beetle larvae can be quite big in comparison to the size of their parasitoids, thus their curved sting shape may be related with the possibility to sting the host larva from above. The Dufour gland duct of *Myzinum* approaches the sting base, but unlike the venom gland duct does not open through the sting. In this regard, it is different from the situation in ants, where both the venom and Dufour gland ducts open through the sting, and thus release their secretory products via the sting shaft (Billen 1986, 1987). Dufour's gland opening at the base of the sting shaft as is the case in *Myzinum* is similar to the situation in wasps and bees (Billen 1987, Fortunato and Turillazzi 2012, Martin et al. 2005), and corresponds with an opening in the dorsal wall of the oviduct.

Even though the South American species taxonomy of tiphiid wasps is controversial and mostly unknown, we believe that all information on this group of wasps is very welcome and important.

Acknowledgements

We are very grateful to An Vandoren for her assistance in making the sections for light and electron microscopy, to Eduardo Almeida for allowing us to use his laboratory to make the entire specimen photographs and to Lynn Kimsey and an anonymous reviewer for making valuable improvements in the manuscript. This research was supported through project 3E150873 from the Explorative Scientific Co-operation Program between UNESP and KU Leuven.

References

- Abdalla FC, Velthuis H, Cruz-Landim C, Duchateau MJ (1999) Changes in the morphology and ultrastructure of the Dufour's gland during the life cycle of the bumblebee queen, *Bombus* terrestris L. (Hymenoptera: Bombini). Netherlands Journal of Zoology 49: 251–261. https:// doi.org/10.1163/156854299505722
- Abdalla FC, Cruz-Landim C (2001a) Dufour glands in the Hymenopterans (Apidae, Formicidae, Vespidae): a review. Revista Brasileira de Biologia 61: 95–106. https://doi.org/10.1590/ S0034-71082001000100013
- Abdalla FC, Cruz-Landim C (2001b) Changes in the morphology of the Dufour gland of *Apis mellifera* L. (Hymenoptera, Apinae, Apini) during the life stages of the female castes. Revista Brasileira de Biologia 61: 123–129.

- Auber J (1963) Ultrastructure de la jonction myo-épidermique chez les diptères. Journal de Microscopie 2: 325–336.
- Billen J (1982) The Dufour gland closing apparatus in *Formica sanguinea* Latreille (Hymenoptera, Formicidae). Zoomorphology 99: 235–244. https://doi.org/10.1007/BF00312297
- Billen J (1985) Ultrastructure of the worker ovarioles in *Formica* ants (Hymenoptera: Formicidae). International Journal of Insect Morphology and Embryology 14: 21–32. https://doi. org/10.1016/0020-7322(85)90034-0
- Billen J (1986) Comparative morphology and ultrastructure of the Dufour gland in ants (Hymenoptera: Formicidae). Entomologia Generalis 11: 165–181. https://doi.org/10.1127/ entom.gen/11/1986/165
- Billen J (1987) New structural aspects of the Dufour's and venom glands in social insects. Naturwissenschaften 74: 340–341. https://doi.org/10.1007/BF00367931
- Billen J (2006) Morphology and ultrastructure of the Dufour gland in workers of social wasps (Hymenoptera, Vespidae). Arthropod Structure and Development 35: 77–84. https://doi. org/10.1016/j.asd.2006.01.002
- Billen J, Šobotník J (2015) Insect exocrine glands. Arthropod Structure and Development 44: 399–400. https://doi.org/10.1016/j.asd.2015.08.010
- Brothers DJ, Tschuch GT, Burger F (2000) Associations of mutillid wasps (Hymenoptera, Mutillidae) with eusocial insects. Insectes Sociaux 47: 201–211. https://doi.org/10.1007/ PL00001704
- Brown GR (1985) The Australian Myzininae (Hymenoptera: Tiphiidae). Journal of the Australian Entomological Society 24: 135–141. https://doi.org/10.1111/j.1440-6055.1985.tb00210.x
- Fortunato A, Turillazzi S (2012) Dufour's gland possible role in the evolution of sting morphology and function in hover wasps (Hymenoptera Stenogastrinae). Arthropod Structure and Development 41: 259–264. https://doi.org/10.1016/j.asd.2012.02.007
- Hefetz A (1987) The role of Dufour's gland secretions in bees. Physiological Entomology 12: 243–253. https://doi.org/10.1111/j.1365-3032.1987.tb00749.x
- Hermann HR (1968) The hymenopterous poison apparatus. IV. *Dasymutilla occidentalis* (Hymenoptera: Mutillidae). Journal of the Georgia Entomological Society 3: 1–10.
- Howard RW, Baker JE (2003) Morphology and chemistry of Dufour glands in four ectoparasitoids: *Cephalonomia tarsalis, C. waterstoni* (Hymenoptera: Bethylidae), *Anisopteromalus calandrae*, and *Pteromalus cerealellae* (Hymenoptera: Pteromalidae). Comparative Biochemistry and Physiology 135B: 153–167. https://doi.org/10.1016/S1096-4959(03)00076-9
- Kimsey LS (1991) Relationship among the tiphiid wasp subfamilies (Hymenoptera). Systematic Entomology 16: 427–438. https://doi.org/10.1111/j.1365-3113.1991.tb00677.x
- Kimsey LS (2009) Taxonomic purgatory: Sorting out the wasp genus *Myzinum* Latreille in North America (Hymenoptera, Tiphiidae, Myzininae). Zootaxa 2224: 30–50.
- Martin SJ, Dils V, Billen J (2005) Morphology of the Dufour gland within the honey bee sting gland complex. Apidologie 36: 543–546. https://doi.org/10.1051/apido:2005041
- Mitra A (2013) Function of the Dufour's gland in solitary and social Hymenoptera. Journal of Hymenoptera Research 35: 33–58. https://doi.org/10.3897/jhr.35.4783
- Pate VSL (1947) A conspectus of the Tiphiidae, with particular reference to the Neartic forms (Hymenoptera, Aculeata). Journal of the New York Entomological Society 55: 115–145.

- Robertson PL (1968) A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. Australian Journal of Zoology 16: 133– 166. https://doi.org/10.1071/ZO9680133
- Sheehan W, Wäckers FL, Lewis WJ (1993) Discrimination of previously searched, host-free sites by *Microplitis croceipes* (Hymenoptera: Braconidae). Journal of Insect Behavior 6: 323–331. https://doi.org/10.1007/BF01048113
- Spence D, Hodges A (2010) A tiphiid wasp *Myzinum maculata* Fabricius (Insecta: Hymenoptera: Tiphiidae: Myzininae). Featured Creatures from the Entomology and Nematology Department EENY 470: 1–5.

RESEARCH ARTICLE



Labilochus brevipalpis, a new genus and species with extremely long mouthparts (Hymenoptera, Ichneumonidae, Tersilochinae) from Mexico

Andrey I. Khalaim¹, Enrique Ruíz-Cancino², Juana María Coronado-Blanco²

l Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia **2** Facultad de Ingeniería y Ciencias, Universidad Autónoma de Tamaulipas, Cd. Victoria, Mexico

Corresponding author: Andrey I. Khalaim (ptera@mail.ru)

Academic editor: G. Broad	P Received 10 December 2016 Accepted 8 M	arch 2017 Published 28 April 2017
		23D5889B0

Citation: Khalaim AI, Ruíz-Cancino E, Coronado-Blanco JM (2017) *Labilochus brevipalpis*, a new genus and species with extremely long mouthparts (Hymenoptera, Ichneumonidae, Tersilochinae) from Mexico. Journal of Hymenoptera Research 55: 121–127. https://doi.org/10.3897/jhr.55.11452

Abstract

Labilochus brevipalpis gen. & sp. n. from northeast Mexico is described and illustrated. The new genus is distinguished from all other Tersilochinae taxa by its extremely long glossa and galeae in combination with short maxillary and labial palps, and both palps with reduced number of palpomeres. The genus also possesses a remarkable head, which is almost straight behind the eyes in dorsal view and with the occipital carina lacking laterally.

Resumen

Se describe e ilustra *Labilochus brevipalpis* **n. gen. y sp.** del noreste de México. El nuevo género se distingue de todos los taxa de Tersilochinae por su glosa y galeas extremadamente largas en combinación con los palpos maxilares y labiales cortos y con menos palpómeros. El género también tiene cabeza notable, es casi recta detrás de los ojos en vista dorsal y la carina occipital está ausente lateralmente.

Keywords

North America, taxonomy, new genus, new species

Introduction

Tersilochinae is a moderately large ichneumonid subfamily distributed almost worldwide and comprising about 500 described and many undescribed species (Yu et al. 2012; Khalaim pers. obs.). Most host records of Tersilochinae are from various taxa of Coleoptera, but species of the genus *Gelanes* Horstmann are parasitoids of xyelid sawflies (Hymenoptera: Xyelidae) (Khalaim and Blank 2011; Horstmann 2013b), and some European species of *Diaparsis* Förster and *Tersilochus* Holmgren have been recorded as parasitoids of Tenthredinidae (Hymenoptera) and Eriocraniidae (Lepidoptera) (Yu et al. 2012).

Nearctic fauna of the subfamily was partly revised by K. Horstmann who examined types of 24 previously known Nearctic species (Horstmann 2001) and revised eleven genera with 74 species occurring in America north of Mexico (Horstmann 2010, 2012, 2013a, 2013b): *Allophrys* Förster (1 species), *Allophroides* Horstmann (6 species), *Aneuclis* Förster (4 species), *Barycnemis* Förster (13 species), *Ctenophion* Horstmann (1 species), *Diaparsis* Förster (12 species, including one introduced from Europe), *Gelanes* Horstmann (13 species), *Phradis* Förster (18 species), *Sathropterus* Förster (1 species), *Spinolochus* Horstmann (2 species) and *Stethantyx* (3 species, including one introduced from South America). Unfortunately, revisions of Nearctic species of two large genera, *Probles* Förster and *Tersilochus* Holmgren, were not finished due to the untimely death of K. Horstmann.

In his revisions, K. Horstmann identified specimens from Canada and USA but did not include material from Mexico, except for two species: *Allophrys divaricata* Horstmann, widely distributed from southern USA to Argentina and occurring in USA and northern Mexico, and *Stethantyx nearctica* Townes. Besides these two species, two new species of *Barycnemis*, the cosmopolitan *Sathropterus pumilus* (Holmgren), and five species of the large Neotropical genus *Stethantyx* (including one new species) were recorded or described from Mexico by A. Khalaim and co-authors (Khalaim 2002; Khalaim and Ruíz-Cancino 2013; Khalaim et al. 2015). Thus, only four genera of Tersilochinae and ten species are currently known from Mexico while a large number of genera and species occurring in Mexico are still undiscovered.

The aim of this work is to describe a new genus and species with bizarre mouthparts from Mexico.

Materials and methods

The new genus is known from two specimens, one female from the insect collection of the Universidad Autónoma de Tamaulipas, Cd. Victoria, Tamaulipas, México (UAT) and one male from the Townes collection, recently moved to the Utah State University, Logan, Utah, USA (EMUS).

Morphological terminology predominantly follows Townes (1969, 1971) with changes according to Khalaim (2011). Layer photographs were taken in the Texas A&M University, Texas, USA (TAMU) with a DFC 295 digital camera attached to Leica stereomicroscope, and were combined using Helicon Focus software.

Taxonomy

Labilochus Khalaim, gen. n.

http://zoobank.org/66B004C4-99DB-4FDA-8807-90855D90BFB7

Type species. Labilochus brevipalpis Khalaim & Ruíz-Cancino, sp. n.

Composition. The new genus contains only the type species, L. brevipalpis, described below.

Morphological remarks. The genus is immediately recognisable by its extremely long glossa and galeae (Fig. 2) and reduced number of segments of the maxillary and labial palps. This is the only genus in the subfamily (and probably in the family) having such long glossa and galeae in combination with very short palps. Some taxa of Tersilochinae (e.g. genera Heterocola Förster and Palpator Khalaim, some species of Gonolochus Förster) possess long mouthparts including palps (especially maxillary palp), but none has the long glossa and galeae AND short palps in combination. The formula of maxillary and labial palps (3:2) is also unique within the subfamily; normally tersilochine species have 4-segmented maxillary and 3-segmented labial palps. The new genus is also distinct by having the head almost straight behind the eyes in dorsal view and the occipital carina lacking laterally.

Labilochus belongs to the Tersilochus group of genera, having a right-angled radial cell (Fig. 3) and the first metasomal segment with a distinct glymma joining by a deep furrow to the ventral part of the postpetiole. Within this group, Labilochus is most similar to the genus Probles Förster as it has a well-developed foveate groove on the mesopleuron (Fig. 5) and a long thyridial depression (Fig. 6).

Description. Head in dorsal view almost straight, weakly tapered behind eyes (Fig. 4); temple 0.9 times as long as eye width. Mandible with upper tooth much longer than lower tooth. Clypeus broad, lenticular, almost flat in lateral view, separated from face by weak furrow. Glossa and galeae very long, thin, equal in length, reaching past posterior end of hind coxa (Fig. 2); glossa not forked; maxillary palp 3-segmented, labial palp 2-segmented, both are very short (Fig. 2). Malar space 0.8 times as long as basal mandibular width in female and 0.5 times in male. Antennal flagellum slightly tapered towards apex, with 21-22 flagellomeres (Fig. 1). Occipital carina present dorsally and ventrally (next to mandibular base), absent laterally. Hypostomal carina absent.

Notaulus weakly impressed, without wrinkles. Scutellum with lateral longitudinal carinae developed in its anterior 0.3-0.4 (Fig. 4). Foveate groove deep, sharp, with strong transverse wrinkles, strongly oblique, curved, not reaching epicnemial carina anteriorly (Fig. 5). Propodeum (Fig. 6) with transverse carina well developed, complete; basal area strongly impressed, elongate, distinctly widened anteriorly, 0.35 times as long as apical area, with basal longitudinal carinae indistinct. Propodeal spiracle separated from pleural carina by about 1.5 times diameter of spiracle. Apical area flat, pointed anteriorly; apical longitudinal carinae reaching transverse carina anteriorly, distinct posteriorly and rather weak anteriorly.

Fore wing (Fig. 3) with first and second abscissae of radius (Rs+2r and Rs) meeting at right angle; both abscissae straight. Intercubitus and abscissa of cubitus between intercubitus and second recurrent vein (abscissa of M between 2rs-m and 2m-cu) not or weakly thickened. Metacarpus (R1) not reaching apex of wing. Hind wing with nervellus (cu1&cu-a) vertical. Legs slender. Hind femur 4.6 times as long as broad and almost 0.85 times as long as tibia. Hind basitarsus 0.45 times as long as tibia (Fig. 2).

First tergite slender, postpetiole clearly separated from petiole (Fig. 6). Glymma distinct, situated in apical 0.6 of tergite, joining by distinct furrow to ventral part of postpetiole. Thyridial depression deep, about 2.5 times as long as broad (Fig. 6). Ovipositor long, evenly upcurved, slender, with very weak dorsal subapical depression; sheath about 3.5 times as long as first tergite.

Etymology. Named after its extremely long labium. Gender masculine.

Labilochus brevipalpis Khalaim & Ruíz-Cancino, sp. n. http://zoobank.org/AD64ABAD-6B63-466D-ABFE-DF3FBF6F5FA1 Figs 1–6

Description. Female. Body length 4.0 mm. Fore wing length 2.9 mm.

Clypeus smooth, with very fine punctures in upper part. Antennal flagellum with 21 flagellomeres (Fig. 1); all flagellomeres (except basal and apical ones) more or less equally elongate, about 1.2-1.3 times as long as broad; flagellomeres 4 to 6 with subapical finger-shaped structures on outer surface. Face, frons and vertex with very fine, inconspicuous, dense punctures on smooth and weakly shining background. Temple polished, impunctate. Mesoscutum very finely punctate on smooth and weakly shining background. Mesopleuron mostly polished and impunctate. Foveate groove postero-ventrally covered by glue and indiscernible. Propodeum weakly shining, impunctate. Fore wing with intercubitus (2rs-m) somewhat longer than abscissa of cubitus between intercubitus and second recurrent vein (abscissa of M between 2rs-m and 2m-cu). First tergite 4.4 times as long as posteriorly broad, smooth (Fig. 6).

Head black; clypeus brownish yellow in lower half, mandible brownish yellow with teeth blackish; glossa and palps yellow, remaining mouthparts dark brown or fuscous. Antennal flagellum black, scape and pedicel dark brown. Mesosoma black. Tegula yellowish. Pterostigma brown. Legs predominantly brown; all coxae black; mid and hind tibiae and tarsi fuscous; hind femur apically pale. First tergite black. Metasoma behind first tergite predominantly brownish yellow; tergite 2 in basal 0.2, tergite 3 in basal 0.6, and following tergites more or less entirely dark brown to black dorsally.

Male. Labium almost reaching past posterior end of first metasomal tergite. Maxillary and labial palps not discernible, probably short. Antennal flagellum with 22 flagellomeres. Occipital carina dorsally fine but distinct, laterally and ventrally indiscernible. Mesopleuron very finely punctate peripherally, centrally (above foveate groove) polished and impunctate (Fig. 5). Fore wing (Fig. 3) with intercubitus (2rs-m) somewhat shorter than abscissa of cubitus between intercubitus and second recurrent vein (abscissa of *M* between 2rs-m and 2m-cu). Basal metasomal tergites slenderer than



Figures 1–6. *Labilochus brevipalpis* sp. n., holotype female (1, 2, 6) and paratype male (3–5). I antenna 2 head and mesosoma, lateral view **3** fore wing **4** head and mesosoma, dorsal view **5** mesopleuron **6** propodeum and base of metasoma, dorsal view.

in female. Thyridial depression shallow. Fore and mid coxae slightly darkened with brown, tibiae and tarsi less infuscate than in female. Otherwise similar to female.

Type material. Holotype female (UAT), Mexico, Tamaulipas, NE of Miquihuana, Rancho Obed Hernández, 2500 m, Malaise trap, 25.IX–7.X.2011, coll. E. Ruíz-Cancino & J.M. Coronado-Blanco.

Paratype. 1 male (EMUS) Mexico, Nuevo León, 32 km W of Linares, San Pedro Iturbide, 26.X.1962, coll. H. & M. Townes, "Probles sp. 37 Tow. 1969".

Etymology. From the Latin *brevis* (small, short) and *palpus* (palp, feeler), after its short maxillary and labial palps.

Discussion

Mouthpart structure among parasitoid wasps was studied by Jervis (1998) who recognized seven functional types relating to the extraction of floral nectar in the families Braconidae and Ichneumonidae. According to Jervis, most Tersilochinae taxa have a type 1 mouthpart apparatus characterized by slightly to moderately elongated glossa and galeae, and glossa shallowly bilobed/forked at its tip and concealed by the galeae for most of its length in dried specimens; and a type 3, resembling type 1 but with maxillary palps markedly elongated, is known in the tersilochine genus *Heterocola*. Besides *Heterocola*, elongated mouthparts are present in the genus *Palpator* and some species of *Gonolochus*. Mouthpart apparatus in these taxa apparently also belongs to type 3 because the maxillary palps are always very long, with other mouthpart structures short or long.

The mouthpart apparatus of the genus *Labilochus* apparently belongs to type 1, but clearly differs from that of other ichneumonid and braconid wasps by the short palps in combination with the extremely long and slender glossa and galeae (in other taxa, if the galeae/glossae are long then the palps are also elongated). For example, in the family Ichneumonidae similar mouthparts are present in the ophionine genus *Agathophiona* Westwood comprising a single species occurring in Mexico (Townes 1971: 61), but in this genus the palps are also conspicuously elongated and the number of palpomeres are not reduced.

The mouthparts apparatus of *Labilochus* is unique among Tersilochinae, and perhaps among the family Ichneumonidae. Unfortunately, the genus is represented only by two dried specimens, female and male, deposited in two different collections, and their partition and preparation for detailed morphological study is not allowed.

Acknowledgements

We are thankful to David Wahl (EMUS) for the loan of valuable material, and John D. Oswald and Karen Wright (TAMU) for their kind help with taking colour photographs. Also we are grateful to Dmitri R. Kasparyan (Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia) for his important comments on the manuscript, and Gavin Broad (the Natural History Museum, London, UK) and an anonymous referee

for their comments and language corrections. This work was supported by the Russian Foundation for Basic Research (grant no. 16-04-00197) and the PRODEP project "Taxonomical and biological studies of pests and natural enemies in Mexico".

References

- Horstmann K (2001) Type revisions of Tersilochinae described from the Nearctic region (Hymenoptera, Ichneumonidae). Linzer Biologische Beiträge 33(1): 595–601.
- Horstmann K (2010) Revisions of Nearctic Tersilochinae II. Genera *Allophrys* Förster, *Barycnemis* Förster, *Ctenophion* gen. nov., *Sathropterus* Förster, *Spinolochus* Horstmann and *Stethantyx* Townes (Hymenoptera, Ichneumonidae). Spixiana 33(1): 73–109.
- Horstmann K (2012) Revisions of Nearctic Tersilochinae III. Genera *Aneuclis* Förster and *Diaparsis* Förster (Hymenoptera, Ichneumonidae). Spixiana 35(1): 117–142.
- Horstmann K (2013a) Revisions of Nearctic Tersilochinae IV. Genus *Phradis* Förster (Hymenoptera, Ichneumonidae). Spixiana 36(1): 67–92.
- Horstmann K (2013b) Revisions of Nearctic Tersilochinae V. Genera *Allophroides* Horstmann and *Gelanes* Horstmann (partim) (Hymenoptra, Ichneumonidae). Spixiana 36(2): 227–261.
- Jervis M (1998) Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. Biological Journal of the Linnean Society 63(4): 461–493. https://doi.org/10.11-11/j.1095-8312.1998.tb00326.x
- Khalaim AI (2002) Two new species of the genus *Barycnemis* Förster from Mexico (Hymenoptera: Ichneumonidae, Tersilochinae). Zoosystematica Rossica 11(1): 167–169.
- Khalaim AI (2011) Tersilochinae of South, Southeast and East Asia, excluding Mongolia and Japan (Hymenoptera: Ichneumonidae). Zoosystematica Rossica 20(1): 96–148.
- Khalaim AI, Blank SM (2011) Review of the European species of the genus Gelanes Horstmann (Hymenoptera: Ichneumonidae: Tersilochinae), parasitoids of xyelid sawflies (Hymenoptera: Xyelidae). Proceedings of the Zoological Institute RAS, 315(2): 154–166.
- Khalaim AI, Ruíz-Cancino E (2013) Mexican species of the genus Stethantyx Townes (Hymenoptera, Ichneumonidae, Tersilochinae). ZooKeys 360: 83–94. https://doi. org/10.3897/zookeys.360.6362
- Khalaim AI, Ruíz-Cancino E, Coronado-Blanco JM (2015) First record of Sathropterus pumilus (Holmgren) (Hymenoptera: Ichneumonidae: Tersilochinae) from Mexico. Acta Zoológica Mexicana (NS) 31(1): 138–139.
- Townes HK (1969) The genera of Ichneumonidae, Part 1. Memoirs of the American Entomological Institute 11: 1–300. https://doi.org/10.1007/bf02027741
- Townes HK (1971) The genera of Ichneumonidae, Part 4. Memoirs of the American Entomological Institute 17: 1–372.
- Yu DSK, van Achterberg C, Horstmann K (2012) Taxapad 2012, Ichneumonoidea 2011. Database on flash-drive. Ottawa, Ontario, Canada.

RESEARCH ARTICLE



Contribution to the study of the genus Stethantyx Townes (Hymenoptera, Ichneumonidae, Tersilochinae), with the description of a new species from Brazil

Andrey I. Khalaim^{1,2}

l Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia **2** Facultad de Ingeniería y Ciencias, Universidad Autónoma de Tamaulipas, Cd. Victoria, Mexico

Corresponding author: Andrey I. Khalaim (ptera@mail.ru)

Academic	editor:	<i>G</i> .	Broad		Received	19 May	2015		Accepted 21	March	2017		Published 2	8 April	2017
			k	ottp:	//zoobank.o	rg/1E275	5640-D50	C6	5-4048-ACBB-2	A17FFE	C2D09	8			

Citation: Khalaim AI (2017) Contribution to the study of the genus *Stethantyx* Townes (Hymenoptera, Ichneumonidae, Tersilochinae), with the description of a new species from Brazil. Journal of Hymenoptera Research 55: 129–138. https://doi.org/10.3897/jhr.55.5322

Abstract

A new species, *Stethantyx durrelli* **sp. n.** from Brazil, is described and illustrated. The recently described genus *Megalochus* Khalaim & Broad is synonymized with *Stethantyx*. The new species is very similar to *S. grandis* (Khalaim & Broad), **comb. n.** but differs by the first metasomal segment being trapeziform in cross-section, the presence of a distinct glymma, and the metapleuron and dorsolateral area of the propodeum being densely punctate, without coarse irregular rugae. These two species are the largest and most conspicuous representatives of the subfamily Tersilochinae. A partial key to species of *Stethantyx* is provided. Taxonomy and generic limits of *Stethantyx* are discussed.

Keywords

Neotropical region, South America, Megalochus, taxonomy, new species, new synonymy, key

Introduction

Stethantyx Townes is a large New World genus comprising 48 described and many undescribed species, most of which are Neotropical (Khalaim and Broad 2013; Khalaim et al. 2013, 2015; Khalaim and Ruíz-Cancino 2013; Khalaim 2016), as well as *S. nearctica* Townes which ranges from the northern US to Mexico and *S. crassa*

Horstmann known from Canada to the southern United States (Horstmann 2010). *Stethantyx* is closely related to the small Neotropical genus *Megalochus* Khalaim & Broad, with only one widely distributed species, *M. grandis* Khalaim & Broad. The genera were thought to be related based on the following synapomorphies: 1) fore wing with obtusely angled first and second abscissae of radius; 2) slender and usually long intercubitus and abscissa of cubitus between intercubitus and second recurrent vein; 3) the narrow pterostigma; and 4) dorsal end of epicnemial (prepectal) carina not joining the anterior margin of mesopleuron, continuing dorsoposterior to the subtegular ridge, or evanescent dorsally (Khalaim and Broad 2013). The *Stethantyx* genus-group was established for these two genera, comprising the largest and most conspicuous representatives of the subfamily, and recently the endemic Australian genus *Australochus* Khalaim was also included in this genus-group (Khalaim 2015).

Nothing is known about the biology and host preferences of *Megalochus* but some species of *Stethantyx* were recorded as parasitoids of the beetle families Nitidulidae and Curculionidae (Parker et al. 1950, Williams et al. 1984, Horstmann 2010). Although the genus *Stethantyx* has been extensively studied in recent years, a large number of species is still undescribed.

The aim of this work is to describe a new species of *Stethantyx* from Brazil, reconsider the classification of *Megalochus* and provide a partial key to species of *Stethantyx*. The taxonomy of the genus *Stethantyx* is also briefly discussed.

Materials and methods

Material of South American Tersilochinae from the Utah State University, Logan, Utah, USA (EMUS, Townes collection) and the Florida State Collection of Arthropods, Gainesville, Florida, U.S.A. (FSCA) was examined. In this material, a new species of *Stethantyx* was found.

Morphological terminology generally follows Townes (1969) with changes according to Khalaim (2011). Photographs were taken at the Instituto de Biología, Universidad Nacional Autónoma de México, D.F., México (UNAM) with a Leica DFC290 HD digital camera attached to a Leica Z6 APO stereoscopic microscope. Partly focused images were combined using the Leica Application Suite program.

Results and taxonomy

The genus *Megalochus* was described for a single species, *M. grandis*, occurring from Costa Rica to southern Brazil. This genus was considered to be related to the large Neotropical genus *Stethantyx*, forming with the latter and the monotypic Australian genus *Australochus* Khalaim (Khalaim 2015) a distinctive group of genera, the *Stethantyx* genus-group, and originally was distinguished from *Stethantyx* on the basis of the following features (Khalaim and Broad 2013):

	Megalochus	Stethantyx	
Antenna	shortened; flagellomeres strongly transverse	not shortened; flagellomeres weakly transverse to elongate	
Propodeum and metapleuron	with coarse irregular rugae	without rugae	
Sub-basal cell in hind wing	unusually long and narrow	not especially narrow	
First metasomal segment	round in cross-section, very slender, about 6.6 times as long as posteriorly broad	trapeziform centrally in cross-section 3.3–5.0 times as long as posteriorly broad	
Glymma	lacking	present	

A new species from southern and southeast Brazil, Stethantyx durrelli, intermediate between the genera Megalochus and Stethantyx, was recently discovered. This species is apparently closely related to *M. grandis* as both are almost identical morphologically and in coloration, except (suprisingly!) for two important diagnostic characters of the genus Megalochus: in S. durrelli, the glymma is present (Figs 15, 16) and the propodeum and metapleuron are without rugae (Figs 10, 11). In addition, some other species of Stethantyx also have shortened antennae (though not as short as in M. grandis and S. durrelli) and some recently discovered species of Stethantyx (Khalaim et al. 2013) also have the first tergite very slender, upto 5.5 times as long as anteriorly broad in female (6.6 times in *M. grandis* and 5.4 times in *S. durrelli*). Only one of the previous five diagnostic features of *Megalochus* works well for both species: the hind wing mediella (M+Cu) is very weakly arcuate and subparallel to the submediella (1A), thus the sub-basal cell is unusually long, 5.0-6.0 times as long as broad (2.8-4.0 times in Stethantyx; compare Fig. 14 and Khalaim and Broad 2013: Figs 1–10). Thus, most of the diagnostic features of *Megalochus* do not distinguish the two genera with certainty and therefore this genus is synonymized here with Stethantyx (syn. n.). Stethantyx durrelli and S. grandis (comb. n.) can be distinguished from each other, as well as from other congeners using the key below.

Portion of the key to species of Stethantyx

 3 First metasomal segment round in cross-section, without glymma. Metapleuron and dorsolateral area of propodeum with coarse irregular rugae. Fore wing with intercubitus about twice as long as abscissa of cubitus between intercubitus and second recurrent vein. Hind wing with nervellus slightly inclivous or vertical. Female with hind femur strongly clavate. Ovipositor with shallow dorsal subapical depression; sheath about 1.4 times as long as first tergite S. grandis (Khalaim & Broad), comb. n. First metasomal segment trapeziform in cross-section, with a deep glymma (Figs 15, 16). Metapleuron and dorsolateral area of propodeum densely punctate on finely granulate background, without coarse rugae, at most with fine wrinkles peripherally (Figs 10, 11). Fore wing with interubitus about 5.0 times as long as abscissa of cubitus between intercubitus and second recurrent vein (Fig. 13). Hind wing with nervellus strongly inclivous (Fig. 14). Female with hind femur weakly clavate (Fig. 12). Ovipositor with a sharp dorsal subapical notch, distal margin of this notch is almost vertical (Fig. 18); sheath

Stethantyx durrelli Khalaim, sp. n.

http://zoobank.org/8057ADFA-7E53-465E-A982-8CA6BC87316E Figs 1–21

Comparative diagnosis. *Stethantyx durrelli* sp. n. is very similar to *S. grandis* but differs from it by the metapleuron and dorsolateral area of propodeum densely punctate on a finely granulate background (Figs 10, 11, 20), without coarse, irregular rugae; fore wing with intercubitus 5.0 times as long as abscissa of cubitus between intercubitus and second recurrent vein (Fig. 13) (versus 2.0 times in *S. grandis*); hind wing with nervellus strongly inclivous (Fig. 14) (slightly inclivous to vertical in *S. grandis*); hind femur of female weakly clavate (Fig. 12); first metasomal segment trapeziform in cross-section and with deep glymma (Figs 15, 16, 21); and ovipositor with a sharp dorsal subapical notch (Fig. 18). Moreover, the new species is generally paler than *S. grandis* and has a somewhat longer ovipositor. These two species are the largest known Tersilochinae with body length 10.5 to 15.0 mm (the largest specimens of *Barycnemis* and *Stethantyx* have body lengths up to 10.0 mm), and can be distinguished from their congeners using a partial key to species of *Stethantyx* above.

Description. Female. Body length 13.0 mm. Fore wing length about 9.2 mm.

Head rounded posterior to eyes in dorsal view (Fig. 4); temple 0.7 times as long as eye width. Mandible finely and densely punctate basally, upper tooth distinctly longer than lower. Clypeus broad, lenticular, 3.2 times as long as broad (Fig. 3), separated from face by shallow broad impression, densely and coarsely punctate in upper half, smooth and impunctate in lower half, weakly convex in lateral view. Malar space half as long as basal mandibular width. Maxillary and labial palpi short (Fig. 5). Flagellum of antenna short, distinctly narrowed towards apex, with 36 flagellomeres (Fig. 1); all



Figures 1–7. *Stethantyx durrelli* sp. n., female, holotype: 1 antenna, lateral view 2 base of antenna, lateral view 3 head, frontal view 4 head, dorsal view 5 head, ventro-postero-lateral view 6 mesoscutum, dorsolateral view 7 head and scutellum, dorsolateral view.

flagellomeres, except basal and apical ones, distinctly transverse; flagellomeres 2 to 7–9 (weak and inconspicuous on flagellomeres 8 and 9) bearing finger-shaped subapical structures on outer surface (Fig. 2). Inner eye orbits very weakly convergent ventrally (Fig. 3). Face with rather dense and long brownish setae, centrally with blunt prominence. Face and frons densely punctate (distance between punctures mostly shorter than one puncture diameter), very finely granulate to almost smooth between punctures, dull. Vertex and temple with moderately dense punctures, smooth and weakly shining between punctures. Occipital carina complete. Hypostomal carina completely absent (Fig. 5).

Notaulus rather long, weakly impressed, with a strong longitudinal wrinkle and sometimes with weak adjacent wrinkles (Figs 6, 7). Mesoscutum densely punctate (distance between punctures shorter than one puncture diameter), dull, finely granulate between punctures (Fig. 6). Scutellum with moderately dense punctures, dull, finely granulate between punctures, with lateral longitudinal carinae strong, developed in its anterior 0.7 (Fig. 9, arrow). Epicnemial carina not joining anterior margin of mesopleuron, evanescent above (Fig. 8). Foveate groove of mesopleuron long, moderately broad, crenulate, extending almost entire length of mesopleuron, weak anteriorly (evanescent near epicnemial carina) and very deep and sharp centrally and posteriorly (Fig. 8). Mesopleuron distinctly and densely punctate, with impunctate area above foveate groove in its anterior part, smooth between punctures centrally and finely granulate peripherally (Fig. 8). Dorsolateral area of propodeum and metapleuron very densely punctate, dull (Figs 10, 11); lower part and periphery of dorsolateral area with shallow irregular wrinkles. Basal area of propodeum slightly widened anteriorly, 1.6 times as long as anteriorly broad and 0.65 times as long as apical area; basal longitudinal carinae weak (Figs 10, 11). Propodeal spiracle separated from pleural carina by 1.0-1.5 times diameter of spiracle (Fig. 8). Apical area anteriorly widely truncate, subrectangular (apical longitudinal carinae parallel), almost twice as long as broad (Figs 10, 11), flat, very densely punctate, dull.

Fore wing (Fig. 13) with second recurrent vein (2m-cu) weakly postfurcal. First and second abscissae of radius (Rs+2r and Rs) angled about 120°. Intercubitus (2rs-m) not thickened, very long, about 5.0 times as long as abscissa of cubitus (M) between intercubitus and second recurrent vein. First abscissa of radius almost straight, 2.5 times as long as width of pterostigma. Metacarpus (R1) not reaching apex of fore wing. Hind wing with nervellus (cu1&cu-a) strongly inclivous (Fig. 14).

Hind femur slightly clavate (Fig. 12), 4.7 times as long as broad, and 0.75 times as long as tibia. Hind basitarsus half as long as tibia. Spurs of hind tibia distinctly curved at apex.

First metasomal segment very slender, 5.4 times as long as posteriorly broad, trapeziform in cross-section, arcuate in lateral view, smooth, with glymma situated somewhat behind its middle (Fig. 15). Glymma deep, joining ventral part of postpetiole by weak groove (Fig. 16). Second tergite 2.3 times as long as anteriorly broad (Fig. 17). Thyridial depression long (Fig. 17); thyridium slightly elongate, separated from anterior margin of second tergite by 3.5 times times maximum diameter of thyridium. Ovipositor upcurved, with a deep dorsal subapical notch; sheath 1.9 times as long as first tergite and 1.75 times as long as hind tibia.

Head black; palpi, lower half of clypeus and mandible (except black teeth) brownish yellow. Antenna with scape and pedicel dark brown, flagellum black. Mesosoma (including tegula) black. Pterostigma pale brown. Legs brownish yellow; all coxae black; trochanters brown to brownish black; fore and mid femora brownish; hind femur brown, on lower and inner sides brownish black. Metasomal tergite 1 black, following tergites brown. Wings infumate with yellow-brown.



Figures 8–14. *Stethantyx durrelli* sp. n., female, holotype: 8 mesosoma, lateral view 9 mesoscutum and scutellum, lateral view 10 propodeum, dorsal view 11 propodeum, dorso-postero-lateral view 12 hind femur and tibia, lateral view 13 apex of fore wing 14 basal part of hind wing.

Male. Body length 10.5–13.0 mm, fore wing length 8.4–9.5 mm. Flagellum with 38 flagellomeres (Fig. 19); flagellomeres 3 to 8–10 (weak and inconspicuous on flagellomeres 9 and 10) bearing finger-shaped subapical structures on outer surface. Malar space 0.4 times as long as basal mandibular width. Propodeal spiracle separated from pleural carina by 0.5–1.0 times diameter of spiracle. Basal area of propodeum 0.7–0.8 times as long as apical area (Fig. 20). First tergite very slender and almost straight in



Figures 15–21. *Stethantyx durrelli* sp. n., female, holotype (15–18) and male, paratype (19–21): 15 first tergite, lateral view 16 glymma, lateral view 17 first and second tergites, dorsal view (the arrow points to the hind end of second tergite) 18 apex of ovipositor, lateral view 19 antenna, lateral view 20 propodeum, dorsolateral view 21 propodeum and first tergite, lateral view.

lateral view (Fig. 21); groove between glymma and ventral part of postpetiole absent or indistinct. Otherwise similar to female.

Variation. The male from São Paulo has metapleuron almost entirely covered with fine vertical wrinkles; dorsolateral area of propodeum with punctures mostly indistinct because of numerous fine wrinkles; basal area rather indistinct (basal longitudinal carinae weak); apical area hexagonal (apical longitudinal carinae ending anteriorly far from the posterior end of basal longitudinal carinae), impunctate; and nervellus less inclivous.

Type material. Holotype female (EMUS), Brazil, State of Rio de Janeiro, Teresópolis, 13.III.1966, coll. H. & M. Townes.

Paratypes. 1 male (FSCA), Brazil, State of São Paulo, Boracéia Biological Station, Sangre Grande, 18.XI.1976, coll. T. Rogers, 23KMPO93834. 1 male (EMUS), Brazil, State of Paraná, NE of Curitiba, Campina Grande do Sul, 16.II.1966, coll. H. & M. Townes.

Distribution. Southern and southeast Brazil (Rio de Janeiro, São Paulo, Paraná). **Etymology.** The new species is named in honour of Gerald Durrell (1925–1995), a well-known British naturalist and author of many popular books about animals.

Discussion

Originally, Townes (1971) described *Stethantyx* with no differential diagnosis, but according to the key to world genera (Townes 1971: 34) *Stethantyx* is similar to another Neotropical genus described in the same paper, *Meggoleus* Townes, and differs from the latter by small, unspecialized propodeal spiracles (strongly enlarged in *Meggoleus*) and inclivous to weakly reclivous nervellus in the hind wing (distinctly reclivous in *Meggoleus*). Later, one more species of *Meggoleus* with enlarged propodeal spiracles was described from Central Africa (Khalaim 2007) and two species from Peru (Alvarado 2012). Besides species of *Meggoleus* with enlarged propodeal spiracles and variable inclivation of the nervellus have been examined. These taxa probably also belong to *Meggoleus*, although the characters suggested by Townes for separation of these two genera do not work.

Extensive study of *Stethantyx* in the past decade demonstrated a considerable morphological diversity of this genus, e.g. some species possess a right-angled radial cell, short and thick intercubitus and abscissa of cubitus between intercubitus and second recurrent vein, broad pterostigma, epicnemial (prepectal) carina with dorsal end obliterated and first metasomal segment without glymmae, and some undescribed species are not clearly distinguished from the genera *Meggoleus*, *Probles* Förster and *Tersilochus* Holmgren. Thus, most previously used diagnostic features of *Stethantyx* (Townes 1971, Khalaim and Broad 2013) do not work well for separating all *Stethantyx* species from other genera, and the limits of *Stethantyx*, as well as some other tersilochine genera, requires further investigation. Moreover, the generic status of *Stethantyx* must be confirmed by apomorphic features, while currently all diagnostic characters of this genus seem to be plesiomorphic.

Acknowledgements

I am grateful to David Wahl (EMUS) and Kevin A. Williams (FSCA) for loan of valuable material, and Andrew Bennett (Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Ontario, Canada) and Gavin Broad (The Natural History Museum, London, UK) for their important suggestions and criticism. Also I wish to thank Alejandro Zaldívar-Riverón (UNAM) for his kind help with taking high quality photographs. This work was supported by the Russian Foundation for Basic Research, grant no. 16-04-00197.

References

Alvarado M (2012) Discovery of the genus *Meggoleus* Townes, 1971 (Hymenoptera, Ichneumonidae, Tersilochinae) in Peru, with the description of two new species. ZooKeys 163: 83–90. https://doi.org/10.3897/zookeys.163.2291

- Horstmann K (2010) Revision of Nearctic Tersilochinae II. Genera Allophrys Förster, Barycnemis Förster, Ctenophion gen. nov., Sathropterus Förster, Spinolochus Horstmann and Stethantyx Townes (Hymenoptera, Ichneumonidae). Spixiana 33(1): 73–109.
- Khalaim AI (2007) First records of *Meggoleus*, *Heterocola* and *Phradis* (Hymenoptera: Ichneumonidae: Tersilochinae) from the Afrotropical region, with description of four new species. African Invertebrates 48(2): 101–110.
- Khalaim AI (2011) Tersilochinae of South, Southeast and East Asia, excluding Mongolia and Japan (Hymenoptera: Ichneumonidae). Zoosystematica Rossica 20(1): 96–148.
- Khalaim AI (2015) To the study of Australian Tersilochinae (Hymenoptera: Ichneumonidae). Russian Entomological Journal 24(1): 77–83.
- Khalaim AI (2016) A new species of *Stethantyx* Townes (Hymenoptera: Ichneumonidae: Tersiochinae) from Argentina. Euroasian Entomological Journal 15, Suppl. 1: 167–170.
- Khalaim AI, Broad GR (2013) Tersilochinae (Hymenoptera: Ichneumonidae) of Costa Rica, part 2. Genera *Megalochus* gen. nov. and *Stethantyx* Townes. Zootaxa 3693(2): 221–266. https://doi.org/10.11646/zootaxa.3693.2.8
- Khalaim AI, Ruíz-Cancino E (2013) Mexican species of the genus Stethantyx Townes (Hymenoptera, Ichneumonidae, Tersilochinae). ZooKeys 360: 83–94. https://doi.org/10.3897/ zookeys.360.6362
- Khalaim AI, Sääksjärvi IE, Bordera S (2013) Tersilochinae of Western Amazonia (Hymenoptera: Ichneumonidae). Genus Stethantyx Townes, part 1. Zootaxa 3741(3): 301–326. https://doi. org/10.11646/zootaxa.3741.3.1
- Khalaim AI, Sääksjärvi IE, Bordera S (2015) Tersilochinae of Western Amazonia (Hymenoptera: Ichneumonidae). Genus Stethantyx Townes, part 2. Zootaxa 3981(1): 95–106. https://doi. org/10.11646/zootaxa.3981.1.4
- Parker HL, Berry PA, Silveira A (1950) Vegetable weevils and their natural enemies in Argentina and Uruguay. United States Department of Agriculture, Technical Bulletin 1016: 1–28.
- Townes HK (1969) The genera of Ichneumonidae, Part 1. Memoirs of the American Entomological Institute 11: 1–300. https://doi.org/10.1007/bf02027741
- Townes HK (1971) The genera of Ichneumonidae, Part 4. Memoirs of the American Entomological Institute 17: 1–372.
- Williams RN, Weiss MJ, Kehat M, Blumberg D (1984) The hymenopterous parasites of Nitidulidae. Phytoparasitica 12: 53–64. https://doi.org/10.1007/BF02980798

RESEARCH ARTICLE



Biting the bullet: revisionary notes on the Oraseminae of the Old World (Hymenoptera, Chalcidoidea, Eucharitidae)

Roger A. Burks¹, John M. Heraty¹, Jason Mottern^{1,2}, Chrysalyn Dominguez¹, Scott Heacox¹

l Department of Entomology, University of California, Riverside, CA 92521 **2** USDA Systematic Entomology Laboratory, Washington, DC 20013-7012

Corresponding author: John M. Heraty (john.heraty@ucr.edu)

Academic editor: P. Jansta	Received 14 December 2016	Accepted 24 March 2017	Published 28 April 2017
	http://zoobank.org/0E1B0A14-F871	-4CD8-9F29-10B255677621	

Citation: Burks RA, Heraty JM, Mottern J, Dominguez C, Heacox S (2017) Biting the bullet: revisionary notes on the Oraseminae of the Old World (Hymenoptera, Chalcidoidea, Eucharitidae). Journal of Hymenoptera Research 55: 139–188. https://doi.org/10.3897/jhr.55.11482

Abstract

Twelve genera of Oraseminae (Hymenoptera: Eucharitidae) are recognized in the Old World. The genus Orasema Cameron is now considered as found only in the New World, and the Old World species, previously treated as species groups, are now treated as distinct genera. Eight new genera are proposed: Australosema gen. n., Cymosema gen. n., Hayatosema gen. n., Ibitya gen. n., Ivieosema gen. n., Leiosema gen. n., Matantas gen. n., and Zuparka gen. n. The genus Losbanus Watanabe is given revised status from Orasema. Nine new species are proposed: Australosema politurae sp. n. (Australia), A. verghetta sp. n. (Australia), Cymosema capelina sp. n. (Australia), C. waterworthae sp. n. (Australia), Hayatosema plicator sp. n. (Vietnam), Ivieosema confluens sp. n. (Madagascar), Iv. limula sp. n. (Madagascar), Leiosema lesiolouna sp. n. (Republic of Congo), and Zuparka fisheri sp. n. (Madagascar). New combinations (from Orasema) include Australosema valgius (Walker, 1839), A. synempora (Heraty, 1994), Hayatosema assectator (Kerrich, 1963), H. delhiensis (Narendran & G. Kumar, 2005), H. initiator (Kerrich, 1963), H. kailashi (G. Kumar & Sureshan, 2015), H. nigra (Heraty, 1994), H. nirupama (G. Kumar & Narendran, 2007), H. siruvanica (G. Kumar & Sureshan, 2015), Ibitya communis (Risbec, 1952), Ib. seyrigi (Risbec, 1952), Ivieosema fraudulenta (Reichensperger, 1913), Iv. striatosoma (Heraty, 1994), Leiosema glabra (Heraty, 1994), Losbanus bouceki (Heraty, 1994), L. ishii (Heraty, 1994), L. promecea (Heraty, 1994), L. rugulosa (Heraty, 1994), Matantas koghisiana (Heraty, 1994), and Zuparka monomoria (Heraty, 2000). Losbanus uichancoi Ishii, 1932 is given revised status from Orasema. Distribution records, a new host association of Pheidole (Myrmicinae) for Ibitya communis, and an identification key to the Old World genera and species are provided.

Copyright Roger A. Burks et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Keywords

Parasitoid, Formicidae, morphology, revision, Palaeotropical

Introduction

Oraseminae constitutes one of the major lineages of the family Eucharitidae, with the estimated number of species approaching 200 (Heraty 2002), all of which are parasitoids of ants (Hymenoptera: Formicidae). There are verified host records of Oraseminae attacking six genera in the ant subfamily Myrmicinae and dubious records on Ecitoninae and Formicinae (Heraty 1994, 2002, Lachaud and Pérez-Lachaud 2012). Hosts for the Old World Oraseminae are species of the myrmicine genera *Monomorium* Mayr and *Pheidole* Westwood (Table 1). While *Orasema* Cameron is present throughout the New World with a northern-most record from southern Canada, Old World Oraseminae are known only from the tropics and subtropics, with northern-most records in India (New Delhi), Taiwan, Iriomote Island of Japan, and the southwestern highlands of Yemen (Heraty 1994, 2002).

The Old World species of Oraseminae were previously revised by Bouček (1988) and Heraty (1994), with a new species of Orasema from Madagascar added by Heraty (2000). A total of 36 species of Old World Oraseminae were placed into four genera: Indosema Husain & Agarwal, Orasema Cameron, Orasemorpha Bouček, and Timioderus Waterston. The Old World species of Orasema were grouped into six species groups by Heraty (1994), with two new groups added by Heraty (2000). Based on an analysis of 62 morphological and behavioral characters, Indosema, Timioderus and Orasemorpha were monophyletic and sister to Orasema, with the Old World species groups of Orasema paraphyletic to the New World Orasema (Heraty 2000). Among these genera, Timioderus and Indosema were considered distinct because of fusion of the mesosoma across the transscutal articulation between the axillae, and because they have eggs that are cylindrical instead of stalked (Heraty 1994, 2000); all other known eggs of Eucharitidae are stalked with the exception of Gollumiellinae (Heraty et al. 2004). Both *Timioderus* and *Orasemorpha* are the only Oraseminae known to deposit multiple eggs into a single oviposition puncture (unknown in Indosema), whereas all known Orasema sensu lato deposit a single stalked egg into each oviposition puncture made by the specialized ovipositor (Das 1963, Heraty 1994, 2000, Ishii 1932). All Oraseminae can be defined by the presence of an enlarged, toothed and usually anteriorly curved ovipositor that is used to enlarge a hole in plant tissue to deposit their eggs.

When using molecular data, the New World species of *Orasema* are consistently monophyletic (Heraty et al. 2004, Murray et al. 2013). The Old World Oraseminae are either monophyletic (Heraty 1994, Heraty et al. 2004) or paraphyletic (Murray et al. 2013) to the New World *Orasema*. Monophyly of *Orasema* s.l. worldwide is never supported. More recent unpublished analyses consistently support either monophyly of the Old World Oraseminae (ribosomal analyses with 18S, 28S, COI), or their paraphyly (Anchored Enrichment, 366-411 loci) with respect to the New World *Orasema*, but

Table 1. List of Old World Oraseminae, with their geographic distribution and ant host genus. For a morecomplete list of synonymies and host information see Heraty (1994, 2002) and Heraty (2017). Asterisk (*)denotes type species of genus. Australian refers to Australia including Tasmania. NR is new host record.

A. politurate sp. n. Australia Australiseran gen. n. A. symmptora (Heraty, 1994), comb. n. Australia (=valgius group) A. valgius (Walker, 1839), comb. n.* Australia Cymosema gen. n. C. capelina sp. n. Australia Cymosema gen. n. C. capelina sp. n. Australia H. assectator (Kertich, 1963)* Indo-Pacific Pheidole H. assectator (Kertich, 1963) Indo-Pacific Heidole H. assectator (Kertich, 1963) Indo-Pacific Heidole H. nititator (Kertich, 1953) Indo-Pacific Heidole H. nititator (Kertich, 1953) Indo-Pacific Heidole H. nititator (Kertich, 1953) Indo-Pacific Heidole H. nititator (Kertich, 1952), comb. n.* Madagascar Pheidole NR (=communis group) I. sitatosona group I. indica Husain & Agarwal, 1983 * India & Kenya Indosena I. indica Husai	Genus	Species	Distribution	Host genus
Australisema gen. n. A. synempora (Heraty, 1994), comb. n. Australia Pheidale A. valgius (Walker, 1839), comb. n.* Australia Pheidale Cymosema gen. n. C. capelina sp. n. Australia Contention Hayatosema gen. n. H. assectator (Kerrich, 1963)* Indo-Pacific Pheidale H. assectator (Kerrich, 1963) Indo-Pacific Pheidale H. debinesis (Narendran & G. Kumar, 2005) Indo-Pacific Indo-Pacific H. initiator (Kerrich, 1963)* Indo-Pacific Indo-Pacific H. initiator (Kerrich, 1963) Indo-Pacific Indo-Pacific H. initiator (Kerrich, 1963) Indo-Pacific Indo-Pacific H. initiator (G. Kumar & Sureshan, 2015) Indo-Pacific Indo-Pacific H. initiator (G. Kumar & Sureshan, 2015) Indo-Pacific Indo-Pacific Ibitya gen. n. I. communis (Risbec, 1952), comb. n.* Madagascar Pheidale NR (=communis group) I. serving (Risbec, 1952), comb. n.* Madagascar Indiae Husain & Agarwal, 1983 * India & Kenya Indosema I. indiar Husain & Agarwal, 1983 * India & Kenya Indiae Kenya Indiae Kenya Icosema gen. n. I. faudulenta		<i>A. politurae</i> sp. n.	Australia	
(=valgius group) A. valgius (Walker, 1839), comb. n.* Australia Pheidole Cymosema gen. n. C. capelina sp. n. Australia C. apelina sp. n. Australia Cymosema gen. n. C. capelina sp. n. Australia C. apelina sp. n. Australia Hayatosema gen. n. H. ascetator (Kerrich, 1963)* Indo-Pacific Pheidole H. apatosema gen. n. H. kailabi (G. Kumar & Sureshan, 2015) Indo-Pacific H. initiator (Kerrich, 1963) Hayatosema gen. n. H. kailabi (G. Kumar & Sureshan, 2015) Indo-Pacific H. initiator (Kerrich, 1963) Hayatosema gen. n. I. kailabi (G. Kumar & Sureshan, 2015) Indo-Pacific H. initiator (Kerrich, 1963) Ibitya gen. n. I. communis (Risbec, 1952), comb. n.* Madagascar Pheidole NR (=communis group) I. india Husain & Agarwal, 1983 * India & Kenya India & Kenya Indosema I. india Husain & Agarwal, 1983 * India & Kenya India & Kenya Indosema gen. n. I. fauduletnat (Reichensperger), comb. n. Ethiopian India & Kenya Indosema gen. n. I. fauduletnat (Reichensperger), comb. n. Ethiopian India & Kenya I. confluens sp. n. I. fauduletnata	Australosema gen. n.	A. synempora (Heraty, 1994), comb. n.	Australia	
A verghetta sp. n. Australia Cymoxema gen. n. C. capelina sp. n. Australia C. vaterworthae sp. n. * Australia H. sexectator (Kerrich, 1963)* Indo-Pacific H. delhiensis (Narendran & G. Kumar, 2005) Indo-Pacific H. delhiensis (Narendran & G. Kumar, 2005) Indo-Pacific H. initiator (Kerrich, 1963) Indo-Pacific H. initiator (G. Kumar & Narendran, 2007) Indo-Pacific H. initiator (G. Kumar & Sureshan, 2015) Indo-Pacific H. initiator (Risbec, 1952), comb. n. * Madagascar Indosema I confluens sp. n. Madagascar Indosema group) I. fraudulenta (Reichensperger), comb. n. Ethiopian Leiosema gen. n. I. fraudulenta (Reichensperger), comb. n. Ethiopian (=communi group) I. glabara (Heraty), comb. n. * Ethiopian Leiosema gen. n. I. fraudulenta (Reichenspergr), comb. n. Ethiopian </td <td>(=valgius group)</td> <td>A. valgius (Walker, 1839), comb. n. *</td> <td>Australia</td> <td>Pheidole</td>	(=valgius group)	A. valgius (Walker, 1839), comb. n. *	Australia	Pheidole
Cymosena gen. n. C. capelina sp. n. * Australia C. more constrained and the sp. n. * Australia Pheidole H. assectator (Kerrich, 1963)* Indo-Pacific Pheidole H. assectator (Kerrich, 1963)* Indo-Pacific Pheidole H. initiator (Kerrich, 1963)* Indo-Pacific Pheidole H. initiator (Kerrich, 1963) Indo-Pacific Indo-Pacific H. initiator (Kerrich, 1963) Indo-Pacific Indo-Pacific H. nitrupana (G. Kumar & Sureshan, 2015) Indo-Pacific Indo-Pacific H. plicator sp. n. Indo-Pacific Indo-Pacific Ibipa gen. n. I. communic (Risbec, 1952), comb. n. * Madagascar Indosema I. indica Husain & Agarwal, 1983 * India & Kenya Indosema gen. n. I. fraudulenta (Reichensperger), comb. n. Madagascar Ivieosema gen. n. I. glabra (Heraty), comb. n. * Ethiopian I. striatosoma (Heraty), comb. n. * Ethiopian Indo-Pacific I. striatosoma (Heraty), comb. n. * Ethiopian Indo-Pacific I. isbiti (Heraty, 1994), comb. n. * Ethiopian Indo-Pacific		<i>A. verghetta</i> sp. n.	Australia	
Cymonend gen. n.C. waterworthæ sp. n. *AustraliaHayatosema gen. n.H. assectator (Kerrich, 1963)*Indo-PacificHayatosema gen. n.H. kailashi (G. Kumar & G. Kumar, 2005)Indo-PacificH. kailashi (G. Kumar & Sureshan, 2015)Indo-PacificH. nirritaro (Kerrich, 1963)Indo-PacificH. kailashi (G. Kumar & Sureshan, 2015)Indo-PacificH. nirrupama (G. Kumar & Sureshan, 2007)Indo-PacificH. nirrupama (G. Kumar & Sureshan, 2015)Indo-PacificH. plicator sp. n.Indo-PacificH. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Bisbec, 1952), comb. n. *MadagascarPheidole NR(=communis group)I. seyrigi (Risbec, 1952), comb. n. *IndosemaI. confluents sp. n.IndosemaI. confluents sp. n.I. imula sp. n.MadagascarIvicosoma gen. n.I. fraudulenta (Reichensperger), comb. n.EthiopianI. striatosoma (Heraty), comb. n. *EthiopianI. keidouma sp. n.Leiosema gen. n.I. glabra (Heraty), comb. n. *EthiopianI. bouceki (Boucek), comb. n. *EthiopianI. bouceki (Boucek), comb. n.Losbanus rev. stat.I. bouceki (Boucek), comb. n.(=uichancoi group)M. kogbisiana (Heraty), comb. n.I. promecea (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaI. joint (Heraty), comb. n.New GuineaI. joint (Heraty), comb. n.New GuineaI. joint (Heraty), comb. n.<	Cumpany damp a	<i>C. capelina</i> sp. n.	Australia	
Hasterator (Kerrich, 1963)*Indo-PacificPheidoleHayatosema gen. n.H. delbiensis (Narendran & G. Kumar, 2005)Indo-Pacific(=assectator group)H. kailashi (G. Kumar & Sureshan, 2015)Indo-PacificH. nitritator (Kerrich, 1963)Indo-Pacific(=assectator group)H. kailashi (G. Kumar & Sureshan, 2015)Indo-PacificH. nirapama (G. Kumar & Narendran, 2007)Indo-PacificH. nirapama (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarPheidole NR(=communis group)I. seyrigi (Risbec, 1952), comb. n. *MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. limula sp. n.MadagascarI. indula sp. n.I. faudulenta (Reichensperger), comb. n.EthiopianLeiosema gen. n.I. glabra (Heraty), comb. n. *EthiopianI. sivitatosoma (Heraty), comb. n. *EthiopianLeisbanus rev. stat.I. bioli (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaI. bioli (Heraty), comb. n.New GuineaI. septistra (Girault, 1940)AustraliaO. agerbiet (Walker, 1839)*Aust	<i>Cymosema</i> gen. n.	C. waterworthae sp. n. *	Australia	
Hayatosema gen. n.H. delhiensis (Narendran & G. Kumar, 2005)Indo-PacificHayatosema gen. n.H. kailabi (G. Kumar & Sureshan, 2015)Indo-Pacific(-assectator group)H. kailabi (G. Kumar & Narendran, 2007)Indo-PacificH. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. nirupama (G. Kumar & Sureshan, 2015)Indo-PacificH. siruvania (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. confluens sp. n.MadagascarIvieosema gen. n.I. fraudulenta (Reichensperger), comb. n.EthiopianI. sprigi (Risbec, 1952), comb. n. *EthiopianI. sitiatosoma (Heraty), comb. n. *EthiopianI. sitiatosoma group)I. fraudulenta (Reichensperger), comb. n.MadagascarI. sitiatosoma (Heraty), Somb. n. *EthiopianI. sitiatosoma (Heraty), Somb. n. *EthiopianI. sitia (Heraty), comb. n.New GuineaI. sitii (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n. *New GuineaI. vichancoi group)M. koghisiana (Heraty), comb. n. *New GuineaI. vichancoi Watanabe comb. n. *PhilippinesMatantas gen. n.I. didentata (Girault, 1940)AustraliaO. didentata (Girault, 1934)AustraliaOniedeleO.		H. assectator (Kerrich, 1963)*	Indo-Pacific	Pheidole
Hayatosema gen. n. (=assectator group)H. initiator (Kerrich, 1963)Indo-PacificH. aigra (Heraty)EthiopianH. nigra (Heraty)EthiopianH. nigra (Heraty)Indo-PacificH. nigra (G. Kumar & Narendran, 2007)Indo-PacificH. plicator sp. n.Indo-PacificH. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIniosema gen. n.I. confluens sp. n.MadagascarIvieosema gen. n.I. fraudilenta (Reichensperger), comb. n.MadagascarI. eisosema gen. n.I. fraudilenta (Reichensperger), comb. n.PheidoleI. striatosoma (Heraty), 1994), comb. n. *EthiopianPheidoleI. striatosoma (Heraty), comb. n. *EthiopianIndiaLeisosema gen. n.L. glabra (Heraty), comb. n. *EthiopianI. striatosoma (Heraty), 1994), comb. n. *EthiopianIndiaLeisolauna sp. n.L. sibii (Heraty), comb. n.TaiwanLeisolauna sp. n.I. sibii (Heraty), comb. n.New GuineaLosbamus rev. stat.L. sibii (Heraty), comb. n.New GuineaL. rugulosa (Heraty), comb. n.New GuineaI. uichancoi Watanabe comb. n. *Matantas gen. n.L. odenceki (Ginault, 1940)AustraliaO. didentata (Girault, 1934)AustraliaPheidoleO. didentata (Girault, 1934)AustraliaPheidoleOnsemorphaO. pytallus (Walker, 1846)Australia<		H. delhiensis (Narendran & G. Kumar, 2005)	Indo-Pacific	
Hayatosema gen. n.H. kailashi (G. Kumar & Sureshan, 2015)Indo-Pacific(=assectator group)H. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. plicator sp. n.Indo-PacificH. sirupanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. fraudulenta (Reichensperger), comb. n.MadagascarI. fraudulenta (Reichensperger), comb. n.EthiopianLeisema gen. n.I. glabra (Heraty), 1994), comb. n. *EthiopianI. seyrigi (Heraty), comb. n.EthiopianLeisema gen. n.I. glabra (Heraty, 1994), comb. n. *EthiopianI. suchancoi group)I. bouceki (Boucek), comb. n.New GuineaLosbanus rev. stat.I. promecea (Heraty), comb. n.New GuineaI. nucleas (Heraty), comb. n.New GuineaI. ishii (Heraty), comb. n.Lobanus group)Matantas gen. n.New GuineaI. nucleas (Heraty), comb. n. *PhilippinesMatantas gen. n.O. didentata (Girault, 1940)AustraliaO. gethei (Girault, 1934)AustraliaO. gethei (Girault, 1934)AustraliaO. nymnicae (Girault, 1936)AustraliaOrasemorphaO. pytallus Walker, 1846)AustraliaOrasemorphaO. sameenibae Herary, 1994Australia		H. initiator (Kerrich, 1963)	Indo-Pacific	
(=assectator group)H. nigra (Heraty)EthiopianH. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. picator sp. n.Indo-PacificH. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *Madagascar(=communis group)I. seyrigi (Risbec, 1952), comb. n.MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvicosema gen. n.I. confluens sp. n.Madagascar(=striatosoma group)I. fraudulenta (Reichensperger), comb. n.EthiopianI. striatosoma (Heraty), pomb. n. *EthiopianLeiosema gen. n.I. glabra (Heraty), comb. n. *Ethiopian(=glabra group)I. leiolouna sp. n.EthiopianLobbanus rev. stat.I. bit (Heraty), comb. n.New GuineaL. indica (Heraty), comb. n.I. siviatusanaI.L. nuchancoi group)I. koghisiana (Heraty), comb. n.New GuineaL. uichancoi Watanabe comb. n. *PhilippinesMatantas gen. n.O. didentata (Girault, 1940)AustraliaOrasemorphaO. geethei (Girault, 1936)AustraliaOrasemorphaO. goethei (Girault, 1936)AustraliaOrasemorphaO. starsenibae Herary, 1994Australia	<i>Hayatosema</i> gen. n.	H. kailashi (G. Kumar & Sureshan, 2015)	Indo-Pacific	
H. nirupama (G. Kumar & Narendran, 2007)Indo-PacificH. plicator sp. n.Indo-PacificH. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvicosema gen. n.I. confluens sp. n.MadagascarIstitatosoma group)I. fraudulenta (Reichensperger), comb. n.MadagascarI. india duenta (Reichensperger), comb. n.EthiopianPheidoleI. striatosoma (Heraty, 1994), comb. n. *EthiopianIndia & Leisolouna sp. n.Leiosema gen. n.I. glabra (Heraty, 1994), comb. n. *EthiopianI. bouceki (Boucek), comb. n.New GuineaI. isbii (Heraty), comb. n.Lobbanus rev. stat.I. bouceki (Boucek), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.Matantas gen. n.I. bouceki (Boucek), comb. n. *PhilippinesMatantas gen. n.M. koghisiana (Heraty), comb. n.New GuineaI. uichancoi Watanabe comb. n. *PhilippinesI. origibasianaOrasemorphaO. goethi (Girault, 1936)AustraliaOrasemorphaO. pytallus (Walker, 1846)AustraliaOrasemorphaO. pytallus (Walker, 1846)AustraliaOrasemorphaO. pytallus (Walker, 1846)Australia	(=assectator group)	H. nigra (Heraty)	Ethiopian	
H. plicator sp. n.Indo-PacificH. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *Madagascar(=communis group)I. seyrigi (Risbec, 1952), comb. n.MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. confluens sp. n.Madagascar(=striatosoma group)I. fraudulenta (Reichensperger), comb. n.EthiopianLeiosema gen. n.I. glabra (Heraty), comb. n. *Ethiopian(=glabra group)I. leisolouna sp. n.EthiopianLosbanus rev. stat.I. sibii (Heraty), comb. n.Taiwan(=uichancoi group)I. kibii (Heraty), comb. n.TaiwanL. sibii (Heraty), comb. n.New GuineaL. ngulosa (Heraty), comb. n.New GuineaL. sibii (Heraty), comb. n.New GuineaL. sibii (Heraty), comb. n.New GuineaL. sibii (Heraty), comb. n.New GuineaL. ngulosa (Heraty), comb. n.New GuineaL. ngulosa (Heraty), comb. n.New GuineaL. vichancoi Watanabe comb. n. *PhilippinesMatantas gen. n.M. kogbisiana (Heraty), comb. n. *(=koghisiana group)M. kogbisiana (Heraty), comb. n. *OrasemorphaO. didentata (Girault, 1940)AustraliaO. agethei (Girault, 1934)AustraliaO. onymricae (Girault, 1936)AustraliaO. onymricae (Girault, 1936)AustraliaO. onymricae (Girault, 1936)AustraliaO. onymricae (Girault, 1936)Austral		H. nirupama (G. Kumar & Narendran, 2007)	Indo-Pacific	
H. siruvanica (G. Kumar & Sureshan, 2015)Indo-PacificIbitya gen. n.I. communis (Risbec, 1952), comb. n. *MadagascarPheidole NR(=communis group)I. seyrigi (Risbec, 1952), comb. n.MadagascarIndia & KenyaIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIndia & KenyaIvieosema gen. n.I. limula sp. n.MadagascarIndia & Kenya(=striatosoma group)I. fraudulenta (Reichensperger), comb. n.EthiopianPheidoleI. striatosoma (Heraty), comb. n. *EthiopianIndia & KenyaLeiosema gen. n.L. glabra (Heraty, 1994), comb. n. *EthiopianIndia & Kenya(=glabra group)L. lesiolouna sp. n.New GuineaI. ishii (Heraty), comb. n. *EthiopianLosbanus rev. stat.L. bouceki (Boucek), comb. n.New GuineaI. ishii (Heraty), comb. n.TaiwanL. promecea (Heraty), comb. n.New GuineaI. rugulosa (Heraty), comb. n.New GuineaL. uichancoi group)M. koghisiana (Heraty), comb. n. *PhilippinesIndia & Giault, 1940)Matantas gen. n.M. koghisiana (Heraty), comb. n. *New Caledonia(=koghisiana group)M. koghisiana (Heraty), comb. n. *New Caledonia0. didentata (Girault, 1940)AustraliaO. egethei (Girault, 1934)0. agethei (Girault, 1934)AustraliaPheidole0. nymnicae (Girault, 1936)AustraliaPheidole0. spaseniloga Heravy 1994AustraliaPheidole		H. plicator sp. n.	Indo-Pacific	
Ibitya gen. n. I. communis (Risbec, 1952), comb. n. * Madagascar Pheidole NR (=communis group) I. seyrigi (Risbec, 1952), comb. n. Madagascar India & Kenya Indosema I. indica Husain & Agarwal, 1983 * India & Kenya I Indosema I. indica Husain & Agarwal, 1983 * India & Kenya I Ivieosema gen. n. I. confluens sp. n. Madagascar I I. fraudulenta (Reichensperger), comb. n. Ethiopian Pheidole I. striatosoma group) I. fraudulenta (Reichensperger), comb. n. Ethiopian Leiosema gen. n. I. glabra (Heraty), comb. n. * Ethiopian (=glabna group) I. lesiolouna sp. n. Ethiopian L. sbianus rev. stat. I. ishii (Heraty), comb. n. New Guinea L. rugulosa (Heraty), comb. n. I. rugulosa (Heraty), comb. n. New Guinea L. rugulosa (Heraty), comb. n. New Guinea I. rugulosa (Heraty), comb. n. Leksophisiana group) M. koghisiana (Heraty), comb. n. * New Guinea L. vichancoi Watanabe comb. n. * Philippines O. didentata (Girault, 1940) A. koghisiana (Heraty), comb. n. * New Caledonia O. eriobotes (Walker, 1839)* Austra		H. siruvanica (G. Kumar & Sureshan, 2015)	Indo-Pacific	
(=communis group)I. seyrigi (Risbec, 1952), comb. n.MadagascarIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. confluens sp. n.Madagascar(=striatosoma group)I. fraudulenta (Reichensperger), comb. n.EthiopianI. striatosoma (Heraty), comb. n. *EthiopianLeiosema gen. n.L. glabra (Heraty, 1994), comb. n. *Ethiopian(=glabra group)I. leiolouna sp. n.EthiopianLosbanus rev. stat.L. bouceki (Boucek), comb. n.New GuineaL. sibii (Heraty), comb. n.TaiwanL.L. rugulosa (Heraty), comb. n.New GuineaL. rugulosa (Heraty), comb. n.New GuineaL. uichancoi group)M. koghisiana (Heraty), comb. n. *PhilippinesMatantas gen. n.O. didentata (Girault, 1940)AustraliaO. didentata (Girault, 1936)AustraliaDeidoleOrasemorphaO. pytallus (Walker, 1839)*AustraliaOrasemorphaO. spasepiloga Heraty, 1994Australia	Ibitya gen. n.	I. communis (Risbec, 1952), comb. n. *	Madagascar	Pheidole NR
IndosemaI. indica Husain & Agarwal, 1983 *India & KenyaIvieosema gen. n.I. confluens sp. n.Madagascar(=striatosoma group)I. fraudulenta (Reichensperger), comb. n.MadagascarI. fraudulenta (Reichensperger), comb. n.EthiopianPheidoleI. striatosoma (Heraty), comb. n. *EthiopianILeiosema gen. n.I. glabra (Heraty, 1994), comb. n. *Ethiopian(=glabra group)I. leiolouna sp. n.EthiopianLosbanus rev. stat.I. bouceki (Boucek), comb. n.New GuineaL. ishii (Heraty), comb. n.TaiwanL. spomecea (Heraty), comb. n.New GuineaL. uichancoi group)I. koghisiana (Heraty), comb. n.New GuineaL. uichancoi Watanabe comb. n. *PhilippinesMatantas gen. n.M. koghisiana (Heraty), comb. n. *New Caledonia(=koghisiana group)O. didentata (Girault, 1940)AustraliaO. geethei (Girault, 1934)AustraliaOnyrmicae (Girault, 1936)OrasemorphaO. pytallus (Walker, 1846)AustraliaO spareninger Heraty, 1994Australia	(=communis group)	I. seyrigi (Risbec, 1952), comb. n.	Madagascar	
Ivieosema gen. n.I. confluens sp. n.Madagascar[=striatosoma group)I. finula sp. n.Madagascar[=striatosoma group)I. fraudulenta (Reichensperger), comb. n.EthiopianI. finula sp. n.I. striatosoma (Heraty), comb. n. *EthiopianLeiosema gen. n.I. glabra (Heraty, 1994), comb. n. *Ethiopian(=glabra group)I. leiolouna sp. n.EthiopianLosbanus rev. stat.I. bouceki (Boucek), comb. n.New Guinea(=uichancoi group)I. bouceki (Boucek), comb. n.New GuineaL. sihii (Heraty), comb. n.I. promecea (Heraty), comb. n.New GuineaL. rugulosa (Heraty), comb. n.New GuineaL. uichancoi watanabe comb. n. *PhilippinesMatantas gen. n.M. koghisiana (Heraty), comb. n. *New CaledoniaOrasemorphaO. didentata (Girault, 1940)AustraliaOnsemorphaO. pytallus (Walker, 1846)AustraliaO. straliaO. straliaOnstralia	Indosema	I. indica Husain & Agarwal, 1983 *	India & Kenya	
Ivieosema gen. n. I. limula sp. n. Madagascar (=striatosoma group) I. fraudulenta (Reichensperger), comb. n. Ethiopian Pheidole I. striatosoma (Heraty), comb. n. * Ethiopian I. Image: Striatosoma (Heraty), comb. n. * Ethiopian Leiosema gen. n. L. glabra (Heraty, 1994), comb. n. * Ethiopian Image: Striatosoma (Heraty, 1994), comb. n. * Ethiopian Losbanus rev. stat. L. bouceki (Boucek), comb. n. New Guinea Image: Striatosoma (Heraty), comb. n. Image: Striatosoma (Heraty), comb. n. Losbanus rev. stat. L. ishii (Heraty), comb. n. Taiwan Image: Striatosoma (Heraty), comb. n. Losbanus rev. stat. L. ishii (Heraty), comb. n. New Guinea Image: Striatosoma (Heraty), comb. n. Luichancoi group) L. ishii (Heraty), comb. n. New Guinea Image: Striatosoma (Heraty), comb. n. Matantas gen. n. L. wichancoi Watanabe comb. n. * New Caledonia Image: Striatosoma (Heraty), comb. n. * Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia Image: Striatosoma (Heraty), comb. n. * Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia Image: Striatosoma (Heraty), Striatosoma (Heraty), Striatosoma (Heraty), Striatosoma (Heraty), Striatosom		<i>I. confluens</i> sp. n.	Madagascar	
I. fraudulenta (Reichensperger), comb. n. Ethiopian Pheidole I. striatosoma group) I. fraudulenta (Reichensperger), comb. n. Ethiopian Pheidole Leiosema gen. n. L. glabra (Heraty, 1994), comb. n. * Ethiopian Ethiopian (=glabra group) L. lesiolouna sp. n. Ethiopian Ethiopian Losbanus rev. stat. L. isbii (Heraty), comb. n. New Guinea L. isbii (Heraty), comb. n. Losbanus rev. stat. L. promecea (Heraty), comb. n. Taiwan L. isbii (Heraty), comb. n. Luichancoi group) Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Guinea Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia O. didentata (Girault, 1940) O. didentata (Girault, 1940) Australia O. ogethei (Girault, 1934) Australia O. agrenorpha O. pytallus (Walker, 1846) Australia Pheidole O. pytallus (Walker, 1846) Australia O. agrenologe	Ivieosema gen. n.	<i>I. limula</i> sp. n.	Madagascar	
I. striatosoma (Heraty), comb. n. *EthiopianLeiosema gen. n.L. glabra (Heraty, 1994), comb. n. *Ethiopian(=glabra group)L. lesiolouna sp. n.EthiopianLosbanus rev. stat.L. bouceki (Boucek), comb. n.New Guinea(=uichancoi group)L. bouceki (Boucek), comb. n.TaiwanLosbanus rev. stat.L. ishii (Heraty), comb. n.Taiwan(=uichancoi group)L. ishii (Heraty), comb. n.New GuineaL. ishii (Heraty), comb. n.New GuineaL. iuchancoi Watanabe comb. n.New GuineaL. uichancoi Watanabe comb. n. *PhilippinesMatantas gen. n. (=koghisiana group)M. koghisiana (Heraty), comb. n. *New CaledoniaO. didentata (Girault, 1940)AustraliaO. ogethei (Girault, 1934)OnasemorphaO. pytallus (Walker, 1846)AustraliaOnasemorphaO. sparsniloga Herary 1994Australia	(=striatosoma group)	I. fraudulenta (Reichensperger), comb. n.	Ethiopian	Pheidole
Leiosema gen. n. L. glabra (Heraty, 1994), comb. n. * Ethiopian (=glabra group) L. leiolouna sp. n. Ethiopian Losbanus rev. stat. L. bouceki (Boucek), comb. n. New Guinea Losbanus rev. stat. L. ishii (Heraty), comb. n. Taiwan Losbanus rev. stat. L. ishii (Heraty), comb. n. New Guinea L. ishii (Heraty), comb. n. New Guinea L. ishii (Heraty), comb. n. L. rugulosa (Heraty), comb. n. New Guinea L. iuchancoi Watanabe comb. n. * Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia O. didentata (Girault, 1940) Australia O. eribotes (Walker, 1839)* Onsemorpha O. pytallus (Walker, 1846) Australia O. sparsenilosed Herary 1994 Australia		I. striatosoma (Heraty), comb. n. *	Ethiopian	
(=glabra group) L. lesiolouna sp. n. Ethiopian Losbanus rev. stat. L. bouceki (Boucek), comb. n. New Guinea Losbanus rev. stat. L. ishii (Heraty), comb. n. Taiwan L. ishii (Heraty), comb. n. New Guinea L. ishii (Heraty), comb. n. L. inchancoi group) L. inchancoi (Heraty), comb. n. New Guinea L. inchancoi Watanabe comb. n. * Philippines Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia O. didentata (Girault, 1940) Australia O. eribotes (Walker, 1839)* Onasemorpha O. pytallus (Walker, 1846) Australia On sparsenilosed Heraty, 1994 Australia	Leiosema gen. n.	L. glabra (Heraty, 1994), comb. n. *	Ethiopian	
Losbanus rev. stat. L. bouceki (Boucek), comb. n. New Guinea Losbanus rev. stat. L. ishii (Heraty), comb. n. Taiwan L. ishii (Heraty), comb. n. New Guinea L. ishii (Heraty), comb. n. L. rugulosa (Heraty), comb. n. New Guinea L. iuchancoi Watanabe comb. n. * Matantas gen. n. L. uichancoi Watanabe comb. n. * Philippines Matantas group) M. koghisiana (Heraty), comb. n. * New Caledonia O. didentata (Girault, 1940) Australia O. eribotes (Walker, 1839)* Onasemorpha O. goethei (Girault, 1936) Australia Pheidole O. sprenilosa Herary, 1994 Australia Image: Pheidole Image: Pheidole	(=glabra group)	<i>L. lesiolouna</i> sp. n.	Ethiopian	
Losbanus rev. stat. L. ishii (Heraty), comb. n. Taiwan (=uichancoi group) L. promecea (Heraty), comb. n. New Guinea L. rugulosa (Heraty), comb. n. New Guinea L. uichancoi Watanabe comb. n. * Matantas gen. n. L. uichancoi Watanabe comb. n. * Philippines Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia O. didentata (Girault, 1940) Australia O. didentata (Girault, 1934) Australia O. goethei (Girault, 1934) Australia O. myrmicae (Girault, 1936) Australia O. sparsenilosa Heraty, 1994 Australia		L. bouceki (Boucek), comb. n.	New Guinea	
Losbanus rev. stat. L. promecea (Heraty), comb. n. New Guinea (=uichancoi group) L. rugulosa (Heraty), comb. n. New Guinea L. uichancoi Watanabe comb. n. * Philippines Matantas gen. n. M. koghisiana (Heraty), comb. n. * New Caledonia (=koghisiana group) M. koghisiana (Heraty), comb. n. * New Caledonia 0. didentata (Girault, 1940) Australia Oc. eribotes (Walker, 1839)* 0. goethei (Girault, 1934) Australia Pheidole 0. myrmicae (Girault, 1936) Australia Oc. australia 0. sparsenilosa Herary, 1994 Australia Description		L. ishii (Heraty), comb. n.	Taiwan	
(=utchancol group) L. rugulosa (Heraty), comb. n. New Guinea L. rugulosa (Heraty), comb. n. * Philippines Matantas gen. n. (=koghisiana group) M. koghisiana (Heraty), comb. n. * New Caledonia 0. didentata (Girault, 1940) Australia 0. eribotes (Walker, 1839)* Australia 0. goethei (Girault, 1934) Australia 0. myrmicae (Girault, 1936) Australia 0. pytallus (Walker, 1846) Australia 0. sparsenilosa Herary, 1994 Australia	Losbanus rev. stat.	L. promecea (Heraty), comb. n.	New Guinea	
L. uichancoi Watanabe comb. n. * Philippines Matantas gen. n. (=koghisiana group) M. koghisiana (Heraty), comb. n. * New Caledonia 0. didentata (Girault, 1940) Australia 0. eribotes (Walker, 1839)* Australia 0. goethei (Girault, 1934) Australia 0. myrmicae (Girault, 1936) Australia 0. myrmicae (Girault, 1936) Australia 0. sparsenilosa Herary 1994 Australia	(= <i>uichancoi</i> group)	L. rugulosa (Heraty), comb. n.	New Guinea	
Matantas gen. n. (=koghisiana group) M. koghisiana (Heraty), comb. n. * New Caledonia 0. didentata (Girault, 1940) Australia 0. eribotes (Walker, 1839)* Australia 0. goethei (Girault, 1934) Australia 0. myrmicae (Girault, 1936) Australia 0. pytallus (Walker, 1846) Australia 0. sparsenilosa Heraty, 1994 Australia		L. uichancoi Watanabe comb. n. *	Philippines	
O. didentata (Girault, 1940) Australia O. eribotes (Walker, 1839)* Australian O. goethei (Girault, 1934) Australia O. myrmicae (Girault, 1936) Australia Orasemorpha O. pytallus (Walker, 1846) O. sparsenilosa Heraty, 1994 Australia	Matantas gen. n. (=koghisiana group)	<i>M. koghisiana</i> (Heraty), comb. n. *	New Caledonia	
O. eribotes (Walker, 1839)* Australian Pheidole O. goethei (Girault, 1934) Australia O. myrmicae (Girault, 1936) Australia Orasemorpha O. pytallus (Walker, 1846) Q. sparsenilosa Heraty, 1994 Australia		O. didentata (Girault, 1940)	Australia	
O. goethei (Girault, 1934) Australia O. myrmicae (Girault, 1936) Australia Orasemorpha O. pytallus (Walker, 1846) Q. sparsenilosa Heraty, 1994 Australia		O. eribotes (Walker, 1839)*	Australian	Pheidole
O. myrmicae (Girault, 1936) Australia Pheidole Orasemorpha O. pytallus (Walker, 1846) Australia O. sparsepilos Herary, 1994 Australia	Orasemorpha	O. goethei (Girault, 1934)	Australia	
Orasemorpha O. pytallus (Walker, 1846) Australia		O. myrmicae (Girault, 1936)	Australia	Pheidole
O starsenilosa Heraty 1994 Australia		O. pytallus (Walker, 1846)	Australia	
O. spuisepuosu liciacy, 1991	-	O. sparsepilosa Heraty, 1994	Australia	
O. tridentata (Girault, 1915) Australia Pheidole		O. tridentata (Girault, 1915)	Australia	Pheidole
O. varidentata (Girault, 1936) Australian		O. varidentata (Girault, 1936)	Australian	
O. xeniades (Walker, 1839) Australian Pheidole		O. xeniades (Walker, 1839)	Australian	Pheidole
T. acuminatus Heraty, 1994 Ethiopian Pheidole		T. acuminatus Heraty, 1994	Ethiopian	Pheidole
<i>T. coronula</i> Heraty, 1994 Ethiopian		T. coronula Heraty, 1994	Ethiopian	
Timioderus T. peridentatus Heraty, 1994 Ethiopian	Timioderus	T. peridentatus Heraty, 1994	Ethiopian	
<i>T. coronula</i> Heraty, 1994 Ethiopian		T. coronula Heraty, 1994	Ethiopian	1
T. refringens Waterston, 1916 * Ethiopian		T. refringens Waterston, 1916 *	Ethiopian	1
Zuparka gen. n. Z. fisheri sp. n. Madagascar	Zuparka gen. n.	Z. fisheri sp. n.	Madagascar	1
(=monomoria group) Z. monomoria (Heraty, 2000), comb. n. * Madagascar Monomorium	(=monomoria group)	Z. monomoria (Heraty, 2000), comb. n. *	Madagascar	Monomorium

in either case, *Orasema* is never monophyletic. Character support for a monophyletic *Orasema* s.l. as presented in Heraty (1994) is weak. Of the characters discussed, only the basal petiolar flange is likely derived, but this has proven to be highly variable in the Old World taxa although not as prominent as can be observed in the New World taxa. Heraty (2000) proposed only a single unambiguous morphological synapomorphy (#52:0) for *Orasema*, the first-instar larvae without a tergopleural line, the absence of which is now regarded as plesiomorphic for the family as based on outgroup comparison.

In support of several upcoming phylogenetic studies, we have decided to recognize the problems inherent in the Old World *Orasema*. Given the wealth of morphological differences in the three other genera of Oraseminae, the associated biological differences, and the lack of morphological and molecular support for *Orasema s.l.*, the best approach is to fragment the Old World species groups of *Orasema* into different genera and recognize only the monophyletic New World clade as *Orasema sensu stricto*. Herein we recognize 12 Old World genera, of which eight are new and one, *Losbanus*, is given revised status. Several new species are described, bringing the number of Old World species to 45, which is far overshadowed by the incredible diversity of *Orasema* in the New World.

Materials and methods

Material was examined from ANIC: Australian National Insect Collection, Canberra; BMNH: Museum of Natural History, London, UK; BPBM: Bernice P. Bishop Museum, Honolulu, HI, USA; CASC: California Academy of Sciences, San Francisco, CA, USA; CNCI: Canadian National Collection of Insects, Ottawa, Canada; MNHP: Muséum National d'Histoire Naturelle, Paris, France; NMPC: National Museum (Natural History), Prague, Czech Republic; PPRI: Plant Protection Research Institute, Pretoria, South Africa; ROME: Royal Ontario Museum, Toronto, ON, Canada; TMP: Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa; UCR: UCR Entomology Research Museum, Riverside, CA, USA; UNMO: University of Montana, Bozeman, MT, USA; USNM: National Museum of Natural History, Washington, DC, USA. Each specimen is labeled with a UCRCENT or CASENT barcode specimen identification number; UCRCENT codes include an additional reference to the museum of deposition. Georeferenced points for specimens estimated from Google Earth are italicized. Photographs were taken using a Leica Imaging System with a Z16 APO A microscope, and stacked using Zerene Stacker (version 1.04, Zerene Systems, LLC).

Morphological terms follow Heraty et al. (2013) and Burks et al. (2015). All terms were verified using the Hymenoptera Anatomy Ontology (http://portal.hymao.org/) when they are represented in that resource, and variations from their preferred terms are discussed here: palpomere formula follows a maxillary:labial format; mandibular tooth count follows a right:left format; surface sculptural terms follow illustrations provided by Harris (1979). Important features include the base of the petiole, which can either

be tapered to the articulating condyle within the propodeal foramen (Figs 20, 25) or truncate basally external to the foramen (Figs 5, 11, 67, 75), and if truncate then with an anterior transverse basal carina (apc, Figs 5, 67, 75).

In the following taxonomic treatments, we provide only new nomenclatorial acts or new information. We do not revisit the genera *Indosema*, *Orasemorpha* and *Timioderus*, which were revised in Heraty (1994). The identification key includes treatments only for the newly decribed species. Two undescribed genera are included along with illustrations that have only been collected as pharate adults (Figs 85, 86).

Key to Oraseminae of the Old World

1	Transscutal articulation medially sinuate; axillae strongly advanced laterally beyond posterior margin of mesoscutum (Figs 19, 24). Fore wing with ante-
	rior margin broadly rounded posterior to stigmal vein making fore wing ap-
	pear ovate (Figs 15, 27). Petiole narrowed gradually into foramen (Fig. 20),
	lacking anterior petiolar flange (Australian; males unknown)
_	Transscutal articulation either absent medially (Fig. 42) or present and at
	most slightly sinuate (usually straight) and axillae not strongly advanced (Figs
	4, 10, 32). Fore wing with anterior margin relatively straight (Figs 7, 33).
	Petiole variable
2 (1)	Mandibles minute and lacking distinct teeth (Fig. 16, md). Mesosomal dor-
	sum entirely smooth (Fig. 19) C. capelina sp. n.
_	Mandibles 3/2 dentate with teeth narrow and weakly curved (Figs 21, 22).
	Mesosoma anteriorly reticulate (Fig. 24)
3 (1)	Upper frons with a large pit immediately below median ocellus (Fig. 39, sdp).
	Antenna with 7 funiculars; anellus transverse and distinct (Fig. 40). Petiole
	without anterior carina. Metasomal tergite margins laterally sinuate (Figs 45,
	46) (Ethiopian and Malagasy)
	Ivieosema gen. n. (striatosoma-group of Heraty 1994)4
_	Upper frons without dorsal pit. Other characters variable7
4 (3)	Face reticulate. Transscutal articulation complete. Fore wing with moderately
	long setae; without swelling posterior to submarginal vein (Ethiopian)5
_	Face smooth (Figs 39, 47) or with fine sculpture (Fig. 50). Transscutal articu-
	lation fused medially. Fore wing with very short setae; with distinct longitu-
	dinal swelling posterior to submarginal vein (Figs 44, 55) (Malagasy)6
5 (4)	Mesoscutellum reticulate dorsally Ivieosema fraudulenta (Reichensperger)
_	Mesoscutellum longitudinally striate Ivieosema striatosoma (Heraty)
6 (5)	Face smooth. Scape brown. Upper frons with two depressions between eye
	and antennal scrobe (Figs 39, 47) Ivieosema confluens sp. n.

_	Face smooth to shallowly reticulate. Scape white. Upper frons with single
	transverse depression between eye and antennal scrobe (Fig. 50)
7 (3)	Transscutal articulation (between mesoscutum and axilla) obliterated medi-
	ally. Maxillary and labial palpi absent8
_	Transscutal articulation complete with a distinct transverse suture (Fig. 4).
	Maxillary and labial palpi present
8 (7)	Body metallic blue or green. Head and mesosoma strongly sculptured and ei-
0(/)	ther corrisceous or rugulose. Apellus present. Mandibles truncate or spatulate
	maxilla small Petiole not fused ventrally. Ovinositor curved ventrally Body
	length at least 3.5 mm (Ethiopian)
	Pody block or brown Head and massage almost smooth Apollus about
-	Mandibles about marrille and mesosonia annost smooth. Anenus absent.
	Mandibles absent, maxilla enlarged and lobate. Petiole fused ventrally. Ovi-
	positor long and relatively straight. Body length about 2 mm (Kenya [New
	Record: UCRCENT 004/8/80, Olorgesailie National Monument, R. Cope-
- ()	land] and India) Indosema Husain & Agarwal
9 (7)	Petiole of female transverse, at most as broad as long. Petiole of male may be
	twice as long as broad, but then distal third or half supported ventrally by
	swollen anterior expansion of first gastral sternite (Gs_1). Base of petiole lack-
	ing an anterior dorsal carina (Australian)10
-	Petiole of both sexes cylindrical and at least as long as broad (Figs 5, 67, 86),
	but usually much longer and gaster never appearing sessile. Petiole of male
	with anterior margin of first gastral sternite (Gs_1) meeting apex of petiole
	(Figs 64, 86). Base of petiole usually truncate and usually with an anterior
	transverse carina (Fig. 75) (Old World tropics)11
10 (9)	Antennal flagellomeres cylindrical. Base of petiole narrowed to condyle
	Orasemorpha Bouček
_	Antennal flagellomeres lobate (Fig. 85). Base of petiole truncate
	Undescribed and unplaced teneral male (new genus 1)
	Antenna encased in exuvia, collected from base of ant-infested termite
	mound, very distinct from other genera and shows some similarities with
	<i>Timioderus</i> (Australia: QLD: Mareeba; ANIC: UCRCENT00238798).
11 (9)	Lower face lateral to clypeus finely reticulate (Fig. 29). Frenum and propo-
. ,	deum evenly sculptured, propodeum lacking a distinctly differentiated nar-
	row median band of areolate sculpture. Prepectus evenly reticulate or rugose.
	dorsal margin without a raised rim and overlapped by ventral margin of mes-
	oscutum Callus at most with a few minute setae. Female antenna with 7–8
	funiculars male with 7–9 funiculars. Ventral valve of ovipositor with several
	minute lateral teeth (Fig. 35)
	Havatosoma gen p (assactator-group of Heraty 1994)
_	Face variously sculptured but if finely reticulate then propodeum with dis
_	tingthy differentiated median channel (Fig. 11) propaging broadly formate
	uncuy unreferituated median channel (Fig. 11), prepectus broadly foveate
	with a distinctly raised dorsal margin (Fig. 12) or callus with dense patch of
	long hairs. Both sexes with 7-9 funiculars. Ventral valve of ovipositor with
---------	--
	3-4 lateral teeth (Figs 13, 76)12
12 (11)	Antenna with 8-9 funiculars, if 7, then labrum with more than 7 digits,
	body black, and propodeal disc evenly sculptured (Ib. seyrigi, Madagascar).
	Ocellar-ocular sulcus usually distinct. Propodeal disc evenly sculptured, rare-
	ly smooth. Fore wing often without speculum
_	Antenna with 7 funiculars, if labrum with more than 7 digits, then body
	metallic blue green and propodeal disc smooth laterally. Ocellar-ocular sulcus
	absent. Fore wing setation variable
13 (12)	Face smooth laterally (Fig. 36). Labrum with more than 9 digits (one unde-
-0 ()	scribed specimen with 5 digits). Antenna with 7–8 funiculars (Madagascar)
	Ibitya gen. n. (communis-group of Heraty, 2000; 2 species described)
_	Face evenly sculptured laterally. Labrum with 4 digits (one undescribed Austra-
	lian species with 6). Antenna with 8–9 funiculars (Paleotropical excluding Mada-
	gascar) Losbanus rev. stat. (uichancoi-group of Heraty, 1994; 5 species)
14 (12)	Propodeal disc evenly sculptured
_ ``	Propodeal disc smooth laterally, usually with a distinct median longitudinal
	channel with strong areolate sculpture (Figs 11, 73), rarely weakly reticulate
	medially (Fig. 5)
15 (13)	Face and frenum completely smooth (Figs 57, 58, 62) (Ethiopian)
-> (-0)	Leiosema gen. n. (glabra-group of Heraty, 1994)16
_	Face completely and evenly reticulate; scutellar disc and frenum rugose-retic-
	ulate (Fig. 86) (Australian)
	Antenna encased in exuvia, no ant host information, close to Australose-
	ma but very distinct from other species (Australia: OLD: Thornton Peak,
	QM:UCRCENT00241816).
16 (15)	Mandibles 3:3 dentate (Fig. 62). Scutellar disc with prominent reticulate
	sculpture (Fig. 61). Pronotal neck extended anteriorly and reticulate (Fig.
	61). Female unknown
_	Mandibles 3:2 dentate. Pronotal neck not extended and smooth. Scutellar
	disc at most with shallow reticulate sculpture anteriorly, weakly reticulate or
	smooth posteriorly (Figs 59–60) Leiosema glabra (Heraty)
17 (14)	Labrum with 6–8 digits. Face smooth (Papua New Guinea [undescribed] and
-, (,	New Caledonia)
	gen. n. (koghisiana-group of Heraty, 1994), M. koghisiana (Heraty)
_	Labrum with 4 digits. Face smooth or reticulate
18 (17)	Antecostal sulcus present, dividing first gastral sternite and separating off a
	distinct acrosternite (Figs 1, 7). Face smooth or with at least some reticulate
	sculpture. Scrobes without parallel median channels. Male scape plands absent
	(Australian) Australosema gen. n. (valgius-group of Heraty. 1994)19
_	Antecostal sulcus absent (first gastral sternite smooth and uninterrupted).
	Face entirely smooth. Scrobes with parallel median channels (Fig. 79). Male
	· · · · · · · · · · · · · · · · · · ·

scape glands present (Malagasy)
Zuparka gen. n. (monomoria-group of Heraty, 2000)22
Face entirely smooth (Fig. 2)
Face with at least frons with reticulate sculpture (Fig. 8)20
Frenum with median longitudinal groove (Fig. 10). Scape dark metallic
brown in both sexes
Frenum without median longitudinal groove. Scape yellow or dark brown21
Lateral lobe of mesoscutum and axilla smooth and polished
Lateral lobe and axilla coriaceous to rugose, axilla weakly carinate with sur-
face imbricate to reticulate. Scape yellow to dark brown (see Heraty 1994 for
discussion of variants)
Face entirely smooth (Figs 69, 79). Propodeal disc with lateral areas smooth
(Fig. 73) Z. fisheri sp. n.
Frons weakly coriaceous (Fig. 81). Propodeal disc with lateral areas weakly
sculpturedZ. monomoria (Heraty)

Australosema Heraty & Burks, gen. n.

http://zoobank.org/9A5268EF-48B5-4293-9562-46A528062AAE Figs 1–14

Type species. *Eucharis valgius* Walker: 412–414. Heraty 1994: 79–81, figs 122, 124, 131, 192, 221, 238, 248, 262–263.

Etymology. Random combination of letters and referring to the distribution; gender feminine.

Discussion. Defined by Heraty (1994) as the *Orasema valgius* group for two species from Australia, and was distinguished from the *glabra* and *koghisiana* groups in part by an at least partly reticulate face and a labrum with 4 digits (Heraty, 1994). *Australosema politurae* and related species expand the definition of the group to include an almost or completely smooth face. Originally recognized to include two species, *Australosema synempora* (Heraty) and *A. valgius* (Walker). Herein we add two new species, *A. politurae* and *A. verghetta*.

Diagnosis. Separated from *Orasema s.s.* by a relatively weak or absent basal petiolar flange, and smooth lateral areas on the propodeal disc in combination with a rugose-areolate or reticulate median channel. Distinguished from other Old World genera by the head subtriangular in frontal view (Fig. 2); scrobal depression evenly impressed and lacking parallel channels or dorsal depressions; dorsal occipital margin abrupt and rounded or carinate; funicle 7-segmented; labrum with 4-digits; mesonotum with only minute setae; mesoscutal lateral lobes and frenum sculptured or smooth; transscutal articulation complete and relatively straight; propodeal disc with lateral areas at most weakly sculptured (Fig. 5), but usually smooth (Fig. 11), and with a broad sculptured

median channel; prepectus foveate and tightly articulated with pronotum ventrally (Fig. 12); fore wing with basal area bare and specular area either bare or pilose (Figs 1, 7), wing disc with very short setae; postmarginal vein much longer than stigmal vein and reaching about half distance to wing apex; petiole base truncate with weak basal flange (Fig. 5); antecostal sulcus present and smooth, at most weakly foveate laterally; first valvula of ovipositor with 3–4 lateral teeth and robust oblique subapical carina. Male scape lacking ventral pores.

Similar genera that have a smooth face and smooth lateral regions on the propodeal disc include *Leiosema*, *Matantas*, and *Zuparka*. *Australosema* is distinguished from *Leiosema* and *Zuparka* by several features, including the absence of a parallel channeled scrobes with dorsal depressions, 3–4 large teeth on the ventral (first) valvula of the ovipositor instead of 9–10 minute teeth, and absence of ventral pores on the male scape. It differs from *Matantas* primarily by having a 4-digitate rather than 6–8 digitate labrum.

Host association. Myrmicinae: *Pheidole* (Girault 1913[175], Heraty 2000). **Distribution.** Four species. Australia including Tasmania.

Australosema politurae Burks, sp. n.

http://zoobank.org/D4F9B53D-B548-4676-832B-68DD3FD08CC8 Figs 1–6

Etymology. Latin noun in genitive case meaning "a polishing," referring to the smooth face.

Diagnosis. Differs from most *Australosema* by having an almost entirely smooth face, with the frons not swollen and the dorsal occipital carina weak. It differs from *A. synempora* in several features, including having a completely sculptured axilla and mesoscutal lateral lobe and a less densely setose fore wing. *Matantas koghisiana* also has a smooth face and frenum, but *A. politurae* has four labral digits and a more elongate mesosoma. Additional features include the lateral lobe of mesoscutum almost entirely rugose-reticulate, smooth near posterior edge; axilla reticulate (Fig. 4); mesepisternum not swollen anterior to mesocoxae (Fig. 1). Propodeum sublaterally nearly smooth (Fig. 5), and in the female the F2 is longer than F3 and expanding apically (Fig. 3).

Female. Length 2.2–3 mm. Head and mesosoma dark metallic green, petiole black, gaster brown with faint metallic luster. Scape, pedicel, anellus yellowish, funiculars and clava brown. Coxae metallic green basally, becoming yellowish apically, femora pale brown except yellowish at tips, remainder of leg yellowish. Fore wing venation pale brown, setae dark. Gaster brown to dark brown, with metallic luster.

Head (Figs 2–3), 1.1–1.2× as broad as high. Face almost entirely smooth except for minute setal pits ventrally, dorsally with shallow irregular sculpture near ocellar triangle; scrobal depression narrow and impressed, without dorsal scrobal foveae; without longitudinal furrow between torulus and eye; supraclypeal area and clypeus smooth, supraclypeal area slightly protruding, anteclypeus present; vertex weakly carinate posterior to ocellar triangle. Labrum with 4 digits. Palpal formula 3:3. Flagellum



Figures 1–6. *Australosema politurae.* Paratype female: **1** habitus, lateral **2** head, anterior **3** antennae, ventral **4** mesosoma, dorsal **5** propodeum and petiole, oblique dorsal. Paratype male: **6** antennae, lateral. acl = anteclypeus; acr = acrosternite; acs = antecostal sulcus; apc = anterior petiolar carina; ax = axilla; cal = callus; cly = clypeus; F = flagellomere; fr = frons; Fu = funicular; F1/an = anellus; llm; mesoscutal lateral lobe; lpr = lateral propodeal disc; mlm = mesoscutal midlobe; mpr = median propodeal disc; pet = petiole; not = notauli; scd = scutellar disc.

 $1.1-1.3 \times$ head height, with 7 funiculars; anellus transverse; F2 2.0–2.8× as long as broad, F2 1.4–1.6× as long as F3.

Mesosoma (Figs 4–5). Mesoscutal midlobe densely reticulate, lateral lobe shallowly transversely rugose-reticulate and becoming smooth posteriorly. Axilla rugose-reticulate, with longitudinal carinae posteriorly that extend across the scutoscutellar suture;

mesoscutellar disc finely rugose-reticulate, with some wrinkle-like carinae posteriorly; frenal line carinate, frenum rugose-reticulate; axillular sulcus carinate, axillula glossy and very shallowly sculptured aside from a few longitudinal carinae. Mesepisternum anterodorsally mostly smooth but not overlapping posterior edge of prepectus, poster-oventrally smooth, not becoming horizontal anterior to mesocoxa; upper and lower mesepimeron mostly smooth except for foveate area at posterior edge, transepimeral sulcus foveate. Propodeum with broad rugose-reticulate median channel, sublaterally nearly smooth; callus smooth, with a few tiny setae. Metacoxa shallowly rugose-reticulate dorsolaterally. Fore wing $2.3-2.4\times$ as long as broad; costal cell with 1 uninterrupted row of ventral setae; basal cell bare; speculum present; cubital fold with uninterrupted ventral row of setae; subcubital fold setose posterior to speculum, bare posterior to basal cell; stigmal vein $1.5-2.0\times$ as long as broad, only slightly expanded at uncus; marginal vein about $6\times$ as long as stigmal vein. Hind wing costal cell with a few ventral setae in apical third.

Metasoma. Petiole 4.0–4.8× as long as broad, 1.6–1.7× as long as metacoxa, finely longitudinally rugose-reticulate, with some incomplete longitudinal carinae laterally and ventrally (Fig. 5). Antecostal sulcus of Gs_1 smooth, very shallow medially; acrosternite smooth, uniformly rounded or with a transverse elevation near midlength. Cercus with a curved seta that is much longer than the others. Hypopygium with a few short setae and a slightly longer posterolateral seta on each side. Ovipositor yellow medially, orange laterally, dorsal valve with 7–8 medially interrupted sawtooth-like annuli; ventral valve with 3–4 weakly defined teeth along lateral carina, and with oblique lateral carina immediately basal to toothed apex (as in Fig. 7).

Male. Length 2.1–2.6 mm. Antennal flagellum (Fig. 6) densely covered with long decumbent setae, with longitudinal sensilla extending beyond funicular apices, funiculars separated by stalk-like constrictions; F7 as long or longer than F6, shorter than F8; scape and pedicel yellow, flagellum brown. Mesoscutal midlobe transversely rugose-reticulate; mesoscutellum rugose-areolate with underlying reticulate sculpture. Petiole 5.7–6.8× as long as broad, 1.9–2.4× as long as metacoxa, narrowest slightly beyond midlength, finely reticulate but becoming smooth posteriorly.

Material examined. Holotype: Australia: QLD: Mt. Glorious, 27°19'54"S, 152°45'29"E, 7-13.ii.1998, N. Power, Malaise trap $[1]^{\circ}$, ANIC: UCR-CENT00091415]. Paratypes: Australia: QLD: Brisbane Forest Pk, 27°25'04"S, 152°49'48"E, 29.xi-5.xii.1997, N. Power, dry sclerophyll, Malaise Trap 3 $[1]^{\circ}$, ANIC: UCRCENT00312131]. Lamington Nat. Park, Binna Burra, 28°11'53"S, 153°11'16"E, 10.xii.2002, George, Hawks, Munro, & Owen, rainforest, sweep $[1]^{\circ}$, UCRC: UCRCENT00312128]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 10-16.i.1997, N. Power, Malaise Trap $[1]^{\circ}$, UCRC: UCRCENT00312135]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 13-24.iii.1998, N. Power, Malaise Trap $[1]^{\circ}$, UCRC: UCRCENT00312133]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 24-30. xi.1997, T. Hiller, MT 3 $[3]^{\circ}$, UCRC: UCRCENT00312060 – UCRC: UCRCENT00312060–62]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 24-30. xi.1997, T. Hiller, MT 3 $[3]^{\circ}$, UCRC: UCRCENT00312060 – UCRC: UCR-CENT00312060–62]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 24-30. xi.1997, T. Hiller, MT 3 $[3]^{\circ}$, UCRC: UCRCENT00312060 – UCRC: UCR-CENT00312060–62]. Mt. Glorious, 27°19'54"S, 152°45'29"E, 3-9.i.1998, T. Hiller, MT 2 $[1]^{\circ}$, UCRC: UCRCENT00312063].

Similar species. A single specimen (gaster missing, likely female; UCR-CENT0092152, D0161) from southeast QLD is molecularly similar and is placed as the sister of *A. politurae*. It is distinct by having a completely smooth face with a strongly swollen frons. Two other series (all males from QLD) likely represent another two species that share similar features to the D0161 specimen. All specimens have a 4-digitate labrum, 7 funiculars, a completely smooth face, and a strongly carinate dorsal occipital margin.

Australosema verghetta Burks, sp. n.

http://zoobank.org/F282DE42-2C64-4FF4-B131-0752F56D00BA Figs 7–14

Etymology. Italian noun used in heraldry to refer to a line along the middle, referring to the longitudinal scutellar groove present in females.

Diagnosis. Differs from other *Australosema* by the presence of a longitudinal median groove on the frenum of females, and similar to some of the included species, the frons is rugose-reticulate and the lower face smooth. The female also has F2 much narrower than F4, not longer than F3, with few longitudinal sensilla (Fig. 9). Males are very similar to those of *A. valgius* (Walker), but differ in having a mostly or entirely dark brown scape (Fig. 8), while that of *A. valgius* is almost entirely yellow.

Female. Length 2.1–2.6 mm. Head and mesosoma metallic green to blue-green, metasoma brown with metallic green luster. Scape and pedicel dark brown; anellus pale brown; flagellum dark brown. Coxae metallic green basally, becoming brownish to yellowish apically, remainder of leg yellowish except femora mostly dark brown and with yellowish tips. Fore wing venation brown, setae dark. Gaster metallic green.

Head (Figs 8–9) 1.2–1.3× as broad as high. Face mostly reticulate, smooth ventrally adjacent to mouthparts; vertex with weak carina posterior to ocellar triangle; scrobal depression narrow and impressed, without dorsal scrobal foveae; longitudinal furrow present amidst sculpture between torulus and eye; supraclypeal area and clypeus smooth and separated by only a very shallow depression, with short decumbent setae, supraclypeal area protruding, anteclypeus present. Labrum with 4 digits. Palpal formula 3:3. Flagellum 1.1–1.2× height of head, with 7 funiculars, dark brown; anellus transverse; F2 1.7–2.3× as long as broad, 0.7–1.0× as long as F3, nearly parallelsided and having few longitudinal sensilla (Fig. 9, F2).

Mesosoma (Figs 10–12). Mesoscutum transversely rugose-reticulate, lateral lobe nearly smooth at posterior margin. Axilla rugose-reticulate and with longitudinal carinae that extend across the scutoscutellar suture; mesoscutellar disc rugose-reticulate except peripherally with many subparallel carinae; frenal line posteriorly carinate, frenum rugose-reticulate and with median longitudinal groove; axillular sulcus foveate, axillula with reticulate sculpture laterally, and with subparallel longitudinal carinae. Mesepisternum anterodorsally smooth and overlapping posterior lower



Figures 7–12. *Australosema verghetta*. Paratype female: **7** habitus, lateral **8** head, anterior **9** antennae, dorsal **10** mesosoma, dorsal; **11** propodeum and petiole, dorsal **12** mesosoma, lateral. acs = antecostal sulcus; apc = anterior petiolar carina; axlg = axiullar groove; cal = callus; F = flagellomere; frg = frenal groove; lpr = lateral propodeal disc; not = notaulix; SSS = scutoscutellar sulcus; tsa = transscutal articulation.

margin of prepectus, posteroventral surface with horizontal shelf that is shorter than mesepimeron but swollen and smooth anterior to mesocoxa; upper and lower mesepimeron smooth, transepimeral sulcus foveate. Propodeal disc with a meandering median carina crossed by short transverse carinae, sublaterally smooth; callus smooth and with very short setae. Metacoxa basally rugose-reticulate, apically smooth. Fore wing $2.4-2.5\times$ as long as broad; costal cell ventrally setose in apical half; basal cell



Figures 13–14. *Australosema verghetta.* Paratype female: **13** ovipositor, lateral. Paratype male: **14** antenna, ventral. Fu = funicle; dv = dorsal valve; lhs = lateral hypopygial seta; ocv = oblique carina of ventral valvula; vv = ventral valve; vvlt = ventral valve lateral teeth.

bare; speculum present; cubital fold setose ventrally posterior to basal cell but bare posterior to speculum; subcubital fold setose along speculum but bare posterior to basal cell; stigmal vein $1.5-2.0\times$ as long as broad, only slightly expanded at uncus; postmarginal vein about $5.0\times$ as long as stigmal vein. Hind wing costal cell setose in apical third, bare in basal two thirds.

Metasoma (Figs 11, 13). Petiole $0.9-1.1\times$ as long as metacoxa, $2.4-3.1\times$ as long as broad, transversely rugose-reticulate and with a few short longitudinal wrinkle-like carinae; basally truncate with at most a weak basal flange. Antecostal sulcus of Gs₁ smooth to finely sculptured laterally; acrosternite smooth. Cercus with 1 curved seta that is much longer than the others. Hypopygium with a few short setae and 1 longer posterolateral seta on each side (Fig. 13, lhs). Ovipositor dorsal valve with 7–8 medially interrupted annuli; ventral valve with 4–5 weakly defined teeth, and with oblique subapical carina immediately basal to toothed apex (Fig. 13, ocv).

Male. Length 2.4–2.6 mm. Scape dark brown for most or all of its length (Fig. 14), yellowish in only a small basal area if at all; antennal flagellum densely covered with short decumbent setae, with longitudinal sensilla extending beyond funicular apices; F7 shorter than F6 and F8; entire antenna dark brown and scape with metallic luster. Frenum without longitudinal groove; axillula with reticulate sculpture and longitudinal carinae. Metatibia dark brown except at apices. Petiole 5.9–7.4× as long as broad, 2.2–2.6× as long as metacoxa, narrow at midlength, reticulate.

Material examined. Holotype: Australia: SA: Mt. Barker, 511m, 35°04'00"S, 138°55'17"E, 22-23.i.1999, J. Heraty, Eucalyptus scrub [1♀, ANIC: UCR-CENT00091308]. Paratypes: Australia: SA: Mt. Barker, 511m, 35°04'00"S, 138°55'17"E, 22-23.i.1999, J. Heraty, Eucalyptus scrub [14♂ 19♀, ANIC: UCR-CENT00311977–81, UCRC: UCRCENT00091307, UCRCENT00091309, UCR-CENT00311982–89, UCRC: UCRCENT00312042–59].

Cymosema Heraty & Burks, gen. n.

http://zoobank.org/8A987051-99CE-482E-ABB1-165B9ACDB8FF Figs 15–27

Type species. Cymosema waterworthae Burks & Mottern sp. n.

Etymology. Based on the Greek κύμα (*kyma*) for wave and referring to the sinuate transscutal articulation; gender feminine.

Discussion. The two species in this group are each known from single specimens collected in Australia, both among the smallest known Eucharitidae. They differ from previously described species of *Orasema* by having a cylindrical ventrally fused petiole that tapers basally to the articulating condyle (Figs 20, 25), reduced mouthparts (Figs 16, 21), and advanced axillae (Figs 19, 24). The mesoscutum and mesoscutellum are separated by a distinct transscutal articulation, but the sclerites are tightly associated and the axillae are advanced (thus somewhat resembling the state in *Timioderus* and *Indosema*). Based on morphological (reduced anellus, reduced mouthparts, smooth head and mesosoma) and molecular evidence, they are the potential sister group of *Indosema*. The fore wing shape is unique within Eucharitidae, with the anterior leading edge of the fore wing anteriorly curved at the stigmal vein giving the wing an oval-shaped appearance (Fig. 27); in other Eucharitidae the wing margin beyond the stigmal vein is straight (Fig. 7). Male unknown.

Diagnosis. Recognized from most Oraseminae by the sinuate closely associated transscutal articulation, minute discoidal anellus, reduced mouthparts that are at most bidentate and medially directed (not falcate), basally tapered petiole and elongate slightly curved ovipositor. Distinguished from other Old World genera by the head transverse in frontal view and mostly smooth (Figs 16, 21); scrobal depression strongly impressed and forming weak parallel channels, but without dorsal foveae; dorsal occipital margin abrupt and rounded; funicle 7-segmented; mandibles, chisel-shaped and slightly broader than long or bidentate with both teeth projecting medially (not falcate as in other Eucharitidae); labrum appears to be membranous and without digits; palpi greatly reduced; mesonotum appearing bare, at most with minute setae; mesoscutal lateral lobes entirely smooth or weakly reticulate laterally; frenum smooth; transscutal articulation sinuate and distinct but sclerites closely associated and appearing fused; callus bare; propodeal disc smooth (Fig. 20) or weakly reticulate with single median carina (Fig. 24); prepectus foveate and loosely articulated with pronotum ventrally (Fig. 18); fore wing with basal area and specular area evenly covered with minute setae, and anterior margin of fore wing disc curved at stigmal vein (Fig. 27); postmarginal vein short and about 1.5× as long as stigmal vein; petiole base tapered and without transverse flange (Figs 20, 25); petiole fused ventrally, basally tapering to condyle and without basal flange; acrosternite swollen and finely reticulate, antecostal sulcus not apparent, but a distinct transition to the smooth posterior region of Gs,; ovipositor long and slightly curved anteriorly (Fig. 26); first valvula with 3-4 lateral teeth and with a strong oblique subapical ridge.

Host association. Unknown.

Distribution. Two species. Australia (Queensland and Western Australia).

Cymosema capelina Burks & Mottern, sp. n.

http://zoobank.org/4E96F380-F80F-417C-B154-D49256EABA22 Figs 15–20

Etymology. Noun from Spanish, meaning wide-brimmed floppy hat, referring to the head shape.

Diagnosis. Mandibles highly reduced, broader than long and truncate. Funiculars tapering to apex. Frons smooth. Submarginal vein with several long setae, fore wing with distinct marginal fringe.

Female. Length 1.3 mm. Head and mesosoma dark brown with very faint metallic luster. Scape, pedicel and anellus pale brown, funiculars and clava brown. Leg brown to milky brown, with slightly darker areas on the coxa basally, femur except at its tips, tibia subbasally, and last two tarsomeres. Fore wing hyaline; venation pale brown, setae dark. Gaster brown with faint metallic luster.

Head (Figs 16–17) transverse, 1.4× as broad as high. Head receding ventral to toruli (Fig. 18); face dorsally smooth, ventrally coriaceous; supraclypeal area and cl-ypeus medially smooth and laterally shallowly coriaceous, anteclypeus absent; vertex not carinate. Mandibles truncate and broader than long, broadly separated. Palpal formula 2:1, palpi long. Pedicel broader than F2; anellus small but easily visible; flagellum 1.4× head height, with 7 funiculars that expand apically and have semi-erect long setae arising from their bases; F2 1.3× as long as broad, 1.0× as long as F3.

Mesosoma (Figs 18–19). Mesoscutum smooth and glossy, notauli evenly impressed and smooth. Axilla strongly advanced, smooth; scutoscutellar suture finely foveate; mesoscutellar disc and axillula smooth, without axillular sulcus; frenum distinguished by a slight change in elevation at frenal line, smooth. Propodeal disc with median carina, weakly sculptured laterally; callus bare, separated from propodeal disc by wrinkle-like longitudinal carinae. Metacoxa smooth to shallowly reticulate. Fore wing spatulate, 2.6× as long as broad; costal cell with 1 complete row of ventral setae; submarginal vein with several long hairs; basal cell setose dorsally and ventrally; speculum absent; cubital and subcubital folds setose; marginal fringe present; stigmal vein 1.5× as long as broad; dorsal setae of disc much longer than ventral setae; postmarginal vein about 1.5× as long as stigmal vein. Hind wing costal cell with a few setae in apical third.

Metasoma. Petiole 0.7× as long as metacoxa, 1.8× as long as broad, smooth except for longitudinal carinae, including a median carina dorsally, narrowing anteriorly to abruptly expand at the anterior condyle, without anterior transverse carina, ventrally smooth (Fig. 20). Antecostal sulcus of Gs_1 crossed by many longitudinal carinae; acrosternite smooth. Cercus with all setae subequal in length. Hypopygium bare. Ovipositor only slightly exerted in holotype and features not distinguished.

Male. Unknown.

Material examined. Holotype: Australia: Queensland: Heathlands, 11°27'00"S, 142°21'00"E, 25.vii-18.viii.1992, P. Zborowski, J. Cardale, Malaise trap [12, ANIC: UCRCENT00238787], deposited in ANIC.



Figures 15–20. *Cymosema capelina*. Holotype female: **15** habitus, lateral **16** head, anterior **17** antennae, lateral **18** mesosoma, lateral **19** mesosoma, dorsal **20** propodeum and petiole, oblique dorsal. ax = axilla; F = flagellomere; md = mandible; pet = petiole; prp = propodeum; tsa = transscutal articulation.

Cymosema waterworthae Burks & Mottern, sp. n. http://zoobank.org/8C723EBE-7AFA-4B38-8671-285CF7E2B443 Figs 21–27

Etymology. Named in honor of the collector, Rebeccah Waterworth.

Diagnosis. Mandibles bidentate and overlapping, teeth of equal length and projecting medially. Funiculars cylindrical. Frons weakly reticulate. Submarginal vein bare, fore wing without marginal fringe.



Figures 21–26. *Cymosema waterworthae*. Holotype female: 21 head, anterior 22 antennae, lateral 23 mesosoma, lateral 24 mesosoma, dorsal 25 petiole, lateral 26 ovipositor. pet = petiole.

Female. Length 1.4 mm. Head, mesosoma, and metasoma brown with metallic luster. Scape yellowish-brown, pedicel and flagellum brown. Legs brown, with tibial apices, and first four tarsomeres pale brown. Fore wing hyaline; venation pale brown, setae dark. Gaster brown with faint metallic luster.

Head (Figs 21–22) transverse, 1.6× as broad as high. Head receding ventral to toruli; face reticulate, including supraclypeal area; clypeus shallowly transversely rugosereticulate, anteclypeus present; vertex not carinate. Mandibles bidentate, both teeth projecting medially, narrow and only weakly curved (Fig. 21). Palpal formula 2:1, palpi minute. Pedicel broader than F2; scape and pedicel reticulate; flagellum 1.5×



Figure 27. Cymosema waterworthae. Holotype female: fore wing. arrow points to end of postmarginal vein.

head height, with 7 parallel-sided funiculars; anellus minute and hardly visible; F2 1.6× as long as broad, F2 1.1× as long as F3.

Mesosoma (Figs 23–24, 27). Mesoscutal midlobe coriaceous anteriorly, becoming smooth posteriorly, lateral lobe mostly smooth but with shallow irregular sculpture anteriorly and laterally; notauli deep anteriorly but very shallow posteriorly. Axilla strongly advanced, smooth anteriorly, coriaceous posteriorly; mesoscutellar disc smooth to very shallowly coriaceous; frenal line indicated by narrow groove, frenum smooth; axillular sulcus narrow, axillula coriaceous. Mesepisternum reticulate anterodorsally, becoming smooth ventrally and forming a rounded horizontal shelf anterior to mesocoxae; mesepimeron shallowly reticulate and without a transepimeral sulcus. Propodeal disc finely reticulate, with a weak median carina, sublaterally reticulate and with an oblique elevation anterior to a steep descent towards the broad petiolar foramen; callus bare, with a flange-like elevation posterolateral to spiracle (Fig. 24, flange). Metacoxa shallowly reticulate dorsolaterally. Fore wing spatulate (Fig. 27), 2.7× as long as broad; costal cell and submarginal vein bare; basal cell ventrally setose, also with a few dorsal setae near basal fold; speculum absent; cubital and subcubital folds setose; marginal fringe absent; stigmal vein 2.0× as long as broad; postmarginal vein about 1.5× as long as stigmal vein. Hind wing costal cell bare.

Metasoma (Figs 25–26). Petiole 1.6× as long as broad, 1.0× as long as metacoxa, finely longitudinally rugose-reticulate, with a pair of complete lateral longitudinal carinae and some additional incomplete longitudinal carinae anteriorly, narrowing anteriorly to abruptly expand anteriorly at the condyle, without anterior transverse carina, ventrally with a longitudinal groove that expands at apices. Acrosternite with irregular raised sculpture, swollen and differentiated across indistinct antecostal sulcus from remaining smooth Gs_1 . Cercus with all setae subequal in length. Hypopygium bare. Ovipositor elongate and slightly recurved, dorsal valve with 7 medially interrupted annuli; ventral valve with 5–6 teeth, and with oblique carina ending in a notch immediately basal to toothed apex.

Male. Unknown.

Material examined. Holotype: Australia: Western Australia: D'Entrecasteaux N.P., Coastal Survivors Walk, 105m, 34°50'19"S, 116°00'17"E, 8.xii.2009, R. Waterworth, sweep [1 \bigcirc , UCRC: UCRCENT00364784], deposited in UCRC. Gaster mounted separately on card.

Hayatosema Heraty & Burks, gen. n.

http://zoobank.org/D6C6360D-85FB-458C-9EC8-DFAD4F930030 Figs 28–35

Type species. Orasema assectator (Kerrich, 1963: 367–368). Heraty, 1994: 74–75, figs 111–112.

Etymology. Named after Mohammad Hayat of Aligarh Muslim University; gender feminine.

Discussion. This group and three of its seven previously described species were characterized as the Orasema assectator-group by Heraty (1994: 73-74). The four Indian species described in Narendran and Girish Kumar (2005), Girish Kumar and Narendran (2007) and Girish Kumar and Sureshan (2015) are readily placed in the assectator-group and hence in this genus (Table 1). Hayatosema is morphologically similar to species in the New World placed in the cockerelli and bakeri species groups. They were not resolved from these taxa based on the morphological analyses of Heraty (1994, 2000), and molecular data clearly place them as distinct and placed with the other Old World genera (Murray et al. 2013, Heraty unpublished). The only consistent differentiating feature from Orasema is that the lateral aspect of the mesepisternum is reticulate with the ventral aspect smooth and shining in all Hayatosema, whereas if it is reticulate laterally in Orasema s.s., it is at least weakly sculptured ventrally. The antennal funicular count is unusual in the African species, with O. nigra Heraty having from 7-8 funiculars in females and 8-9 funiculars in males, all from the same collecting event. The Indo-Pacific species all have 7 funiculars in both sexes. Notably, molecular analyses fail to support the monophyly of the African and Indo-Pacific species, although sampling is currently very poor.

Diagnosis. Distinguished from other Old World genera by the head subtriangular in frontal view (Fig. 29); lower face excluding clypeal region finely reticulate; scrobal depression evenly impressed, lacking parallel channels and dorsal foveae; dorsal occipital margin abrupt with a rounded or carinate margin; antenna with 7-8 funiculars in females (Fig. 30) and 7–9 funiculars in males; labrum with 4-digits; mesonotum appearing bare, at most with minute setae, notauli deeply and broadly impressed; mesoscutal lateral lobes and frenum evenly sculptured; transscutal articulation complete and weakly sinuate, axillae not advanced; propodeal disc evenly sculptured without distinctly differentiated narrow median area (Fig. 34); prepectus finely reticulate or rugose with undifferentiated dorsal margin that is partially overlapped by lateral margin of mesonotum (Fig. 31); tightly articulated with mesepisternum ventrally (Fig. 31); fore wing with basal area and specular area bare (Fig. 33), wing disc with dense long setae; postmarginal vein relatively short, less than 1/3 distance to apex of wing; petiole base truncate with weak basal flange (Fig. 34); antecostal sulcus foveate or irregularly sculptured; first valvula of ovipositor with 7-10 minute lateral teeth (Fig. 35). Male scape lacking ventral pores.

Host association. *Hayatosema initiator* (Kerrich) reared from *Pheidole* (Das 1963; Kerrich 1963).

Distribution. Four species. Ethiopian and Indo-Pacific (Heraty, 1994).

Hayatosema plicator Burks, sp. n.

http://zoobank.org/0F73EB6C-36D2-4BB8-AC07-45177DDE900B Figs 28–35

Etymology. A noun meaning "one who folds clothing," derived from the Latin verb plicare (to fold). Refers to the rough propodeal and petiolar surface sculpture.

Diagnosis. Flagellum with 7 funiculars (Fig. 30). Prepectus rugose, mostly smooth, and without evenly reticulate sculpture as in all other species. Supraclypeal area and clypeus smooth (Fig. 29). Mesoscutal midlobe strongly elevated anteriorly; pronotum with rounded anterolateral protrusions (Fig. 32). Propodeal disc evenly areolate, with irregular, incomplete median carina (Fig. 34). This species keys to *O. initiator* in Heraty (1994), but differs by having a proportionally longer antennal flagellum to head height (1.3 versus 1.1–1.2), longer F2 (2.0 versus 1.4–1.5), frenum finely rugosereticulate (versus reticulate), and a distinctly areolate (versus finely reticulate or nearly smooth) propodeum. It will key to *O. assectator* in Girish Kumar and Sureshan (2015), but differs most distinctly by the rugose versus reticulate prepectus.

Female. Length 3.5 mm. Head, mesosoma, and petiole black with slight metallic blue to purple luster. Antenna pale yellow. Coxae black to dark brown, with faint metallic purple luster; femora dark brown except white at tips; tibiae and tarsi pale yellow. Fore wing venation yellowish-white. Gaster dark brown.

Head (Figs 29–30) 1.4× as broad as high. Face rugose-reticulate; supraclypeal area and clypeus smooth; anteclypeus absent; vertex reticulate. Labrum with 4 digits. Palpal formula 3:3 but with minute 2nd palpomeres. Flagellum $1.3\times$ height of head; anellus transverse; F2 2.0× as long as broad, F2 $1.3\times$ as long as F3.

Mesosoma (Figs 31–34). Pronotum with small protrusion ventral to mesothoracic spiracle (Fig. 32: protrusion). Mesoscutum finely rugose-reticulate, posterior margin sinuate and midlobe strongly convex posteromedially, mesoscutal midlobe abruptly elevated above lateral lobes; notauli broadly and deeply impressed anteriorly. Axilla finely rugose-reticulate; mesoscutellar disc finely rugose-reticulate; frenal line as a deep groove with a carinate edge posteriorly; frenum finely rugose-reticulate; axillular sulcus not indicated, axillula finely rugose-reticulate. Mesepisternum anteriorly with a smooth area dorsolaterally, laterally finely reticulate and ventrally smooth; not overlapping prepectus; ventrally smooth and forming a rounded horizontal surface anterior to mesocoxae; upper mesepimeron elevated and smooth; transepimeral sulcus foveate;



Figures 28–33. *Hayatosema plicator*. Holotype female: 28 habitus, lateral 29 head, anterior 30 antennae, dorsal 31 mesosoma, lateral 32 mesosoma, dorsal 33 fore wing, dorsal.

lower mesepimeron glossy, shallowly irregularly sculptured. Propodeal disc medially areolate with some underlying irregular sculpture, with irregular median carina that is present only for a short distance near propodeal midlength, sublaterally rugose-reticulate; callus bare, smooth over most of surface but coarsely areolate to foveate peripherally, including foveate depression separating metapleuron from hind wing base. Metacoxa rugose-reticulate, glossy posteriorly. Fore wing 2.4× as long as broad; costal cell with ventral row of setae apically, bare basally; basal cell with 2 ventral setae anteriorly; speculum present, partially crossed by a patch of ventral setae near midlength of fore



Figures 34–37. 34–35 *Hayatosema plicator*. Holotype female: **34** propodeum and petiole, dorsal oblique **35** ovipositor, dorsal **36–37**: *Ibitya communis*. Female: **36** head, frontal **37** pupa. hcx = hind coxa; pet = petiole.

wing; cubital fold with only a single ventral seta posterior to basal cell, bare posterior to speculum; subcubital fold bare posterior to basal cell, with only some ventral setae posterior to speculum; wing disc covered by dense long setae (Fig. 33); stigmal vein 2.0× as long as broad, only slightly expanded at uncus; postmarginal vein about 3.0× as long as stigmal vein. Hind wing costal cell with only a few ventral setae apically.

Metasoma (Figs 34–35). Petiole $1.7\times$ as long as broad; $0.9\times$ as long as metacoxa, with sharp anterior transverse carina, areolate and with a complete dorsal median carina. Antecostal sulcus of Gs₁ finely sculptured laterally, becoming smooth and very shallow medially; acrosternite smooth. Hypopygium with a few short setae, and 1 slightly longer posterolateral seta on each side. Ovipositor dorsal valve with 7 medially interrupted annuli; ventral valve with 7–8 minute teeth along lateral carina, with only a rounded elevation basal to toothed apex.

Male. Unknown.

Material examined. Holotype: Vietnam: Thua Thien-Hue: Bach Ma Natl. Pk. Parashorea Trail, 9 km from park entrance, 100m, 16°12'02.4"N, 107°50'49.6"E, 26.v-13.vi.2001, D.C. Darling, N. Tatarnic, B. Hubley, Dipterocarp forest-closed canopy, Malaise trap (fine) [12, ROME 2001504], deposited in ROME.

Ibitya Heraty & Burks, gen. n.

http://zoobank.org/F1DA0653-6359-4DB9-9110-3703880DDB18 Figs 36, 37

Type species. Orasema communis Risbec, 1952: 412–414. Heraty 1994: 59–60, figs 80, 82, 84–85.

Etymology. Named after one of the Madagascar collecting localities, Ibity; gender feminine.

Discussion. Heraty (1994) proposed a *uichancoi*-group that included *Ibitya seyrigi* (Risbec) and *I. communis* (Risbec) as well as five other Indo-Pacific species of *Orasema* (now *Losbanus*). Based largely on all of the Malagasy species having more than 8 labral digits (Fig. 36), Heraty (2000) proposed a separate *communis*-group. Herein we recognize the two currently described *communis*-group species as the genus *Ibitya*, although other potential species from Madagascar have been identified. Illustrations and a key to species, as *Orasema*, are provided in Heraty (1994).

Diagnosis. Separated from other Oraseminae by having the apex of the first valvula of the ovipositor with sinuate ridges as opposed to distinct lateral teeth. Distinguished from other Old World genera by the head subtriangular in frontal view; face entirely smooth laterally, scrobal depression evenly impressed and lacking parallel channels and dorsal foveae; dorsal occipital margin abrupt and rounded or carinate; antenna with 7 or 8 funiculars (11–12 antennal segments); labrum with 8-10 digits (rarely 5) (Fig. 36); mesonotum appearing bare, at most with minute setae; mesoscutal lateral lobes and frenum evenly sculptured and never smooth and shining; transscutal articulation complete; propodeal disc evenly sculptured; prepectus foveate and tightly articulated with pronotum ventrally; fore wing with basal area pilose or bare, and with specular area pilose, wing disc with dense long setae; postmarginal vein much longer than stigmal vein and reaching beyond half distance to wing apex; petiole base truncate with weak basal flange; antecostal sulcus smooth and distinctly impressed; first valvula of ovipositor with 3-4 sinuate lateral ridges. Male scape lacking ventral pores.

Host association. Myrmicinae: *Ibitya communis* reared from *Pheidole veteratrix* Forel. Distribution. Madagascar.

Ibitya communis (Risbec), comb. n.

Fig. 37

Orasema communis Risbec, 1952: 412–414. Type data: Madagascar: Bekily. Lectotype male (examined), by subsequent designation Heraty, 1994: 59. Type depository: MNHP. Citations: Heraty, 1994: 59-61 (subsequent description, both sexes, illustrated); Heraty, 2002: 51 (catalog).

Discussion. A new host record is made for *Pheidole veteratrix* Forel based on a single collection that included a soldier gripping the wing of an adult *I. communis*, 5 female

and 1 male pupae, and two unparasitized ant larvae. The pupa has the basic features of an *Orasema*, but with additional pustulate swellings not found in other taxa.

Pupa (Fig. 37). Length 5.1–5.5 mm. Typical morphology for *Orasema*, including three swollen tubercles over the petiolar region and pronounced linear swellings along the posterior margins of Mt_{1-5} . Additional atypical tubercular swellings occur over each anellus, each side of the occiput, on the dorsal margin of each flagellomere, laterally on the anterior face of the mesoscutal midlobe, axilla, laterally (paired) on the mesoscutellum as well as a single medial posterior tubercle, and with paired lateral swellings associated with the linear swellings on each of Mt_{1-5} .

New host record. Myrmicinae: Pheidole veteratrix.

New material examined. Madagascar: 45 km S Ambalavao, 785m, 22°13'00"S, 47°01'00"E, 2.x.1993, B.L. Fisher, nest, rotten log rainforest, ex: Pheidole vetera*trix* $[1^{\circ}], 1^{\circ}], 6^{\circ}$ pupae, 1 $^{\circ}$ pupa: CASC: UCRCENT00417452, UCRC: UCR-CENT00417446-00417451, UCRC: UCRCENT00417453]. La Mandraka, 18°54'19"S, 47°55'13"E, ii.1944, A. Seyrig [1∂, NMPC: UCRCENT00416474]. Antananarivo Prov.: Ankokoy Forest, 3 km E of Ibity, 1700m, 20°04'03"S, 46°59'58"E, 14-24.xi.2008, M.Irwin, R.Harin'Hala, Uapaca forest, Malaise trap [13], CASC: CASENT02212472]. Antsiranana Prov.: botanical garden near the entrance to Andasibe National Park, 1025m, 18°55'35"S, 48°24'28"E, 1-5.ix.2001, R. Harin' Hala, tropical forest, Malaise trap [23, CASC: UCRCENT00091471-72]. Fianarantsoa Prov.: 7 km W Ranomafana, 1100m, 24°34'04"S, 46°50'13"E, 15-21. ix.1988, C. Kremen, montane rainforest, small clearing, Malaise Trap [1∂, EMEC: UCRCENT00404908]. 7 km W Ranomafana, 900m, 21°15'33"S, 47°23'12"E, 23-28.ii.1990, W.E. Steiner, montane rainforest, Malaise trap in small clearing $[1^{\circ}]$, USNM: UCRCENT00416660]. Parc National Ranomafanae, radio tower at forest edge, 1130m, 21°15'03"S, 47°24'26"E, 16.x-8.xi.2001, 6-17.vii.2003, R. Harin'Hala, mixed tropical forest, Malaise trap $[3\stackrel{?}{\partial} 1\stackrel{?}{\downarrow}$, CASC: UCRCENT00417457–59, UCR-CENT00417550].

Distribution. Madagascar.

Ibitya seyrigi Risbec, comb. n.

Orasema seyrigi Risbec, 1952: 414–416. Type data: Madagascar: Bekily. Holotype female (examined), by monotypy. Type depository: MNHN. Citations: Heraty 1994: 61–62 (subsequent description of female, illustrated); Heraty 2002: 55 (catalog).

Discussion. The redescription and illustrations provided by Heraty (2002) are accurate for this species. The holotype was missing the antennae and the labrum was not visible. Based on the new material: antenna with 11 segments, all flagellomeres beyond anellus densely pilose with numerous longitudinal sensilla; flagellum 1.5× head height; 7 funiculars; F2 1.9× as long as broad, 1.1× as long as F3; clava as long as preceding

two flagellomeres. Labrum with 9 long digits, each with a long apical seta, digits arranged in clusters of 1-1-3-3-1. Ovipositor as described for *O. communis* Risbec in Heraty (2002: fig. 82), but distinctly curved cephalad.

A single male of a different species (Reserve Betampona, from sifted litter; CAS, UCRCENT 00417456) also has an antenna with 11 segments and 7 funiculars, a labrum with 7 digits, and a long petiole about as long as the hind femur. The male shares many features with *I. seyrigi*, and may be the same species, however there are dramatic differences in especially the coarsely rugose scutellar disc.

New material examined. Madagascar: Fianarantsoa Prov.: Parc National Ranomafanae, radio tower at forest edge, 1130m, 21°15′03″S, 47°24′26″E, 6-17. vii.2003, R. Harin'Hala & M. Irwin, mixed tropical forest, Malaise trap (1 $^{\circ}$, CAS: UCRCENT00417549).

Distribution. Madagascar.

164

Ivieosema Heraty & Burks, gen. n.

http://zoobank.org/11180142-ED8D-4F39-AE24-6358C767A9D8 Figs 38–54

Type species. Orasema striatosoma Heraty, 1994: 68-70, figs 98-105.

Etymology. Named after Michael Ivie of Montana State University; gender feminine.

Discussion. Defined by Heraty (1994: 68) as the Orasema striatosoma-group. Ivieosema previously contained two mainland African species, which Heraty (1994) noted as being very different from other Orasema. The two new Malagasy species that we include are even more different from other Oraseminae in many ways, but share several features with Ivieosema striatosoma (Heraty), and to a lesser degree with Ivieosema fraudulenta (Reichensperger): a large pit immediately ventral to the median ocellus (Fig. 39), continuous striae extending from the axillae to the mesoscutellar disc (Figs 42, 52), propodeal shape and sculpture (Figs 41, 43, 52), and the laterally sinuate posterior margin of the gastral tergites (Figs 45–46, 49). They differ from the African I. striatosoma and I. fraudulenta in several major ways, including the presence of two additional pairs of depressions between the eye and antennal scrobe, prepectus slightly swollen rather than weakly foveate, lack of any indication of an anterior transverse petiolar carina, and presence of a thickened basal fold in the fore wing. They also exhibit further reductions in surface sculpture, mouthparts and wing setation. All of the species have a closely appressed pronotum and prepectus that appear fused in the Malagasy species, a nearly quadrate anellus, and a thickened marginal vein. Notably the anterior margin of the fore wing beyond the stigmal vein is rounded similar to that of Cymosema.

Diagnosis. Separated from other Oraseminae by the deep sharply impressed pit just below the median ocellus (Fig. 39). Distinguished from other Old World genera by the head subtriangular in frontal view (Figs 39, 50); scrobal depression below pit

broadly impressed, lacking parallel channels or dorsal scrobal foveae; dorsal occipital margin abrupt and rounded; funicle 7-segmented; labrum with 4-digits; mesonotum appearing bare, at most with minute setae; mesoscutal lateral lobes and frenum finely sculptured; transscutal articulation complete or fused medially; propodeal disc evenly and finely sculptured (Figs 43, 52); prepectus with upper panel broad and flat, at most with a slightly raised posterior margin, very tightly appressed to posterior margin of pronotum (Figs 41, 52); fore wing with basal area pilose or bare (Figs 44, 55), wing disc with dense long setae (African species) or lacking setae but with sockets apparent (Malagasy species); marginal vein thickened along entire length; postmarginal vein absent or not much longer than stigmal vein; petiole base narrowed into foramen and lacking basal flange (Figs 45, 52); antecostal sulcus present and smooth; posterior lateral margin of gastral tergites 1–4 sinuate; first valvula of ovipositor with several fine lateral teeth. Male scape lacking ventral pores.

Host association. Myrmicinae: *Ivieosema fraudulenta* reared from *Pheidole mega-cephala* Fabricius (Reichensperger 1913).

Distribution. Ethiopian and Malagasy regions.

Ivieosema confluens Burks, sp. n.

http://zoobank.org/DD89153A-F762-43D6-80DE-B823E00EC907 Figs 38–48

Etymology. Latin noun meaning "a place where rivers meet," referring to the mesosomal surface sculpture.

Diagnosis. Recognized from other *Orasema* and African *Ivieosema* by the fore wing lacking setae and with a medial longitudinal fold. Distinguished from *I. limulus* by the smooth face, frons with 2 depressions between eye and antennal scrobe (Fig. 39), and the basal gastral tergite with a laterally carinate median longitudinal depression extending the equivalent length of the petiole.

Female. Length 2.8 mm. Head and mesosoma dark brown. Scape, pedicel, and anellus light brown, rest of flagellum darker brown. Coxae, trochanters, most of femora and last tarsomere dark brown; femoral apices, tibiae and tarsi pale white yellow with last tarsomere brown. Fore wing venation glossy and brown. Gaster brown.

Head (Figs 39–40) broadly subtriangular, $1.4\times$ as broad as long. Face flat and smooth; scrobal depression broad and shallow, extending laterally well beyond toruli and forming a single dorsal frontal depression (Fig. 39, dfd); lower frons with a vague longitudinal groove; scrobal area with a single medial large pit just below median ocellus; supraclypeal area smooth, clypeus with shallow transverse sculpture, anterior tentorial pits very deep and broad, anteclypeus short laterally and absent medially; scrobal depression shallow and hardly evident; vertex not carinate. Labrum with 4 digits. Maxillary and labial palps absent. Mandibular formula 3:2, mandibles small but falcate. Flagellum 1.0× head height, 7 funiculars; anellus longer than broad (Fig. 40, F1); F2 1.7× as long as broad, 1.1× as long as F3.



Figures 38–43. *Ivieosema confluens.* Paratype female: **38** head and mesosoma, lateral **39** head, anterior **40** antenna, medial **41** mesosoma, lateral **42** mesosoma, dorsal **43** mesosoma, posterior. dfd = dorsal frontal depression; F1/an = anellus; lg = longitudinal groove; sod = subocellar depression; tsa = transscutal articulation.

Mesosoma (Figs 41–44). Mesoscutal midlobe finely reticulate, lateral lobe mostly coriaceous, notauli very shallow and with vague margins; transscutal articulation represented only by a vague depression medially (Fig. 42, tsa). Axilla anteriorly reticulate, posteriorly longitudinally striate; mesoscutellum and axillula finely longitudinally striate; frenal line as a smooth raised strip. Metascutellum protruding, not separated from rest of metanotum. Mesepisternum reticulate dorsally, smooth ventrally, forming a short rounded horizontal area anterior to mesocoxae; mesepimeron reticulate, without



Figures 44–48. *Ivieosema confluens.* Paratype female: **44** fore wing **45** metasoma, lateral, lateral view of ovipositor in top left corner. Holotype male: **46** habitus, lateral **47** head, anterior **48** antennae, dorsal. $dv = dorsal (2^{nd}) valvula$, F1/an = anellus; $vv = ventral (1^{st}) valvula$.

transepimeral sulcus. Propodeum finely reticulate, callus bare and smooth to shallowly reticulate. Metacoxa smooth. Fore wing 2.3× as long as broad; slightly infuscate along cubital fold and posterior to marginal and submarginal veins, and between the oblique folds in the speculum; venation with only a few tiny setae, including on submarginal vein; costal cell bare; basal cell bare; speculum present, with two oblique folds (Fig. 44, fold) that converge towards stigma and basal fold; marginal vein very thick basally and

narrowing apically, not separate from wing margin at base of stigmal vein; stigmal vein 4.5× as long as broad, without an uncus; postmarginal vein absent; cubital and subcubital folds bare; marginal fringe absent. Hind wing costal cell bare.

Metasoma (Fig. 45). Petiole $1.7 \times$ as long as broad, $0.9 \times$ as long as metacoxa, longitudinally shallowly rugose-reticulate. Gt₁ with a deep longitudinal median depression with carinate lateral margins equal to length of petiole; shallower smooth depression present on Gt₂. Antecostal sulcus of Gs₁ smooth, very shallow medially; acrosternite swollen and with shallow irregular sculpture; posterior Gs₁ smooth to finely punctate. Cercus with all setae subequal in length. Hypopygium with a few small subapical setae laterally. Ovipositor dorsal valve with 9 annuli, including a basal annulus that is broadly separated from the rest; ventral valve with 5–6 lateral teeth and with transverse carina basal to toothed apex.

Male (Figs 46–48). Length 2.5 mm. Antennal flagellum densely covered with long decumbent setae, with only a few longitudinal sensilla extending beyond funicular apices; F7 shorter than F6 and F8; entire antenna brown. Petiole $1.3 \times$ as long as broad, $2.5 \times$ as long as metacoxa. Gaster with broad, striate longitudinal depression on Gt₁. Digitus with 6 spines; parameres present.

Holotype. Madagascar: Toliara Prov.: 18 km NNW Betroke, 825m, 23°09'48"S, 45°58'07"E, 24.x-4.xii.1994, M.A.Ivie & D.A.Pollock, FIT [1♂, UNMO: UCR-CENT00435300], deposited in TMP. Paratype: Madagascar: Toliara Prov.: Tsi-manampetsotsa National Park, Mitoho Forest, 120m, 24°02'55"S, 43°45'08"E, 24-29.x.2008, M. Irwin & R. Harin'Hala, transitional forest, Malaise trap [1♀, CASC: CASENT2022276].

Ivieosema limula Burks, sp. n.

http://zoobank.org/2985A405-15F7-4588-A216-E1C5C76FC5D6 Figs 49–55

Etymology. Latin noun meaning "small file (carpenter's or sculptor's tool)," referring to the finely striate mesosomal surface sculpture.

Diagnosis. Recognized from other *Orasema* and African *Ivieosema* by the fore wing lacking setae and presence of a medial longitudinal fold. Distinguished from *I. confluens* by the reticulate facial sculpture, frons with a single depression between eye and antennal scrobe (Fig. 50), and the basal gastral tergite with a laterally smooth median longitudinal depression extending the entire length of the tergite.

Female. Length 3.1 mm. Head and mesosoma almost entirely dark brown, without metallic luster; pronotum ventrally, prepectus, and acropleuron yellowish-brown. Scape white; pedicel and flagellum pale brown. Coxae and most of femora pale brown; trochanters, femoral apices, tibiae, and tarsi white. Fore wing venation glossy and milky brown. Gaster brown to dark brown.

Head (Figs 50–51) 1.4× as broad as long. Face flat and smooth; medial scrobal depression absent, but frons with paired dorsal frontal depressions lateral to scrobal



Figures 49–54. *Ivieosema limula.* Holotype female: **49** habitus, lateral **50** head, anterior **51** antenna, lateral **52** mesosoma, lateral **53** mesosoma, dorsal **54** ovipositor, lateral. dfd = dorsal frontal depression; F1/an = anellus; lg = longitudinal groove; mts = metascutellum; tsa = transscutal articulation.

area (Fig. 50, dfd); lower frons with a distinct vertical groove (Fig. 50, lg); scrobal area with a single medial large pit just below median ocellus; supraclypeal area smooth, clypeus shallowly irregularly sculptured, anterior tentorial pits very deep and broad, anteclypeus very short; scrobal depression broadly and shallowly impressed; vertex not carinate. Labrum with 4 digits. Maxillary and labial palps absent. Flagellum 1.2× head height, 7 funiculars; anellus slightly broader than long, expanding apically (Fig. 51, F1); F2 2.0× as long as broad, F2 1.1× as long as F3.



Figure 55. Ivieosema limula. Holotype female: fore wing.

Mesosoma (Figs 52-53, 55). Mesoscutum finely reticulate, with a shallow median depression; notauli finely reticulate in their troughs, with vague margins and not foveate, merging posteriorly as a transverse depression anterior to the transscutal articulation, which is present medially (Fig. 53, tsa). Axilla anteriorly reticulate, posteriorly longitudinally striate; mesoscutellum and axillula finely longitudinally striate; frenal line as a pale strip slightly elevated above frenum. Metascutellum narrow and protruding, not separated from rest of metanotum but with fine reticulate sculpture anteromedially. Mesepisternum finely reticulate dorsally and anteriorly, smooth posteroventrally, forming a short protruding horizontal surface anterior to mesocoxa. Propodeum finely reticulate, with a shallow and vague median carina; callus bare, glossy and more shallowly reticulate than propodeal disc. Metacoxa smooth. Fore wing (Fig. 55) 2.2× as long as broad; venation with only a few tiny setae, including on submarginal vein; costal cell bare; basal cell bare; speculum present, with two oblique folds that converge anteriorly towards stigma and diverge posteriorly; marginal vein very thick basally and narrowing apically, separating from wing margin to smoothly form the stigmal vein; stigmal vein 1.4× as long as broad; postmarginal vein absent; cubital and subcubital folds with only a few tiny setae beyond speculum; marginal fringe absent. Hind wing costal cell bare.

Metasoma (Fig. 54). Petiole $1.7 \times as$ long as broad, $0.9 \times as$ long as metacoxa, nearly smooth medially but longitudinally rugose-reticulate laterally, without transverse anterior carina and narrowest anteriorly immediately posterior to the condyle. Gt₁ with a deep longitudinal median depression extending length of tergite and with smooth lateral margins. Antecostal sulcus of Gs₁ smooth; acrosternite smooth to very shallowly reticulate. Cercus with all setae subequal in length. Hypopygium with a few setae sub-medially. Ovipositor dorsal valve with 8 medially interrupted annuli, including a basal annulus that is broadly separated from the rest; ventral valve with 4 lateral teeth and with a vague transverse elevation immediately basal to toothed apex.

Male. Unknown.

Material examined. Holotype: Madagascar: Toliara Prov: Manderano, 70m, 23°31'39"S, 44°05'18"E, 23.vi-28.vii.2002, Frontier Wilderness Project, gallery forest at the edge of marsh, 5m from road, Malaise trap [1Q, CAS: CASENT2022276], deposited in CAS.

Leiosema Heraty & Burks, gen. n.

http://zoobank.org/F7181858-49AC-491A-ABD2-6E035D26DBFF Figs 56–67

Type species. Orasema glabra Heraty, 1994: 72–73, figs 119, 125–128, 130, 132.

Etymology. Combination of the Greek $\lambda \varepsilon \widetilde{i} \circ \zeta$ (*leios*) for smooth and a contraction of *Orasema*, referring to the smooth and polished head and frenum; gender feminine.

Discussion. Originally treated within *Orasema* as the *glabra* group by Heraty (1994: p. 72). Heraty (1994) speculated that some of the characteristic features were shared with species in the New World *coloradensis* group. However, there is a greater similarity with *Zuparka* (Madagascar), including the entirely smooth face (Figs 57–58, 62), scrobal channels with dorsal foveae (Fig. 57), labrum with 4 digits (Figs 57, 62), and fore wing with bare basal area and speculum (Fig. 65). However, *Zuparka* has a laterally smooth or very weakly sculptured propodeal disc (Figs 73, 82) and the pronotum and prepectus are more rigidly associated ventrally (Fig. 82). *Australosema synempora* Heraty also has the mesosomal sidelobes, axillae and frenum smooth, but the face is reticulate and the propodeum has lateral glabrous areas. *Matantas* also has a similar smooth face, axilla and frenum, but the face is distinctly subtriangular, the labrum has 6-8 digits and the propodeum is laterally glabrous. Each of these other genera have only 3 or 4 lateral subapical teeth on the first valvula in contrast to the 6–10 minute lateral teeth of *Leiosema*.

Diagnosis. Separated from *Orasema* by the presence of male scape glands (pores) (Fig. 56, vp), broadly impressed rugulose antecostal sulcus and the combination of smooth head, 4-digitate labrum, and smooth frenum (Figs 59–61). Distinguished from the other Old World genera by having the head smooth and subcircular in frontal view (Figs 57–62); scrobal depression with parallel channels and dorsal foveae (Fig. 57); dorsal occipital margin rounded; funicle 7-segmented; labrum with 4 digits; mesonotum with scattered short setae; mesoscutal lateral lobes and frenum smooth; transscutal articulation complete; propodeal disc evenly rugose; prepectus foveate and loosely articulated with pronotum ventrally (Fig. 63); fore wing with basal area and specular area bare (Fig. 65), with dense and relatively long wing disc setae; postmarginal vein 1.5–3.2× as long as stigmal vein; petiole base truncate with prominent basal flange (Fig. 67); antecostal sulcus broad and reticulate; first valvula of ovipositor with 6–10 minute lateral teeth. Male scape with distinct ventral pores (glands) set in circular depressions across entire ventral surface (Fig. 56).

Distribution. Sub-saharan Africa (Democratic Republic of the Congo, South Africa, Tanzania, Zimbabwe), and Yemen.

Leiosema lesiolouna Heraty & Burks, sp. n. http://zoobank.org/9AA354CA-AF78-4523-ACB0-170734056A65 Figs 61–62, 64, 66

Etymology. Named for the collection locality of the holotype.

Diagnosis. The female is unknown, but the male is easily distinguished by the 3:3 dentate mandibles (Fig. 62), strongly reticulate mesoscutal midlobe and scutellar disc, and all tibiae yellow. It can be further differentiated from *L. glabra* by the anteriorly extended reticulate pronotal neck (Fig. 61), and petiole 4.7× as long as broad, with a strong transverse basal carina (flange) but without a lateral carina.

Male. Length 1.6 mm. Head and mesosoma blue. Scape brown; pedicel brown; anellus yellowish brown; flagellum brown. Mandible yellow, ventral mandibular setae acute; maxilla and labium yellowish brown. Coxae dark blue; fore and mid femur mostly brown, apically yellowish; hind femur mostly dark brown to black, apically yellow; tibiae yellow, but with hind tibia slightly darker basally. Fore wing hyaline; venation clear. Petiole same color as mesosoma; gaster dark brown; acrosternite same color as petiole.

Head (Figs 61–62) 1.2× as broad as high; inter-ocular distance 1.2× eye height; malar space 0.4× eye height; supraclypeal area longer than broad, smooth; clypeus smooth; epistomal sulcus distinct and sharply defined; anteclypeus distinct, straight. Mandibular formula 3:3, apical tooth elongate. Maxilla and labium of normal size, palpal formula 3:2. Occiput striate, shallowly emarginate in dorsal view, dorsal margin evenly rounded, temples present, rounded and coriaceous. Antenna 11-segmented; scape narrow and cylindrical, not reaching median ocellus; pedicel subconical, as broad as F1; flagellum 1.4× head height; anellus minute, difficult to distinguish, F2 1.2× as long as broad, 1.2× as long as F3; following funiculars subequal in length, equal in width; clava subcylindrical, longer than preceding 2 funiculars, clava without distinct separation of fused clavomeres.

Mesosoma (Figs 61, 64). Mesoscutal midlobe reticulate, interstices rounded, dorsally with few sparse setae; lateral lobe smooth and shining; notauli deeply impressed. Axilla smooth; dorsally rounded, on roughly same plane as scutellum; scutoscutellar sulcus broad, irregularly foveate. Scutoscutellar sulcus meeting transscutal articulation; scutellar disc about 1.5× as long as broad, reticulate, smooth just anterior to frenal line; frenal line as distinct crenulate groove; axillular sulcus distinct and foveate; axillula very weakly reticulate. Propodeal disc broadly rounded, without depression or carina, rugose-areolate; callus smooth, with several long hairs; callar nib absent. Prepectus evenly triangular, sculpture broadly foveate. Mesepisternum reticulate laterally, smooth ventrally, broadly rounded anterior to mid coxa. Upper mesepimeron smooth; lower mesepimeron smooth; transepimeral sulcus distinct. Propleuron convex, smooth. Postpectal carina prominent. Hind coxa 1.8× as long as broad, smooth with very weak reticulate sculpture; hind femur 5.7× as long as broad, with even cover of appressed long setae; hind tibia densely setose. Fore wing 2.4× as long as broad; basal cell and speculum bare, costal cell and wing disc densely setose, wing disc setae



Figs 56–67. *Leiosema glabra.* Male: **56** antenna, lateral (Tanzania, TZ) **57** head, frontal, (Yemen) **58** head, oblique (TZ). Female holotype **59** head and mesosoma, dorsal; Male: **60** head and mesosoma, dorsal (South Africa) **63** mesosoma, lateral (SA) **65** wings, dorsal (TZ) **66** stigmal vein (TZ) **67** propodeum and petiole, oblique (TZ). *Leiosema lesiolouna.* Holotype male: **61** head and mesosoma, dorsal **62** head, oblique **64** head and mesosoma, lateral.acr = acrosternite; apc = anterior petiolar carina; F = flagellomere; frn = frenum; lbr = labrum; no₁ = pronotum; scp = scape; vp = ventral pores.

long; marginal fringe relatively long; submarginal vein with several long setae; marginal vein with minute setae; stigmal vein more than 2.5× as long as broad, slightly angled, slightly narrowed basally and capitate apically (Fig. 66); uncus absent; stigma with 3 sensilla in a straight line; postmarginal vein 1.9× as long as stigmal vein. Hind wing costal cell with a broad bare area.

Metasoma. Petiole cylindrical, linear in profile, 4.6× as long as broad, 1.7× as long as hind coxa, reticulate, anterior carina strong, lateral margin rounded, ventral sulcus present with margins narrowly separated. Antecostal sulcus rugulose; acrosternite posteriorly angulate, raised and smooth medially and laterally broadly impressed and reticulate. Genitalia protruding: parameres elongate, digitus broad and flattened with 4 marginal spines.

Female. unknown.

Holotype. Republic of Congo: Pool Dept.: Iboubikro, Lesio-Louna Pk., 340m, 3°16'12"S, 15°28'16"E, 23.vii.2008, Sharkey & Braet, Malaise trap #3 [13, UCRC: UCRCENT00408466].

Leiosema glabra (Heraty), comb. n.

Figs 56-60, 63, 65-67

Orasema glabra Heraty, 1994: 72–73. Holotype, South Africa, Transvaal [♀, CNCI]. Mistakenly figured in Heraty (1994) with 6 funicular segments (cf. Fig. 126) instead of 7.

Diagnosis. Both sexes with mandibles 3:2 dentate, mesoscutal midlobe and scutellar disc weakly reticulate, becoming smooth posteriorly (Figs 59–60). The pronotal neck is not extended, and is reticulate only along the anterior margin (Fig. 60). Male petiole 2.6–2.9× as long as broad, female petiole 1.5–2.1× as long as broad, with a strong basal carina continuous with a lateral carina and extending 1/3 to 2/3 length of petiole (Fig. 67).

Variation. The few specimens that are known were collected across a broad geographic range from Yemen to South Africa. Females from South Africa, Yemen and Zimbabwe all have a pale brown scape and a completely yellow fore and mid tibia, whereas the female from Tanzania has an almost black scape and all tibiae are basally dark brown. Males generally have the scape and tibiae dark brown, but again these are much darker in specimens from Tanzania. In the description below, the primary measurements are for what appear to be typical *L. glabra* specimens from South Africa and Zimbabwe. There are a few minor ratio differences for specimens from Tanzania and Yemen (included in parentheses) that are outside of the range of variation from the typical *L. glabra* specimens. While these are currently considered to be one species, as more material becomes available, additional species will likely need to be recognized. An additional collection from Gambia shows variation that is likely representative of another species that has a more distinctly reticulate mesoscutellum, but we do not treat this as there seems to be a need to collect more material across Africa to assess the patterns of variation.

Male. Length 1.8–2.4 mm. Head and mesosoma dark blue, violet or green. Scape dark brown to black; pedicel black; anellus brown; flagellum black. Mandibles dark

brown; maxilla and labium brown. Coxae dark blue; femora mostly dark brown to black, with tips pale; fore and mid tibia yellow to almost completely black with pale apex; hind femur dark brown to black with metallic reflections; hind tibia mostly dark brown to black, tips pale. Fore wing hyaline; venation pale brown. Petiole and acrosternite same as mesosoma; gaster dark metallic.

Head (Figs 61–62) 1.1–1.2× as broad as high; inter-ocular distance 1.4–1.5× eye height; malar space 0.3-0.7× eye height; supraclypeal area slightly broader than long, longer than clypeus, smooth; clypeus smooth; epistomal sulcus distinct and sharply defined; anteclypeus weakly differentiated, straight. Mandibular formula 3:2. Flagel-lum 1.0–1.2× head height. F2 1.2–1.3× as long as broad, 1.2–1.3× as long as F3; clava subconical, longer than preceding two funiculars and weakly segmented.

Mesosoma (Figs 61, 64). Mesosoma $1.5-1.7 \times$ as long as high. Mesoscutal lateral lobe smooth and shining dorsally, weak rugulose laterally. Scutellar disc $1.5-1.7 \times$ as long as broad, reticulate; axillula weakly rugulose, nearly smooth. Pronotal neck not extended, at most reticulate along anterior margin. Mesepisternum straight anterior to mid coxa. Propleuron coriaceous. Hind coxa $1.1-2.0 \times$ as long as broad, smooth to coriaceous; hind femur $4.2-5.4 \times$ as long as broad, with even cover of elongate, semierect setae. Fore wing $2.1-2.3 \times$ as long as broad; marginal vein with long setae; stigmal vein $1.5-2.6 \times$ as long as broad, slightly angled; stigma nearly quadrate but with short apical anterior extension; stigma with 3 sensilla in a straight line; postmarginal vein $1.1-3.2 \times$ as long as stigmal vein. Hind wing costal cell bare.

Metasoma. Petiole 2.6–2.9× as long as broad, 1.2–1.4× as long as hind coxa, lateral margin rounded with only short lateral carina in basal 1/4. Acrosternite posteriorly rounded with rugulose sculpture, antecostal sulcus rugulose.

Female (redescription) (Fig. 59, holotype). Length 2.0–2.6 mm. Scape yellow. Fore femur mostly dark brown to black, tip pale; fore tibia yellow; mid femur mostly dark brown to black, tip pale; mid tibia yellow; hind femur mostly dark brown to black, tip pale; hind tibia pale brown basally, yellow apically.

Head 1.0-1.1x as broad as high; eyes separated by 1.3-1.5x eye height; malar space 0.4-0.6x eye height. Flagellum length 0.8-1.0x head height (0.9-1.0 in type material); flagellum with 7 funiculars, anellus disc-shaped, F2 1.1-1.4x as long as broad, 1.1-1.2x as long as F3.

Mesosoma 1.6–2.1x as long as high. Fore wing 2.3–2.6× as long as broad.

Metasoma. Petiole 1.5–2.1× as long as broad, 0.9–1.3× as long as hind coxa, apical setae of hypopygium with 2–4 long hairs clustered on each side of midline. Ovipositor slightly curved cephalad; first (ventral) valvula with 6–10 small, narrowly separated teeth, second (dorsal) valvula with 6–7 annuli that are broadly separated dorsally by smooth area; subapical carina present; third valvula separated.

Material examined. South Africa: Eastern Cape: Port St. John, 31°37'00"S, 29°32'00"E, i.1974, A. Watsham [1♂, NMPC: UCRCENT00416408]. Orange Free State: Koppies Nat. Res., 26°10'11"S, 27°59'46"E, 22-23.ii.1993, M. Stiller, Acacia karroo, sweep [1♀, NMPC: UCRCENT00416471]. Transvaal: Blyderiviers-poort, 1200m, 24°53'00"S, 30°45'00"E, iii.1981, G. L. Prinsloo [1♂, PPRI: UCR-

CENT00298795]. Waterberg nr Nylstroom [Modimolle], 1200m, 24°48'00"S, 28°25'51"E, i.1980, G. L. Prinsloo [1 \Diamond , PPRI: UCRCENT00298796]. Strijdom Tunnel, 730 m, 24°27'47"S, 30°36'31"E, 24-25.xi.1991, G.L. Prinsloo [1 \heartsuit , NMPC: UCRCENT00416472]. **Tanzania: Tanga:** West Usambara, Mgwashi env., 1460m, 4°45'47"S, 38°28'30"E, 31.i-1.ii.2015, P. Jansta & J. Straka [3 \Diamond 1 \heartsuit 2?, UCRC: UCRCENT00479260–65]. **Zimbabwe: Harare:** Chishawasha, 1416m, 17°45'46"S, 31°12'31"E, A. Watsham [2 \heartsuit , NMPC: UCRCENT00416454, UCR-CENT00416456]. **Zimbabwe: Mashondland:** Mazowe, 125m, 17°30'32"S, 30°58'19"E, i.1975, A. Watsham [6 \heartsuit , NMPC: UCRCENT00416459–61, UCR-CENT00416466–67, UCRCENT00416519]. Makumbi Miss., 17°31'12"S, 31°15'22"E, A. Watsham [1 \Diamond , NMPC: UCRCENT00416462].

Orasema near glabra: Gambia: Banjul: Kotu Stream, 3m, $13^{\circ}27'41"N$, $16^{\circ}42'13"W$, 14.xi.1981, K-J. Hedqvist $[5\overset{\circ}{\circ}4^{\bigcirc}, BMNH: UCRCENT00309860-68]$. Kotu Stream, 4m, $13^{\circ}27'42"N$, $16^{\circ}42'13"W$, 18.xi.1981, K-J. Hedqvist $[1^{\bigcirc}, BMNH: UCRCENT00309871]$. North Bank Division: Upper Baddibu, Farafenni, 13m, $13^{\circ}34'03"N$, $15^{\circ}44'56"W$, 1-2.xi.1977, Michael Söderlund, Meadow (mostly resorts) with baobab $[1\overset{\circ}{\circ}, BMNH: UCRCENT00309873]$. Western Division: Kombo St Mary, Bakau, 10m, $13^{\circ}28'47"N$, $16^{\circ}40'14"W$, 28-29.x.1977, Michael Söderlund, shore meadow $[1\overset{\circ}{\circ}, BMNH: UCRCENT00309872]$. Kombo St Mary, Sara Job Kunda, 25m, $13^{\circ}26'40"N$, $16^{\circ}42'46"E$, 29.x.1977, Michael Söderlund, grassland with palms $[1\overset{\circ}{\circ}, BMNH: UCRCENT00309859]$.

Losbanus Ishii, rev. stat.

176

Losbanus Ishii, 1932: 210. Type species: Losbanus uichancoi Ishii 1932: 210–211, by monotypy.

Losbanus; Hedqvist, 1978: 229. Short redescription and key to species, most of which are now attributed to *Neolosbanus* (Eucharitinae).

Losbanus; Watanabe, 1958, 26. Subsequent description.

Gollumiella; Bouček, 1988: 521. Incorrectly placed as senior synonym of *Gollumiella*. *Orasema*; Heraty, 1992: 586. Synonymy based on transfer of *L. uichancoi* to *Orasema*. *Orasema*; Heraty, 1994: 54–57. Description and treatment as *Orasema uichancoi*-group. *Orasema*; Heraty, 2000: 378. Separation of *communis* and *uichancoi* species groups.

Discussion. Losbanus was first described for a single species, L. uichancoi. Bouček (1988) incorrectly used this as a senior synonym of Gollumiella. Heraty (1992) transferred the type species to Orasema, then used it to represent the Orasema uichancoigroup in Heraty (1994), and in a more restricted sense for all of the Indo-Pacific species in Heraty (2000). Herein we recognize this more restricted uichancoi group (sensu Heraty, 2000) as Losbanus. We have discovered two new species (not described) that expand the geographic and morphological limits of Losbanus. A single male from the Republic of the Congo (UCRC: UCRCENT00434658) fits all of the characteristics of the group and extends the distribution to Africa. Another series of males from northeastern Queensland in Australia (Charmillin Creek and Baldy Mountain Rd; QM: UCRCENT00241810–14) overall fit the description of the genus, but lack the ocellar-ocular sulcus and have a 5-7 digitate labrum, whereas the other species have 4 digits. All species of *Losbanus* have 8–9 funiculars, a 12-13 segmented antenna, and densely pilose wings. The following species are transferred from *Orasema: L. bouceki* (Heraty), comb. n., *L. ishii* (Heraty), comb. n., *L. promecea* (Heraty), comb. n., *L. rugulosa* (Heraty), comb. n., and *L. uichancoi* Ishii comb. n. (key in Heraty, 1994).

Diagnosis. Separated from most Orasema and other Oraseminae by having 8-9 funiculars versus 7, a weak basal petiolar flange, usually a distinct ocellar-ocular sulcus, 4-7 digitate labrum, and the callar region usually with several long setae (African male with a single long seta). Distinguished from other Old World genera by the head broadly subtriangular to transverse in frontal view; face smooth or sculptured; presence of an ocellar-ocular sulcus in all but the Australian species; scrobal depression evenly impressed and lacking parallel channels and dorsal foveae; dorsal occipital margin abrupt and rounded or carinate; funicle 8-9 segmented; labrum with 4-7 digits (usually 4); mesonotum appearing bare, at most with minute setae; mesoscutal lateral lobes and frenum sculptured or smooth; transscutal articulation complete and only slightly sinuate; propodeal disc evenly sculptured, smooth laterally only in the Australian species; prepectus foveate and tightly articulated with pronotum ventrally; fore wing with basal area and specular area pilose or bare, wing disc with dense long setae; postmarginal vein much longer than stigmal vein and reaching over half distance to wing apex; petiole base truncate with weak basal flange; antecostal sulcus broad and smooth or foveate; first valvula of ovipositor with 3-5 lateral teeth, subapical teeth sometimes formed by oblique ridges. Male scape lacking ventral pores.

Biology. The oviposition habits and morphology of the egg and first instar were described by Ishii (1932) for *L. uichancoi*. The egg is stalked as in most Eucharitidae. A revised interpretation of the planidum was presented in Heraty (1994) and larvae are the same as for *Orasema*, with tergites I and II separated and not fused as illustrated by Ishii. Oviposition was made in short parallel rows into incisions made into the undersurface of leaves of *Celtis philippinensis* Blanco (Cannabaceae) and *Leucaena glauca* Benth. (Fabaceae).

Host association. Unknown.

Distribution. Five species described from southeast Asia (Heraty, 1994). Paleotropical (Australia: Queensland (undescribed); Republic of Congo (undescribed), Papua New Guinea, Philippines, Taiwan).

Matantas Heraty & Burks, gen. n. http://zoobank.org/6556925F-B592-4324-B97C-110902691CF2

Type species. Orasema koghisiana Heraty, 1994: 71–72, figs 107–108, 110, 189–190, 211–212, 219, 236, 247.

Etymology. Named after one of the New Caledonia collecting localities, Matanta; gender feminine.

Discussion. Defined by Heraty (1994: 71) as the *Orasema koghisiana*-group. No genetic sequence data are available for the group. *Matantas koghisiana* (Heraty) comb. n. is the only species described for the genus.

Diagnosis. Separated from *Orasema* by the combination of smooth lateral areas on the propodeal disc in combination with a rugose-areolate or reticulate median channel, smooth face, and labrum with 6–8 digits. Distinguished from other Old World genera by the head subtriangular in frontal view; face smooth and relatively flattened, scrobal depression evenly impressed and lacking parallel channels or dorsal foveae; dorsal occipital margin abrupt and rounded, at most with a weak dorsal carina; funicle 7-segmented; labrum with 6–8 digits; mesonotum appearing bare, at most with minute setae; mesoscutal lateral lobes and frenum smooth; transscutal articulation complete and relatively straight; propodeal disc smooth with a broad sculptured median channel; prepectus foveate and tightly articulated with pronotum ventrally; fore wing with basal area and specular area bare, wing disc setae relatively long and dense; postmarginal vein much longer than stigmal vein and reaching about half distance to wing apex; petiole base truncate with strong basal flange; antecostal sulcus present and smooth; first valvula of ovipositor with 3 or 4 lateral teeth. Male scape lacking ventral pores.

Host association. Unknown.

178

Distribution. One species described. New Caledonia (another undescribed species from Vanuatu, BPBM: UCRCENT00422296).

Zuparka Heraty & Burks, gen. n.

http://zoobank.org/17C35918-BF49-424D-BFE0-F3541C898EBB Figs 68–86

Type species. Zuparka monomoria Heraty, 2000: 375–378, figs 1–7.

Etymology. Named after Robert Zuparko of the California Academy of Sciences; gender feminine.

Discussion. Defined by Heraty (2000: 375) as the Orasema monomoria group as based on the single species Z. monomoria (Heraty), comb. n. and on a single recently emerged teneral female. Another distinctive species is recognized herein, Z. fisheri sp. n. The two species are morphologically distinct from each other, and the divergence in their ribosomal and mitochondrial data is generally what is expected between different genera in other Oraseminae. However, morphological features support recognition of a single genus. Zuparka is most similar to the African Leiosema, the only other orasemine with ventral pores on the male scape. Based on Z. monomoria, Zuparka is the only genus with a pupa that lacks pronounced tubercles over the petiolar region (c.f. Fig. 37) or laterally on the lateral abdominal region (Heraty, 2000). It is also the only genus known to attack Monomorium (Myrmicinae).

Diagnosis. Separated from other Oraseminae by the presence of ventral pores on the male scape, 4-digitate labrum (Figs 69, 79), parallel scrobal depressions with a dorsal fovea (Fig. 79, dsd), sculptured frenum (Fig. 70, frn), presence of a basal petiolar carina (Fig. 75, apc), and absence of an antecostal sulcus. Distinguished from the other Old World genera by having the head smooth or very weakly coriaceous, and subtriangular in frontal view (Figs 69, 79, 81); scrobal depression with parallel channels and dorsal fovea (Fig. 79); occiput rounded; funicle 7-segmented; labrum with 4 digits; mesonotum appearing bare, at most with few minute setae; mesosomal lateral lobes and frenum sculptured; transscutal articulation complete and relatively straight; propodeal disc has either smooth or nearly smooth lateral areas on the propodeal disc in combination with a rugose-areolate or reticulate median channel (Fig. 73), or more weakly sculptured propodeum with a weak median channel and a median carina; prepectus foveate dorsally and tightly articulated with pronotum ventrally (Figs 70, 82); fore wing with basal area and specular area bare (Figs 74, 83), wing disc with relatively long dense setae; postmarginal vein less than twice as long as stigmal vein; petiole with prominent basal flange; antecostal sulcus absent; first valvula of ovipositor with 3-4 lateral teeth. Male scape with distinct ventral pores (glands) set in circular depressions across entire ventral surface (Fig. 78).

Host association. Myrmicinae: Z. monomoria reared from Monomorium sp. (Heraty 2000).

Distribution. Madagascar.

Zuparka fisheri Heacox & Dominguez, sp. n.

http://zoobank.org/A2294EE0-09AF-4A98-B9AA-B8D207366A13 Figs 68–80

Etymology. Named after Brian Fisher of the California Academy of Sciences for his tremendous collecting efforts that have contributed to the understanding of the fauna of Madagascar.

Diagnosis. Face entirely smooth. Scutellum vaulted anterior to frenum and medially depressed. Propodeal disc laterally smooth. This species resembles *Zuparka monomoria*, but can be easily differentiated by the presence of an elevated medial region of the scutellar disc (Fig. 70) with a median depression (Figs 71, 72), sculptured axilla (Fig. 71), torulus with ventral margins roughly on the same plane as the ventral margins of the eyes (Figs 69, 79). Based on differing structures of the male antenna, what we are currently recognizing as *Z. fisheri* may ultimately be a complex of species.

Female. Length 1.8–2.4 mm. Head and mesosoma, including mid and hind coxae and petiole, dark bluish-black; fore coxae dark bluish-black and yellow apically. Flagellum brown; scape, pedicel and anellus yellow to brown. Legs beyond coxa yellow with femora medially brown and tarsomeres apically pale brown. Gaster dark brown. Wings hyaline, venation pale yellowish-brown.



Figures 68–73. *Zuparka fisheri*. Paratype female: **68** habitus, lateral **69** head, anterior **70** mesosoma, lateral **71** mesosoma, oblique dorsal **72** mesosoma, anterior **73** propodeum, oblique dorsal. apc = anterior petiolar carina; cal = callus; frn = frenum; lpr; lateral propodeal disc; mts = metascutellum; sct = mesoscutellum; tsa = transscutal articulation.

Head (Figs 69, 77–79) 2.2–2.6× as broad as long; face broadly rounded, smooth and polished with faint indication of cellulate sculpture on upper frons and vertex; interocular distance $1.3-1.4\times$ eye height; malar space $0.5-0.7\times$ eye height; distance from anteclypeus to ventral margin of toruli $0.3-0.4\times$ head height; clypeus smooth and with scattered setae, lateral margins and epistomal sulcus strongly impressed; anteclypeus distinct and subtruncate. Mandibular formula 3:2; palpal formula 3:3.
Occiput transversely aciculate, dorsal margin broadly rounded, occipital carina absent; temples broad. Antenna 11-segmented (Fig. 77); scape narrow and cylindrical, slightly broadening medially and reaching median ocellus, at least 7× as long as broad; pedicel 1.3–2.0× as long as broad, apex broader than anellus; flagellum 0.8–0.9× head height; funicle 7-segmented; flagellar segments beyond anellus densely setose with numerous longitudinal sensilla; F2 1.2–1.6× as long as broad, following segments becoming more transverse; clava subconical, about as long as preceding three segments.

Mesosoma (Figs 70-74). Midlobe of mesoscutum and mesoscutellum finely reticulate; notauli foveate, reaching transscutal articulation (TSA) and broadly separated posteriorly; lateral lobe and axilla broadly rounded; scutellar disc abruptly vaulted anterior to frenum (Fig. 70) and with weak median depression (Figs 71–72); scutellar disc about as long as broad, separated from axillae and TSA by deep foveate scutoscutellar sulcus that is continuous medially; axillular sulcus and frenal line medially foveate with a weak carina along ventral margin of sulcus, continuing laterally as a smooth ridge; frenum semicircular and vertical. Propodeal disc rounded, areolate medially, smooth laterally (Fig. 73); callar region smooth with few setae dorsally; metepimeron smooth dorsally and ventrally reticulate. Upper and lower mesepimeron mostly smooth; transepimeral sulcus irregularly foveate; femoral groove obscure. Prepectus foveate dorsally, with a strong posterior flange, ventrally narrow and smooth. Pronotum reticulate laterally and smooth medially. Propleuron imbricate. Fore and mid coxae imbricate; hind coxae reticulate. Fore wing $2.6-2.9\times$ as long as mesosoma, $2.4-2.6 \times$ as long as broad; basal cell setose; costal cell ventrally pilose, remainder of wing pilose; stigmal vein as long or slightly longer than wide and perpendicular to wing margin; postmarginal vein 0.1-0.2× length of marginal vein, about twice length of stigmal vein. Hind wing costal cell with several ventral setae in apical half.

Metasoma (Figs 75–76) with petiole cylindrical, $1.6-1.9\times$ as long as hind coxa; finely reticulate; ventral sulcus absent. Gt₁ as long as or slightly shorter than femur, smooth and bare; Mt₇ densely pilose anterior to cercus, cercus with 5 long setae; Gs₁ smooth and without antecostal sulcus. Hypopygium with 2 pairs of minute subapical setae. Ovipositor expanded subapically and curved forward; first valvula with 3 lateral teeth and sinuate subapical ridge; second valvula with 8 lateral teeth (Fig. 76).

Male. Length 1.7–1.8 mm. Scape yellow to brown, flagellomeres brown. Fore coxa bluish-black and brown apically; legs yellow to yellowish-brown, hind femur darker with yellow tips, tarsomeres yellow to brown. Scape ventroapically with dense minute pores. Gs_8 apically strongly convex with sparse ventral hairs; Ms_8 densely setose near cerci. Genitalia with broad flattened parameres with two subapical setae, digiti with 4 lateral spines; aedeagus subapically expanded (Fig. 80).

Holotype. Madagascar: Fianarantsoa Prov.: Parc National Ranomafana, Belle Vue at Talatakely, 1020m, 21°15′59″S, 47°25′07″E, 2-10.i.2002, R. Harin' Hala, secondary tropical forest, Malaise trap [1Q, CASC: UCRCENT00417485]. Paratypes: Madagascar: Antananarivo Prov.: 3 km 41 degrees NE Andranomay,



Figures 74–78. *Zuparka fisheri*. Paratype female: **74** fore wing **75** petiolar base **76** ovipositor. Paratype male: **77** antenna **78** pores on scape ventrally. ads = anterodorsal swelling of petiole; apc = anterior petiolar carina; dv = dorsal (2nd) valvula; F = flagellomere; F1/an = anellus; lhp = petiolar lateral hair patch; vp = ventral pore of scape; pmv = postmarginal vein; stv = stignal vein; vv = ventral (1st) valvula.

11.5 km 147 degrees SSE Anjozorobe, 1300m, 18°28'24"S, 47°57'36"E, 5-13. xii.2000, Fisher, Griswold et al., montane rainforest, Malaise trap [13, CASC: UCRCENT00417369]. Antsiranana Prov.: Parc National Montagne d'Ambre,



Figures 79–80. *Zuparka fisheri.* Paratype male: **79** head, anterior **80** genitalia and subgenital plate, ventral. acy = anteclypeus; dsd = dorsal scrobal fovea; msd = median scrobal depression; prm = paramere; sgp = subgenital plate; tor = torulus.

960m, 12°30'52"S, 49°10'53"E, 12.ii-4.iii.2001, 4-19.iii.2001, R. Harin'Hala, Malaise $[5^{\uparrow}_{\circ}, 1^{\circ}_{\circ}, CASC: UCRCENT00175169, UCRCENT00278241-45]$. Parc National Montagne d'Ambre, 1125m, 12°31'13"S, 49°10'45"E, 29.i-11.ii.2001, 5-21.iv.2001, 14-30.v.2001, 30.v-6.vi.2001, R. Harin'Hala, Malaise trap [4] 12, CASC: CASENT02014649, CASENT02015483, CASENT02015488, UCR-CENT00417343, UCRCENT00417345]. Sakalava Beach, 10m, 12°15'46"S, 49°23'51"E, 16-31.v.2001, R. Harin' Hala, dwarf littoral forest, sandy trail, Malaise trap [13, CASC: UCRCENT00417339]. Fianarantsoa Prov.: Parc National Ranomafana, Belle Vue at Talatakely, 1020m, 21°15′59″S, 47°25′13″E, 28.xi-6.xii.2001, M. Irwin & R. Harin'Hala, secondary tropical forest, Malaise Trap $[1 \stackrel{?}{\circ} 1 \stackrel{?}{\circ}$, CASC: UCRCENT00417551, UCRCENT00417553]. Parc National Ranomafana, radio tower at forest edge, 1130m, 21°15'03"S, 47°24'26"E, 16.x-8.xi.2001, 24.v-4.vi.2002, 7-17.v.2003, R. Harin' Hala, mixed tropical forest, Malaise $[2 \stackrel{?}{\circ} 4 \stackrel{\circ}{\downarrow},$ CASC: UCRCENT00417386-487, UCRCENT00417388, UCRCENT00417489, UCRCENT00417490, UCRCENT00417492]. Parc National Ranomafana, Vohiparara at broken bridge, 1110m, 21°13'34"S, 47°22'11"E, 21-28.i.2002, 4-12. ii.2002, M. Irwin and R. Harin'Hala, high altitude rain forest, Malaise trap [1] 29, CASC: UCRCENT00417509-10, UCRCENT00417537]. Toamasina Prov.: bot. garden near entrance to Andasibe National Park, 1025m, 18°55'35"S, 48°24'28"E, 16-24.x.2001, 24.x-1.xi.2001, 1-7.xi.2001, R. Harin'Hala, tropical forest, Malaise Trap $[2 \stackrel{?}{\odot} 2 \stackrel{\circ}{\downarrow}$, CASC: UCRCENT00417486, UCRCENT00417497, UCRCENT00417513, UCRCENT00417538].

Additional material examined. Madagascar: Antsiranana Prov.: Parc National Montagnad'Ambre, 1125m, 12°31'13"S, 49°10'45"E, 12.ii-4.iii.2001, 19.iii-5.iv.2001, 12-14.v.2001, R. Harin'Hala, Malaise trap $[3 \ 1 \ 3 \ CASC$: CASENT02015492, UCRCENT00417340, UCRCENT00417344, UCRCENT00417346]. Sakalava Beach, 10m, 12°15'46"S, 49°23'51"E, 16-31.v.2001, R. Harin' Hala, dwarf littoral forest, sandy trail, Malaise trap $[1 \ CASC$: UCRCENT00417338].

Zuparka monomoria (Heraty), comb. n.

Figs 81-84

184

Orasema monomoria Heraty, 2000: 376-378.

Diagnosis. Frons weakly coriaceous. Scutellum evenly rounded anterior to frenum. Propodeal disc laterally weakly sculptured.

Discussion. Previously described from a single female that had recently emerged. The new material examined fits the description of the single female.

Distribution. Madagascar.

Holotype. Madagascar: Fianarantsoa Prov.: Res. Andringitra, 8.5 km SE of Antanitotsy, 1990m, 22°10'00"S, 46°58'00"E, 6.iii.1997, Sylvian, montane rainforest [1 \mathcal{Q} , UCRC: UCRCENT00417370]. Additional material examined: Madagascar: Majunga Ampijoroa National Park, 160 km N of Maevatanana on RN 04, 43m, 16°19'10"S, 46°48'48"E, Rin'ha Harin'Hala, deciduous forest, Malaise trap [12, CASC: UCRCENT00417389]. Antananarivo Prov.: 3km 41d NE Andranomay, 1300m, 18°28'24"S, 47°57'36"E, 5-13.xii.2000, Fisher, Griswold, et al. CASC, montane rainforest, Malaise trap [13, CASC: UCRCENT00278242]. Ankokoy Forest, 3 km E of Ibity, 1700m, 20°04'03"S, 46°59'58"E, 12-22.xii.2008, M.Irwin, R.Harin'Hala, Uapaca forest, Malaise trap [1º, CASC: UCRCENT00352446]. Antsiranana Prov.: Parc National Montagne d'Ambre, 960m, 12°30'52"S, 49°10'53"E, 4-19. iii.2001, 5-21.iv.2001, R. Harin' Hala, Malaise trap [32, CASC: CASENT02015482, CASENT02015484, CASENT02015487]. Diego Suarez: PN Montange d'Ambra, 960m, 12°30'52"S, 49°10'53"E, 21-26.i.2001, M.E. Irwin, E.I. Schlinger & R. Harin'Hala, Malaise trap [1?, CASC: UCRCENT00417358]. Fianarantsoa Prov.: Miandritsara Forest, 40 km S Ambositra, 825m, 20°47'34"S, 47°10'32"E, 28.xii.2006-4.i.2007, M. Irwin, R. Harin'Hala, low altitude rainforest, Malaise trap [19, CASC:CASENT02174550]. near Isalo National Park, at stream E of Interpretive Cntr., 750m, 22°37'36"S, 45°21'29"E, 7-17.v.2003, R. Harin' Hala, mixed tropical forest, Malaise trap in open area [19, CASC: UCRCENT00417378]. Parc Nacional Ranomafana, Belle Vue at Talatalely, 1020m, 21°15'59"S, 47°25'13"E, 22.xi.2001, 6-12.xii.2001, 28.xi-6.xii.2001, 19-26.ii.2002, 10-14.i.2002, 12-19.ii.2002, 23-28.iv.2002, 5-13.v.2002, 15-22.xi.2002, 16-26.ii.2003, 26.ii-10.iii.2003, 10-21.iii.2003, 28.v-6.vi.2003, R. Harin' Hala, secondary forest, Malaise [4] 21, CASC: CASENT02174558-60, CASENT02174556, CASENT02174592, CASENT02174594-97, UCRCENT00 417360; UCRC: UCRCENT00417481, UCRCENT00417495-96, UCRCENT0 0417503, UCRCENT00417514, UCRCENT00417531-33, UCRCENT004175 35, UCRCENT00417390–93]. Parc National Ranomafana, JIRAMA water works, 690m, 21°14'55"S, 47°27'08"E, 28.i-4.ii.2002, R.Harin Hala, near river, Malaise Trap $[1^{\circ}]$, CASC: CASENT02174591]. Parc National Ranomafana, radio tower at forest edge, 1130m, 21°15′03″S, 47°24′26″E, 14-21.i.2002, 28.i-4.ii.2002, 4-12.ii.2002, 7-17.v.2003, 7-18.vi.2003, 27.vi-7.vii.2003, R. Harin' Hala, mixed tropical forest, Malaise trap [14♀ 3♂, CASC: UCRCENT00417467, UCRCENT00417371-77,



Figures 81–86. 81–84 *Zuparka monomoria*. Female: **81** head, frontal **82** mesosoma, lateral **83** habitus, lateral **84** head and mesosoma, dorsal **85** unknown male Oraseminae, Australia: UCRCENT00238798 (couplet 10) **86** unknown male Oraseminae, Australia: UCRCENT00241816 (couplet 15).

UCRCENT00417379–85, UCRCENT00417387, UCRCENT00417530]. Parc National Ranomafana, Vohiparara at broken bridge, 1110m, 21°13'34"S, 47°22'11"E, 6-15.xii.2001, 14-21.i.2002, 21-28.i.2002, 4-12.ii.2002, 19-26.ii.2002, 6-15.v.2002, M. Irwin and R. Harin'Hala, high altitude rain forest, Malaise trap [5♂ 9♀ 3?, CAS: CASENT02174562, CASENT02174583, CASENT02174587–89; UCRC: UC RCENT00417508, UCRCENT00417511–12, UCRCENT00417525–29, UC RCENT00417534, UCRCENT00417465-66, UCRCENT00417468]. Parc National Ranomafanae, radio tower at forest edge, 1130m, 21°15'03"S, 47°24'26"E, 12-19.ii.2002, R. Harin'Hala, mixed tropical forest, Malaise trap [23] 12, CASC: UCRCENT00417443, UCRCENT00417501-02]. Parc National Ranomafanae, radio tower at forest edge, 1130m, 21°15'03"S, 47°24'26"E, 21-28.i.2002, 4-12. iii.2002, 12-19.iii.2002, 27.ii-9.iii.2003, 20.iii-3.iv.2003, 15-27.iv.2003, 24.v-4. vi.2002, 6-17.vii.2003, R. Harin'Hala, mixed tropical forest, Malaise trap [6379]1?, CASC: CASENT02174580-81, UCRCENT00417441, UCRCENT00417488, UCRCENT00417491; UCRCENT00417493-94, UCRCENT00417498, UCRCENT00417504-07, UCRCENT00417536, UCRCENT00417554]. Ranomafana National Park Talatakely area, 900m, 21°15'02"S, 47°25'10"E, 9-19.i.2001, D.H. & K.M. Kavanaugh, R.L. Brett, E. Elsom, F. Vargas, mixed tropical forest, flight intercept trap [12, CASC: UCRCENT00417347]. Res. Andringitra, 8.5 km SE of Antanitotsy, 1990m, 22°10'00"S, 46°58'00"E, 6.iii.1997, Sylvian, montane rainforest [1º 1?, UCRC: UCRCENT00412588-89]. Toamasina Prov.: bot. garden near entrance to Andasibe National Park, 1025m, 18°55'35"S, 48°24'28"E, 16-23.xi.2001, R. Harin'Hala, tropical forest, Malaise Trap [1⁽²⁾, CASC: UCRCENT00417494].

Acknowledgements

We would like to thank Gary Gibson and Lisa Bearss for imaging the holotype of *Orasema glabra*. We would like to thank Austin Baker, Chris Darling and Javier Torréns for comments on earlier drafts of the manuscript. This research was supported by NSF DEB 1257733 and UCR Hatch grants to JMH. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA; USDA is an equal opportunity provider and employer.

References

- Bouček Z (1988) Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species. CAB International.
- Burks RA, Mottern J, Heraty JM (2015) Revision of the Orasema festiva species group (Hymenoptera: Chalcidoidea: Eucharitidae). Zootaxa 3972: 521–534. https://doi.org/10.11646/ zootaxa.3972.4.4
- Das GM (1963) Preliminary studies on the biology of Orasema assectator Kerrich (Hymenoptera: Eucharitidae) parasitic on Pheidole and causing damage to leaves of tea in Assam. Bulletin of Entomological Research 54: 393–398. https://doi.org/10.1017/S0007485300048884
- Girault AA (1913[175]) New genera and species of chalcidoid Hymenoptera from the South Australian Museum, Adelaide. Transactions of the Royal Society of South Australia 37: 67–115.

- Girish Kumar P, Narendran TC (2007) A new species of *Orasema* Cameron (Hymenoptera: Eucharitidae) of Indian subcontinent. Journal of Environment & Sociobiology 4: 149–153.
- Girish Kumar P, Sureshan PM (2015) Description of two species of *Orasema* Cameron (Hymenoptera: Eucharitidae) from Kerala, India. Journal of Insect Systematics 2: 97–105.
- Harris RA (1979) A glossary of surface sculpturing. Occasional Papers of the California Department of Food and Agriculture 28: 31 pp.
- Hedqvist KJ (1978) Some Chalcidoidea collected in the Philippine, Bismarck and Solomon Islands. 2. Eucharitidae, with keys and check-lists to Indo-Australian genera (Insecta, Hymenoptera). Steenstrupia 4: 227–248.
- Heraty JM (1992) Revision of the genera Gollumiella Hedqvist and Anorasema Bouček (Hymenoptera: Eucharitidae). Invertebrate Taxonomy 6: 583–604. https://doi.org/10.1071/ IT9920583
- Heraty JM (1994) Classification and evolution of the Oraseminae in the Old World, with revisions of two closely related genera of Eucharitinae (Hymenoptera: Eucharitidae). Life Sciences Contributions, Royal Ontario Museum 157: 1–174. https://doi.org/10.5962/bhl.title.53489
- Heraty JM (2000) Phylogenetic relationships of Oraseminae (Hymenoptera: Eucharitidae). Annals of the Entomological Society of America 93: 374–390. https://doi.org/10.1603/0013-8746(2000)093[0374:PROOHE]2.0.CO;2
- Heraty JM (2002) A revision of the genera of Eucharitidae (Hymenoptera: Chalcidoidea) of the World. Memoirs of the American Entomological Institute 68: 1–359.
- Heraty JM (2017) Catalog of World Eucharitidae. University of California, Riverside 107 pp. http://hymenoptera.ucr.edu/EucharitidaeCatalog2014.pdf
- Heraty JM, Burks BD, Cruaud A, Gibson G, Liljeblad J, Munro J, Rasplus J-Y, Delvare G, Janšta P, Gumovsky AV, Huber JT, Woolley JB, Krogmann L, Heydon S, Polaszek A, Schmidt S, Darling DC, Gates MW, Mottern JL, Murray E, Dal Molin A, Triapitsyn S, Baur H, Pinto JD, van Noort S, George J, Yoder M (2013) A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). Cladistics 29: 466–542. https://doi.org/10.1111/cla.12006
- Heraty JM, Hawks D, Kostecki JS, Carmichael AE (2004) Phylogeny and behaviour of the Gollumiellinae, a new subfamily of the ant-parasitic Eucharitidae (Hymenoptera: Chalcidoidea). Systematic Entomology 29: 544–559. https://doi.org/10.1111/j.0307-6970.2004.00267.x
- Ishii T (1932) Some Philippine eucharids with notes on their oviposition habits. Bulletin of the Imperial agricultural Experiment Station, Nishigahara 3: 203–212.
- Kerrich GJ (1963) Descriptions of two species of Eucharitidae damaging tea, with comparative notes on other species (Hymenoptera: Chalcidoidea). Bulletin of Entomological Research 54: 365–371. https://doi.org/10.1017/S0007485300048872
- Lachaud JP, Pérez-Lachaud G (2012) Diversity of species and behavior of hymenopteran parasitoids of ants: A review. Psyche 2012: 1–24. https://doi.org/10.1155/2012/134746
- Murray E, Carmichael AE, Heraty JM (2013) Ancient host shifts followed by host conservatism in a group of ant parasitoids. Proceedings of the Royal Society, B 280: 9 pp., 20130495
- Narendran TC, Girish Kumar P (2005) Description of a new species and a key to species of *Orasema* Cameron (Hymenoptera: Eucharitidae) from India. Cobios 3: 10–14.

- Reichensperger A (1913) Zur kentnis von Myrmecophilen aus Abessinen, I. Zoologische Jahrbücher. https://doi.org/10.1098/rspb.2013.0495
- Risbec J (1952) Contribution à l'étude des Chalcidoides de Madagascar. Mémoirs de L'Institute Scientifique de Madagascar, Séries E 2: 449 pp.
- Walker F (1839) Monographia Chalciditum, Vol. 2., London. https://doi.org/10.5962/bhl. title.67725
- Watanabe C (1958) Eucharidae. Insects of Micronesia 19: 19-34.

RESEARCH ARTICLE



On the natural history of the willow sawfly Nematus oligospilus (Hymenoptera, Tenthredinidae) inhabiting Salix humboldtiana, in Colombia

Leonardo A. Malagón-Aldana¹, Francisco Serna¹, David R. Smith²

I Museo Entomológico UNAB, Grupo Sistemática de Insectos Agronomía SIA, Facultad de Ciencias Agrarias, Universidad Nacional de Colombia, Cra 30 #45-03, Bogotá, D.C., Colombia 2 Systematic Entomology Laboratory, Agricultural Research Service, U. S. Department of Agriculture, c/o National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, MRC 168, Washington, D.C. 20013-7012, USA

Corresponding author: Leonardo A. Malagón-Aldana (landresmalagon@gmail.com.co)

Academic editor: M. Prous	Received 20 December 2016 Accepted 13 February 2017	Published 28 April 2017
	http://zoobank.org/6D8168AF-9803-4F22-AAA1-649BD46A33DB	

Citation: Malagón-Aldana LA, Francisco S, Smith DR (2017) On the natural history of the willow sawfly *Nematus oligospilus* (Hymenoptera, Tenthredinidae) inhabiting *Salix humboldtiana*, in Colombia. Journal of Hymenoptera Research 55: 189–199. https://doi.org/10.3897/jhr.55.11566

Abstract

The willow sawfly, *Nematus oligospilus* Förster, has recently been recorded from Colombia. Natural populations were searched for in Bogotá City, where one of the host plants, *Salix humboldtiana*, grows as an ornamental tree. Larvae and cocoons were found, which thrive on the leaves of this plant. Parthenogenetic reproduction of this sawfly was confirmed. Fecundity of every female was estimated through counting the number of eggs laid on the leaves of the host. In addition, some variations in the color pattern of the adult are described and several of its morphological traits measured. For the larval stage, the body length of each instar was measured and their stadium (intermoult period or instar duration) calculated. Six larval instars were observed regularly; only one case of seven instars occurred.

Keywords

Symphyta, development, introduced species, Neotropics, Bogotá

Introduction

The presence of the willow sawfly, *Nematus oligospilus* Förster, was recently recorded for Colombia (Malagón-Aldana et al., in press); two female specimens were found deposited at different entomological collections (Entomological Museum UNAB and the biological collection from Alexander Von Humboldt Institute IAvH), both distributed in central region of Colombia, departments of Cundinamarca and Boyacá. In early 1980s, this species was recorded for the first time for southern South America, in Argentina and Chile (Smith 1983, González et al. 1986, Dapoto and Giganti 1994, Koch and Smith 2000), where this introduced species is a pest occurring at very high larval densities, causing severe defoliation, tree mortality, and economic losses on plantations of different species of *Salix* (Dapoto and Giganti 1994). Populations identified as *N. oligospilus* in different regions of the world could involve different members of a species group (Koch and Smith 2000, Smith 2003, Caron et al. 2013a).

The natural history of N. oligospilus has been addressed in several studies from different biogeographical regions (De Santis and De Sureda 1984, Dapoto and Giganti 1994, Urban and Eardley 1995, Ede et al. 2007, Alderete et al. 2010). Some common features regarding these studies include absence of males and reproduction by parthenogenesis (apomictic thelytoky) in the invasive populations (De Santis and De Sureda 1984, González et al. 1986, Ede et al. 2007, Caron et al 2013b). Regarding immature forms, larvae hibernate as prepupae when their deciduous hosts lose their leaves; the larvae move from the host into the soil, where they build cocoons and dwell until spring when they pupate and adults eventually emerge (Ede et al. 2007). A small proportion of the population may pupate directly either on leaves or trunks within the summer and winter season (Dapoto and Giganti 1994, Alderete et al. 2010). Concerning their development, stadia (timing) of various stages have been estimated several times (Ede et al. 2007), the number of larval instars varies between four to seven (González et al. 1986, Ovruski 1991, Charles and Allan 2000). However, little information of the intermoult growth and stadia of larval instars has been reported. As to their natural enemies, several parasitoids of the families Ichneumonidae, Eurytomidae, Pteromalidae, Eulophidae, Eupelmidae, and Chalcididae, as well as predators of the families Pentatomidae and Vespidae have been recorded (De Santis and De Sureda 1984, González et al. 1986, Dapoto and Giganti 1994).

In Colombia, *Salix* is represented primarily by the species *S. humboldtiana* (Alford 2015), which is naturally distributed from Mexico to Argentina (STRI 2015). Likewise, though much less common, some introduced species, including *S. babylonica*, *S. viminalis*, and *S. purpurea* have also been recorded. Contrary to other countries in the region, in Colombia there are no extensive plantations of *Salix* spp.; the main purpose of urban plantings of the introduced species are ornamental, landscaping, soil conservation, and protection of water bodies. In cities such as Bogotá, the planted trees of *S. humboldtiana* are easily found, albeit scattered.

Based on a previous record of some specimens of *N. oligospilus* from localities in central Colombia, and the abundance of *Salix humboldtiana* thriving in Bogotá City,

the main goals of this study were to discover populations of *N. oligospilus* in the city, corroborate parthenogenetic reproducing populations, the presence/absence of males, and highlight some traits of the populations, including phenotypic variation of adults, larval development, oviposition behavior, and occurrence of parasitoids.

Materials and methods

Field work

To locate the larvae, cocoons, or any other indication of the occurrence of *N. oligospilus*, we inspected approximately 25 trees of *S. humboldtiana* scattered around Bogotá, including the campus of the Universidad Nacional de Colombia. Following recommendations from the literature (Charles and Allan 2000, Loetti et al. 2012), we collected branches with numerous leaves, on heights between 0 and 3 m on each tree, for 10 to 15 minutes per tree. Sampling was carried out during July and August, 2015, from 10 am to 4 pm. The foliage accumulated was placed into several plastic boxes and transported to the laboratory.

Laboratory procedures and data analysis

Laboratory work was conducted at the Entomological Museum UNAB (Universidad Nacional Agronomía Bogotá). Several specimens were mounted, curated, and housed in the Central Taxonomic Collection (CTC) of UNAB, following the curatorial standards of Martínez-Alava and Serna (2015). To confirm the identity of the collected specimens, we needed adults, because this is the main stage of development for which taxonomic keys, diagnosis, and descriptions are available (Benson 1958, Förster 1854, Koch and Smith 2000, Smith 2003). To obtain adults, the larvae and in-cocoon pupae were put individually in Petri dishes. Larvae were maintained with leaves of *S. humboldtiana*, while cocoons were placed on a filter paper that was the same size as the Petri dish, and into which 10 drops of water was daily applied to guarantee moisture. The breeding was kept at room temperature (with oscillations between 5–18 °C, between night and day).

All stages of development were observed under a Nikon SMZ-1 stereo microscope. Measurements were taken with a micrometric scale, and photographs were taken with a Canon EOS RevelXS camera, adapted to the stereo microscope. Adult specimens were preserved in 96%-ethanol. The ovipositors were cleared in 10% KOH for 12 hours, then cleaned in diluted acetic acid (3 drops into 30 ml of distilled water) for one minute, and subsequently rinsed in 75% and 96% ethanol for 5 minutes each; finally, they were slide-mounted, using Canada balsam partially diluted with Xylene. To observe details of the ovipositor, an Olympus CX31 microscope was employed. Morphological terminology was based on Snodgrass (1935), Gibson (1985, 1993) and Viitasaari (2002).

Results

Field collections

Larvae, pupae, and cocoons of *Nematus oligospilus* were found on the collected foliage of *S. humboldtiana*. Populations of *N. oligospilus* had low densities, 1-10 individuals per tree, including the larvae and pupae. We did not observe any adults in the field. The green color of eggs, larvae and cocoons of the sawfly made them cryptic on the willow leaves. Neither the individuals nor their damage were immediately noticeable in the trees examined. No symptoms from moderate to severe defoliation occurred.

Fifteen adult females were obtained from rearing. These specimens are housed in the CTC, UNAB (Figs 1–6), with the following data: COLOMBIA, Cundinamarca, Bogotá, Campus Universidad Nacional de Colombia, N 4°38'34", W 74°04'58", 2600 m, Ago.-2015, L. Malagón (11 Ω); COLOMBIA, Cundinamarca, Bogotá, Barrio Guacamayas, N 4°33'09", W74°05'49", 2730 m, 22-Ago-2015, L. Malagón (2 Ω); COLOM-BIA, Cundinamarca, Bogotá, Barrio Santa Ana Occidental, N4°41'36", W74°02'23", 2580 m, 19-Ago-2015, L. Malagón (2 Ω). All under catalogue number 733.

Phenotypic variation of females

Supplemental to the descriptions by Koch and Smith (2000) and Smith (2003), information about some variation may be useful in recognizing females of *N. oligospilus*.

Measurements (n = 15): Total length 5.3-7.8 mm; ranges of metric ratios include antenna length / head width 3-3.2; lower interocular distance/ eye length 1.8-1.9; upper interocular distance/ eye length 1.7-1.8; width / length of postocellar area 2-2.5; malar space length / median ocellus diameter 1.4-1.6; cercus length / valvulae 3 length, in dorsal view, 0.7-0.8.

Color. Head (Figs 4, 5): vertex, genae, and frons above antennae dark yellow; facial area below antennae, including clypeus, labrum, and malar areas pale yellow; limit between vertex and occiput either with or without a mesal triangular black spot; areas surrounding ocelli containing linear black spots; frons lacking a black spot; in living individuals, all areas of head lack green color. Antenna black, being clearer distally to the third flagellomere. Mandible yellow, with a brown apical tooth. Thorax (Figs 1, 2): pronotum light yellow; propleuron yellow, with its anterodorsal margin from black to entirely yellow; basalare, tegula, and postspiracular sclerite yellow; mesoscutum reddish yellow, with lateral lobes either having or lacking black spots; antecostal suture and medial sulcus of mesoscutum black; axilla from entirely black to white, or with a black spot on the disc of its posterior margin; mesoscutellum yellow, with its posterior margin black to yellow entirely; mesopostnotum white with a black discal spot; middle of upper half of mesepisternum pale yellow, and middle of lateroventral lower area reddish yellow; epicnemium yellow; metascutum white, with cenchri yellow; metascutellum dark



Figures 1–6. *Nematus oligospilus*, \mathcal{Q} , reared from immatures collected on *Salix humboldtiana* (Salicaceae) in Bogotá, Colombia. I Dorsal view **2** Lateral view **3** Ovipositor sheath, lateral view **4** Vertex with a conspicuous black spot **5** Vertex with a reduced black spot **6** Housed specimens at the Entomological Museum UNAB (Catal. Number 733).

yellow with posterior margin black to entirely black; metapleuron and metasternum yellow; metapostnotum black mesally and white laterally. Abdomen: Green in living individuals, segments VII-X yellow (green color sometimes preserved (Figs 1, 2), but the entire abdomen usually turns yellow in mounted specimens); urotergites (segmental abdominal terga) I, II and III with or without black wide medial spot, which when present may be very narrow and anteroposteriorly extended on dorsum, as a longitudinal medial line. Legs (Fig. 2): yellow, darker on each segment apically. Genitalia: valvulae 1 (= lancet) and 2 (= lance) hyaline yellow, with annuli dark yellow; valvula 3 (= sheath) (Fig. 3) dark yellow, with posteroventral margin black; cerci dark brown. Wings hyaline (Fig. 1); Costal vein and pterostigma yellow; remaining veins dark brown.

	Fecu		longevit						y (days)		
	number of		Larval instar					Pupae	A .l		
	eggs/female	eggs/leaf		1	2	3	4	5	6	(in cocoon)	Adult
Maximum	53	17	Maximum	8	2	3	3	4	4	11	9
Average	30	3.7	Average	6.5	2	3	3	4	3	9.78	7.1
Minimum	9	1	Minimum	5	2	3	3	4	2	9	4

Table 1. Fecundity and longevity of *N. oligospilus* in laboratory. Females, n= 15; pupae, n = 15; larvae, n= 11 (from several instars); eggs, n= 490.

Notes on the development of N. oligospilus on S. humboldtiana in Bogotá

From the immature forms reared in the lab, we obtained only females. Immediately after emergence, a female lays an average of 31 eggs (n = 15) on the leaves of the host plant (Table 1). Postembryonic development lasts from 32 to 44 days (Table 1). The larval stage has the longest time span, between 19 and 24 days. Most eggs obtained in the lab did not hatch, a few viable eggs lasted between six and eight days before hatching.

Six larval instars (n = 10) were recognized; each instar varied in size; most instars did not overlap in body length, except 5th and 6th where overlap was close to 0.15mm. Regarding intermoult size increment (Gullan and Cranston 2014), 3rd instar had the lowest (0.1 mm) and the 5th instar the highest (0.55mm). Concerning stadia (Gullan and Cranston 2014), intermoult duration was highest in the 1st instar, varying between five and eight days, while 2nd instar had a two-day shortest stadium (Table 1). One larva went through seven instars.

Darkening of the head capsule of the larvae in early instars marks the initiation of the moulting process (Fig. 8). Right after completing each ecdysis, the new larvae are light green (except for eyes and mandibles) (Fig. 9). Prepupae build the cocoon and pupate directly on foliage of *Salix humboldtiana* (Figs 12, 13). In the lab, larval ecdysis tends to occur during night hours, whereas adults emerge around noon. No parasitoids were obtained from the reared larvae or pupae.

Oviposition behavior

For oviposition, the first and second valvulae work together as a sharp structure tapering distally. With the teeth of ventral margin of the 1st valvula of the ovipositor, the sawfly produces an incision in the cuticle of the leaf, generating a small swelling (Fig. 14) in the epidermis or between the epidermis and the chlorenchyma (Braccini et al. 2013). During oviposition, the valvulae are inserted in the leaf initially in a position perpendicular to the body axis; as the valvulae penetrate deeper, they rotate anteriorly, being parallel to the body axis at the end of oviposition. This forms a kidney-shaped pocket, which is immediately filled with an egg, turning back the ovipositor in the opposite direction.



Figure 7. Box-whisker plot of total length variation with reference to each larval instar (n=10).

Discussion

The presence of *N. oligospilus* in Colombia was confirmed by finding specimens feeding on the foliage of *Salix humboldtiana*, in the City of Bogotá. According to records from other parts of South America, *N. oligospilus* is distributed between 0 and 1700m above sea level (Koch and Smith 2000); in Colombia it reaches higher elevations (2600m) in Bogotá.

Regarding phenotypic characters of this species, contrary to what was written by Koch and Smith (2000) for the lectotype, we did not find black spots on the frons or on the interocellar area; additionally, we observed intraspecific variation in the coloration of the individuals reared in the lab. Whereas the specimens housed in different collections have black color pattern characteristic of the species, the adults we reared lack or have the triangular spot on the vertex reduced, whereas the spots on the mesoscutum and abdominal terga are retained. Similar variations regarding the reduction of spots and black color patterns are found in specimens from several countries around the world (Koch and Smith 2000). Characteristics of the ovipositor agree with other descriptions (Malagón-Aldana et al., in press); similarly, the coloration of the larva coincides with what is described in the literature.



Figures 8–14. Nematus oligospilus. **8** Larval instar 1 immediately before ecdysis **9** Larval instar 3 immediately after ecdysis **10** Larval instar 6 feeding on a leaf of *Salix humboldtiana* **11** Frontal view of head of 6th larval instar **12** A sixth larval instar spinning its own cocoon **13** Pupa **14** A female ovipositing.

Parthenogenetic reproduction is confirmed in *N. oligospilus*. For the first time, we observed and compared the different intermoult larval instar stadia and growth; likewise, the number of larval instars coincides with the data in Ovruski (1991) and Charles and Allan (2000); other development stages agree with data recorded in different studies (Ede et al. 2007). Contrary to what was previously reported for other parts of the Southern Hemisphere (Ede et al. 2007), the larvae of *N. oligospilus* in Colombia make cocoons directly on leaves of *S. humboldtiana* and not in the soil. This difference is probably due to climate seasonality in other regions, usually subtropical (Argentina, South Africa, Australia), where the photoperiod and temperature change abruptly from one season to the next (especially winter and spring), and favoring strategies as winter diapause (Ede et al. 2007), and pupation underground.

Compared to other countries in the Southern Hemisphere, population densities of *N. oligospilus* are low in Bogotá. It is noteworthy that in different studies *S. humboldtiana* and its varieties exhibit lower levels of both oviposition and phytophagy by the willow sawfly (Cerillo et al. 2011, Braccini et al. 2013), compared to exotic species such as *S. nigra*, *S. babylonica*, *S. alba*, and *S. matsudana*. Moreover, in the other countries where the introduction of *N. oligospilus* has been recorded, there are extensive commercial plantations, or additional natural communities of *Salix* spp., which favor establishing sawfly populations. In Colombia, the larvae seldom devour the leaves entirely. This behavior is similar to that described by Carr et al. (1998) in native populations of *N. oligospilus* in Arizona, on *Salix lasiolepis* (Arroyo Willow), the sawfly displays moderate movements between leaves, and populations remain low and stable.

Concerning the expansion of the distribution of this sawfly from Argentina, and the wide distribution of *S. humboldtiana* in South America, it is likely that *N. oligospilus* is present in neighboring countries. In Colombia, it is necessary to determine whether this sawfly is also present on other species of planted *Salix*.

Acknowledgments

Marko Prous, Veli Vikberg, Jean-Luc Boevé and Lars Vilhelmsen provided very important suggestions to the manuscript. We thank UNAB museum, for providing the equipment and space for the development of this study. Also, we thank Javier Martínez, who produced some photographs, Diana Suárez and Helber Arévalo who supported collecting process in the field, and Valentina Vergara who cataloged collected specimens.

References

- Alford MH (2015) *Salix humboldtiana* Willd. In: Bernal R, Gradstein SR, Celis M (Eds) Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. http://catalogoplantascolombia.unal.edu.co
- Alderete M, Liljesthrom G, Hidalgo P (2010) Bio-ecología y perspectivas para el manejo de la avispa sierra del sauce, *Nematus oligospilus*. In: Villacide J, Corley J (Eds) Serie Técnica: Manejo Integrado de Plagas Forestales. Cuadernillo 10, 10 pp.
- Benson RB (1958) Hymenoptera, Symphyta. Handbooks for the Identification of British Insects 6(2c): 139–252.
- Braccini CL, Vega AS, Chludil HD, Leicach SR, Fernandez PC (2013) Host selection, oviposition behaviour and leaf traits in a specialist willow sawfly on species of *Salix* (Salicaceae). Ecological Entomology 38: 617–626. doi: 10.1111/een.12053
- Carr TG, Roininen H, Price PW (1998) Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. Environmental Entomology 27(3): 615–625.
- Caron V, Ede F, Sunnucks P, O'Dowd DJ (2013a) Distribution and rapid range expansion of the introduced willow sawfly *Nematus oligospilus* Förster in Australasia. Austral Entomology 53: 175–182. doi: 10.1111/aen.12067
- Caron V, Norgate M, Ede FJ, Nyman T, Sunnucks P (2013b) Novel microsatellite DNA markers indicate strict parthenogenesis and few genotypes in the invasive willow sawfly *Nematus oligospilus*. Bulletin of Entomological Research 103: 74–88.
- Cerrillo T, Braccini C, Martínez R, Chludil H, Leicach S, Fernández P (2011) Susceptibilidad de distintos genotipos experimentales de *Salix* spp. a la avispa sierra *Nematus oligospilus* -

Evaluación de daños a campo y estudios de preferencia en laboratorio. Trabajo técnico, Tercer Congreso Internacional de Salicáceas en Argentina.

- Charles JG, Allan DJ (2000) Development of the willow sawfly, *Nematus oligospilus*, at different temperatures, and an estimation of voltinism throughout New Zealand. New Zealand Journal of Zoology 27(3): 197–200.
- Dapoto G, Giganti H (1994) Bioecologia de *Nematus desantisi* Smith (Hymenoptera: Tenthredinidae: Nematinae) en las provincias de Rio Negro y Neuquen (Argentina). Bosque 15: 27–32.
- De Santis L, De Sureda G (1984) La falsa oruga de los sauces y álamos (*Nematus desantisi*). Academia Nacional de Agronomía y Veterinaria (Buenos Aires) 38(7): 1–22.
- Ede FJ, Caron V, Clements D (2007) Willow Sawfly Activity in Victoria: The 2006/07 Season. Victorian Department of Primary Industries, Frankston, Australia.
- Förster A (1854) Neue Blattwespen. Verhandlungen des Naturhistorischen Vereins der Preussichen Rheinlande 11: 265–350.
- Gibson GAP (1985) Some pro- and mesothoracic structures important for phylogenetic analysis of Hymenoptera, with a review of the terms used for the structures. Canadian Entomologist 117: 1395–1443.
- Gibson GAP (1993) Groundplan structure and homology of the pleuron in Hymenoptera based on a comparison of the skeletomusculature of Xyelidae (Hymenoptera) and Raphidiidae (Neuroptera). In: Ball GEB, Danks H (Eds) Systematics and Entomology: Diversity, Distribution, Adaptation and Application. Memoirs of the Entomological Society of Canada 165: 165–187.
- González RH, Barría G, Guerrero MA (1986) *Nematus desantisi* Smith, a new species of forest importance in Chile (Hymenoptera: Tenthredinidae). Revista Chilena de Entomología 14: 13–15.
- Gullan PJ, Cranston PS (2014) The Insects: An Outline of Entomology (5th edn). Wiley-Blackwell, 624 pp.
- Koch F, Smith DR (2000) Nematus oligospilus Förster (Hymenoptera: Tenthredinidae), an introduced willow sawfly in the Southern Hemisphere. Proceedings of the Entomological Society of Washington 102: 292–300.
- Loetti V, Rubio A, Bellocq MI (2012) Feeding preferences of the willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinidae) for commercial *Salix* clones. Revista de la Sociedad Entomológica Argentina 71(1/2): 145–150.
- Malagón-Aldana L, Serna F, Smith DR (in press) The introduced willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinidae: Nematinae): first record for Colombia and in north of northern South America, Colombia, with some notes of on its ovipositor anatomy. Entomological news.
- Martínez-Alava JO, Serna F (2015) Managing insect collections. Micropezidae (Diptera: Nerioidea) of the Entomological Museum UNAB. Agronomía Colombiana 33(3): 339–347.
- Ovruski S (1991) Estudios biológicos y ecológicos de la falsa oruga de los sauces y álamos (*Nematus desantisi*) y consideraciones sobre su distribución. Trabajo de seminario para optar al título de Licenciatura en Ciencias Biológicas, orientación Zoología, Universidad Nacional de Tucumán, Facultad de Ciencias Naturales e Inst. M. Lillo. Mecanografiado, 94 pp.

- Ovruski S, Smith DR (1993) Descriptions of immature stages of *Nematus desantisi* (Hymenoptera: Tenthredinidae), a pest of Salicaceae in Argentina and Chile. Entomological News 104(4): 153–160.
- Smith DR (1983) The first record of *Nematus* Panzer from South America: A new species from Argentina (Hymenoptera: Tenthredinidae). Proceedings of the Entomological Society of Washington 85: 260–262.
- Smith DR (2003) A synopsis of the sawflies (Hymenoptera: Symphyta) of America south of the United States: Tenthredinidae (Nematinae, Heterarthrinae, Tenthredininae). Transactions of the American Entomological Society 129: 1–45.
- Snodgrass RE (1935) Principles of Insect Morphology. Comstock Publishing Associates, London, 667 pp.
- STRI Smithsonian tropical research Institute (2015) http://biogeodb.stri.si.edu/herbarium/ species/25561/?search_key=salix+humboldtiana
- Urban AJ, Eardley CD (1995) A recently introduced sawfly, *Nematus oligospilus* Forster (Hymenoptera: Tenthredinidae), that defoliates willows in southern Africa. African Entomology 3: 23–27.
- Viitasaari M (2002) The suborder Symphyta of the Hymenoptera, external morphology. In: Viitasaari M (Ed.) Sawflies (Hymenoptera, Symphyta) 1. Tremex Press, Helsinki, 108–174.