Three new genera of Mymaridae (Hymenoptera) from the Neotropical region

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Abstract

Three new genera and species of Mymaridae from the Neotropical region are described: Megamymar waorani Huber, gen. and sp. nov.; Neopolynemoidea chilensis Huber, gen. and sp. nov.; and Porcepicus herison Huber, gen. and sp. nov. Their possible relationships are discussed to place them in context among the previously described genera of Mymaridae.

Keywords

fairyflies, new genera and species, South America, taxonomy

Introduction

Mymaridae are a relatively large family of Hymenoptera, at present including about 100 valid genera, 90 of them extant and 10 extinct, including 2 fossils that may be misplaced in Mymaridae. This is almost double the number treated in the only world key (Annecke and Doutt 1961). Over the past 60 years but especially during the last 40 large numbers of specimens have accumulated in major institutions. These were sometimes collected using Malaise or yellow pan traps in previously poorly collected countries or areas, or in unusual habitats such as in tree canopies or soil. As a result, many new species continue to be discovered and publications that attempt to define generic limits more precisely must take them into account. Nevertheless, the limits for many previously described valid genera still remain unclear and may become even
more unclear because of the additional species discovered. Their limits could perhaps be redefined to include or exclude species that are near the edge of a given generic concept. If excluded, such species could be placed, perhaps doubtfully, into another genus where they appear to fit better. However, specimens occasionally are found that are clearly so unusual that they cannot be placed reasonably into any existing generic concept. These specimens not only represent new species but also new genera. Three are described below to make their names available for a planned generic key and species catalogue of Mymaridae in the Neotropical region excluding Mexico.

Methods

Specimens were point or card mounted and photographed. Because of its large size, the specimen representing the first genus and species was retained on a point mount and photographed using a ProgRes C14+ digital camera mounted on a Nikon SMZ1500 microscope; its description and, especially, measurements are therefore not as accurate as for the other two species. One specimen of each of the other two species was dissected and slide mounted in Canada balsam. These specimens were photographed at different focal planes using the same camera as above mounted on a Nikon Eclipse E800 compound microscope, and the resulting layers combined and refined using Zerene Stacker™. The layers were edited from the top of the focus stack down to produce one image showing surface structures. For certain views, such as posterior or ventral, the layers were combined and edited from the bottom up. These views were flipped either horizontally or vertically in Adobe Photoshop to appear as if the specimen was photographed from that surface. A unique image number is given to different structures but if different planes of the same structure (from the same individual) are illustrated, e.g., of the metasoma (Fig. 10), then the different planes are given the same number with different letters. Body length of a card-mounted paratype of each of two species was measured with an ocular micrometer mounted in a Leitz-Wetzlar binocular microscope at 64× or 160× magnification, as needed. Morphological terms follow Gibson (1997), with some terms from Huber (2015). Measurements are given in micrometres (μm) except body and ovipositor length of the largest species are in millimetres (mm). Because of rounding errors, it appears that the ratios are slightly incorrect compared to those calculated using the absolute measurements (micrometres) but, in fact, those calculated from the ocular micrometer readings before converting to micrometers are more accurate, so are given in the descriptions.

Abbreviations used

fl = flagellar segment (in males), fu = funicular segment (in females), gt = gastral tergum, LOL = distance between a lateral ocellus and median ocellus, mps = multiporous plate sensillum, OOL = distance between a lateral ocellus and eye margin, POL = distance between lateral ocelli. The specimen depositories are:
Results

**Megamymar Huber, gen. nov.**
https://zoobank.org/F50653C9-CDA8-497F-B141-8A3D0B35884B
Fig. 1

*Type species.* Megamymar waorani Huber, here designated.

**Diagnosis.** With the following combination of features: body huge (for a fairyfly), together with exerted section of the ovipositor well over 9 mm long; median ocellus abutting transverse trabecula; petiole distinctly shorter than gaster and, in dorsal view, completely hidden; metatarsus 1 longer than metatibia; gaster extending as horn anterodorsal to mesosoma.

**Description. Female.** **Head.** Head slightly wider than mesosoma (21: 20), -1.4× as wide as long, -1.1× as wide as high and almost 1.25× as high as long, measured laterally; transverse trabecula entirely dark; supraorbital trabecula with well sclerotized (dark) anterior half short, extending posteriorly only to level of posterior margin of median ocellus, then continuing posteriorly as poorly sclerotized (light) section extending as far as anterior margin of lateral ocellus and further continuing obliquely towards but not reaching occipital foramen as a faint, fine line. Face -0.5× as wide as high, in lateral view upper face receding to transverse trabecula and lower face flat and, in anterior view, with distinct depression medially dorsal to oral cavity and short, narrow vertical depression ventral to torulus; torulus -0.5× its own height from transverse trabecula; preorbital sulci slightly converging medially just ventral to toruli then continuing straight ventrally to dorsolateral angle of oral cavity. Compound eye slightly shorter than malar space and apparently with very few short setae among the ommatidia. Vertex in lateral view slightly curved, posteriorly merging smoothly with occiput; median ocellus abutting transverse trabecula; POL 2.0× LOL and -1.7× OOL. Gena ventrally in lateral view longer than eye length but dorsally much shorter. Back of head without sulci and oral cavity well separated from occipital foramen. **Antenna.** Scape with radicle barely differentiated; funicle 6-segmented; clava 1-segmented. **Mouthparts.** Mandibles apparently with 3 teeth, meeting when closed. **Mesosoma.** Mesosoma almost 2.6× as long as wide, almost 3.2× as long as high, and -0.8× as wide as high. Pronotum entire, in lateral view almost horizontal, with flat dorsum, in dorsal view triangular and, including neck, almost as long as mesoscutum. Prosternum -1.3× as long as wide, and entire. Mesoscutum just over 2.0× as long as scutellum + frenum, in lateral view flat; notauli incomplete, -0.3 as
long as mesoscutum as measured from their junction with anterior margin. Scutellum ~4.0× as long as poorly defined frenum; axilla barely advanced, each ~1.0× as wide as long. Metanotum slightly longer than frenum, without obvious dorsellum. Propodeum slightly longer than scutellum + frenum, with a shallow and narrow longitudinal median depression, in lateral view almost horizontal; spiracle in a shallow wide depression.  

**Wings.** Fore wing fairly wide, with apex rounded and slightly asymmetrical, and with almost straight margin behind venation; venation ~0.2× as long as wing length; parastigma with proximal but apparently without distal macrochaetae, with hypochaeta next to proximal macrochaeta. Hind wing narrow and almost straight. **Legs.** Legs long; tarsi 4-segmented, with tarsomere 1 of all legs longer than tibiae.  

**Metasoma.** Metasoma ~2.3× as long as mesosoma (Fig. 1). Petiole ~3.4× as long as wide, in dorsal view hidden by anterior extension of gaster. Gaster (measured to anterior apex of anteriorly truncate dorsal horn) ~6.4× as long as wide and ~1.2× as high as wide; gt₅ apparently the longest tergum (Fig. 1). Ovipositor with exserted portion extremely long.  

**Male.** Unknown.  

**Derivation of genus name.** A euphonious combination from Greek: megas, meaning large, and Mymar, the name of the type genus of Mymaridae. The genus name is neuter. Mega refers to the large body of the only known species of the genus, which is over 1 mm longer than the next longest Neotropical species, *Erdosiella mina* (Annecke & Doutt), whose body length is 3.7 mm.  

**Relationships.** *Megamymar* is best placed in Mymarini *sensu* Annecke and Doutt (1961) because of the combination of 6-segmented funicle, 4-segmented tarsi and distinctly petiolate gaster. Among the genera of Mymarini, the supraorbital trabecula extending posteriorly only to the level of the median ocellus, the fore wing shape, short fringe setae and venation with relatively long parastigma indicate that *Megamymar* is most closely related to *Erdosiella* Soyka and *Tanyostethium* Yoshimoto in the New World, and perhaps *Narayanella* Subba Rao in the Old World. *Megamymar* is clearly separated from these three genera by the petiole much shorter than the gaster and the anterodorsal extension of the base of the gaster over the apex of the propodeum; none of their species have this combination of features. Instead, in these genera the supraorbital trabecula extends to about the level of the lateral ocelli, the petiole is usually as long or longer than the gaster, and gt₁ does not project anteriorly over the propodeum though occasionally the base of gt₁ may slant slightly anteriorly before receding uniformly and smoothly posteriorly to the anterior margin of gt₂. It could perhaps be argued that the features of *Megamymar* are just one of degree rather than substance and therefore *Megamymar* should be treated as just an extreme representative of *Erdosiella*, but then many of the numerous genera of Mymarini should be placed in synonymy under one another as well. Whether such an approach would clarify generic relationships within Mymarini is debatable.  

*Megamymar* superficially resembles several of the largest species of *Australomymar* Girault and the extralimital genera *Borneomymar* Huber, *Neotriadomerus* Huber and *Paranaphoidea* Girault. At least some species in all these genera, none of which are morphologically closely related to *Megamymar*, have a long ovipositor often greatly exserted posteriorly (*Australomymar*, *Borneomymar*, *Polynemoidea* Girault) or anteriorly.
Three new genera (Neotriadomerus). In the Neotropical region, Australomymar appears superficially to be the most similar looking genus but the body of the largest species is at most ~3.0 mm long and the base of the female gaster does not extend anteriorly in a dorsal horn (the gastral sac). In other genera of Mymaridae the ovipositor may extend anteriorly but it is always ventral to the mesosoma.

Megamymar waorani Huber, sp. nov.
https://zoobank.org/4C5905C4-D5E8-4412-8676-B0146071C225
Fig. 1


Diagnosis. Megamymar waorani is the only described species in the genus. Its diagnosis is therefore the same as for the generic description, i.e., ovipositor extending anteriorly in a short, truncate gastral sac dorsal to propodeum (Fig. 1).

Description. Female. Colour. Body orange-yellow, with metasoma except for apical tergum and sternum slightly lighter; transverse trabecula and mandibles dark reddish-brown; scape and pedicel dark yellow, fu₁–fu₄ brown except slightly lighter apex of fu₅, fu₆ cream coloured, fu₇ and clava dark brown; legs same colour as body except mesotibia slightly darker yellow, mesotarsomere brown, and metatibia and tarsus almost black. Fore wing clear except yellowish suffusion posterior to and slightly distal to venation; hind wing clear (Fig. 1). Body length. 4.8 mm, excluding exserted part of ovipositor, which extends 4.9 mm posterior to apex of gaster. Head. Head width ~535. Entire face with fine engraved but slightly granulate sculpture and with 2 sublateral setae, about 6 lateral setae and a dense patch of thicker setae sublaterally and laterally at mouth margin. Vertex with 2 setae between lateral ocelli, apparently 2 minute setae lateral to median ocellus, and engraved, slightly granulate reticulations at least anteriorly. Back of head with faint engraved reticulations, 1 short seta posterolateral to lateral ocellus, and a few minute setae lateral to foramen and sublaterally on gena. Antenna. Scape with faint, fine transverse sculpture on inner surface and apparently at least 1 very short seta, on dorsal margin at least. Fu₁ with at least one longitudinal row of 6 or 7 short mps; clava with numerous (11 on at least one surface) short scattered mps; funicle slender, with segments barely widening towards apex, each with apex squarely truncate and with numerous short setae. Length/width measurements (ratio, calculated from eyepiece micrometer measurements before converting to micrometres): scape 220/120 (1.83); pedicel 120/60 (2.00), fu₁ 240/30 (8.00); fu₂ 545/30 (18.33); fu₃ 910/40 (23.00); fu₄ 645/50 (13.00); fu₅ 495/60 (8.33); fu₆ 385/80 (4.87), clava 604/90 (6.78). Mesosoma. Pronotum with 2 setae anteriorly and 1 seta posterolaterally, and with faint raised reticulate sculpture. Mesoscutum with faint raised reticulate sculpture, 1 adnotaular seta at extreme anterior
margin and 1 lateral seta posterolaterally on lateral lobe. Scutellum with faint engraved reticulate sculpture and without setae; axilla with 1 small seta; frenum apparently with faint sculpture. Propodeum with 1 propodeal setae well separated from spiracle and with faint reticulate sculpture. **Wings.** Fore wing with a single line of microtrichia separating bare space posterior to parastigma from bare space anterior to retinaculum; hypochaeta next to proximal macrochaeta, distal macrochaeta not visible (absent?); wing length 3900, width 845, length/width 4.62, longest marginal setae 100, venation length 820, spur 100. Hind wing with median row of microtrichia but only a few distally along anterior and posterior margins; wing length 2400, width 50, longest marginal setae 155, venation length 770. **Legs.** Metatibia and tarsomeres 1 and 2 with short, dense setae; tarsomere 1 slightly longer than metatibia. **Metasoma.** Petiole (mostly hidden by metacoxae and gt.) ~310 long, width 90. Gaster with terga and sternae apparently transparent above yellow ground colour; middle terga apparently the longest segments (not accurately measurable). Ovipositor length (visible part only, the part concealed within gaster not measurable) 5500, the exserted length 4900 with hooked apex.

**Derivation of species name.** The species is named after the indigenous Waorani people of Ecuador in whose reserve *M. waorani* was collected. Their way of life has been seriously affected by resource extraction and settlement by colonists. The species name is treated as a noun in apposition.

**Biology.** Unknown, but because of its size, likely a solitary parasitoid in large insect eggs. We suggest that the host is most likely a species of Orthoptera. First, despite *M. waorani* being the third longest fairyfly species known worldwide, after specimens of a species of *Neotriadomerus* from Australia and specimens of one species of *Australomymar* from New Zealand, it has apparently never been collected at ground level, despite considerable Malaise or pan trapping in equatorial rain forests of the Neotropical region. Second, the host egg must be at least 4.8 mm long and eggs of this size are mostly likely to be found among species of Orthoptera. Third, although hosts of any species of Mymaridae with body length over 3.0 mm are unknown, one relatively small (~1.3 mm) species of *Australomymar* has been reared from Tetttigonidae (Orthoptera) and one large (2.5 mm) species of *Acmopolynema* Ogloblin has been reared from *Oecanthus* spp. (Orthoptera: Gryllidae).

**Neopolynemoidea Huber, gen. nov.**
https://zoobank.org/58E1ADB3-3B0C-4EFA-9356-5CCF75554A0C
Figs 2–10

**Type species.** *Neopolynemoidea chilensis* Huber, here designated.

**Diagnosis.** Female with the following combination of features: toruli almost touching transverse trabecula (Fig. 2a); scape over 10× as long as greatest width and 1.4× as long as head width, funicle 6-segmented and clava 3-segmented (Fig. 3); fore wing venation extending almost 0.7× wing length (Fig. 7).

**Description.** **Female. Head.** Head slightly wider than mesosoma (24: 21), ~1.8× as wide as long, ~1.6× as wide as high and almost 1.2× as high as long, measured laterally; transverse trabecula entire (Fig. 2a); supraorbital trabecula apparently entire. Face
Three new genera

1.2× as wide as high; torulus ~0.25× its own height from transverse trabecula; preorbital sulcus not bulging ventral to eye. Compound eye ~2.0× as long as malar space and with a few short setae among the ommatidia. Vertex in lateral view strongly curved, becoming vertical posteriorly so in same plane as occiput; median ocellus well separated from transverse trabecula; POL 2.0× LOL and ~2.7× OOL (holotype with left lateral ocellus missing entirely, with a seta where it should be). Back of head without sulci. Oral cavity posteriorly almost confluent with occipital foramen (Fig. 2b). **Antenna.** Scape with radicle barely differentiated; funicle 6-segmented; clava 3-segmented, with the sutures slightly oblique or transverse (Figs 3, 4). **Mouthparts.** Mandibles apparently with 3 teeth, barely meeting when closed (Fig. 2a). **Mesosoma.** Almost 2.0× as long as wide, almost 1.4× as long as high, and 0.75× as wide as high. Pronotum ~1.9× as wide as long and longitudinally divided medially (Fig. 9b). Mesoscutum just over 0.9× as long as scutellum + frenum, in lateral view strongly curved anteriorly; notauli complete (Fig. 9a). Scutellum ~1.2× as long as frenum, with campaniform sensilla midway between anterior and posterior margins and fenestra an isosceles triangle with rounded corners; axilla slightly but distinctly advanced, ~1.8× as wide as long; second phragma extending to apex of propodeum, with rounded apex. Metanotum ~0.75× as long as frenum, with transversely oval/rhomboidal dorsellum. Propodeum medially about 0.6× as long as metanotum. **Wings.** Fore wing (Fig. 7) fairly wide, with slight lobe posterior to parastigma, and with apex symmetrical and narrowly rounded; venation ~0.6× as long as wing length; parastigma with proximal and slightly longer distal macrochaetae, with hypoachaeta close to proximal macrochaeta (Fig. 7). Hind wing (Fig. 8) narrow and almost straight. **Legs.** Legs fairly long; tarsi 4-segmented, with tarsomere 1 of all legs slightly the longest segment or subequal to tarsomere 4 (Fig. 6). **Metasoma.** Metasoma ~0.8× as long as mesosoma (Fig. 6). Petiole ~3.2× as wide as long, barely visible in dorsal view. Gaster ~2.0× as long as wide, and ~1.3× as high as wide; t, the longest tergum, t, (syntergum) conical, t, ~, subequal in length (Fig. 10a); cerci normal, but almost vertically positioned on sides of syntergum; apical sternum (outer ovipositor plate) much longer and narrower than preceding sterna (Fig. 10b). Ovipositor arising at level of t, (Fig. 10c) and exerted portion ~0.75× length of internal portion (Fig. 6).

**Male.** Unknown.

**Derivation of genus name.** From Greek: *Neo-* meaning new, referring to its occurrence in the New World and *Polynemoidea*, a monotypic genus known so far only from Tasmania. The name *Neopolynemoidea* is given to draw attention to the general similarity the two genera, one from the Old World and one from the New World.

*Neopolynemoidea* differs from *Polynemoidea* by: toruli almost in contact with transverse trabecula (separated from transverse trabecula by almost its own height in *Polynemoidea*), scape over 10× as long as wide (no more than 3× as long as wide in *Polynemoidea*); fore wing venation at least 0.6× as long as fore wing length (no more than 0.4 as long as fore wing length in *Polynemoidea*).

**Relationships.** Worldwide, at least 14 genera or subgenera of Mymaridae have females with a 3-segmented clava: *Allanagrus* Noyes & Valentine, *Allarescon* Noyes &
Valentine, *Eustochomorpha* Girault, *Krokella* Huber, * Nesomyumar Valentine, Nessopatasson Valentine, Neostethynium Ogloblin, Notomyumar Doutt & Yoshimoto, Paracmotemnus Noyes & Valentine, Paranaphoidea (Idiocentrus) Gahan, Platystethynium (Platystethynium) Ogloblin, Polynemoidea, Pseudanaphes Noyes & Valentine, and Stethynium Enoch. Except for *Eustochomorpha*, with an 8-segmented funicle in females, all have a 6-segmented funicle. The majority of these genera occur in the southern hemisphere, particularly in the southernmost areas, though several extend well into the northern hemisphere. Two other genera appear to have the clava with 3-segments in at least one species: one *Eustochus (Eustochus)* from China was described as having 3-segmented clava (the other described species have a 2-segmented clava) but this may be an artefact of partial antennal collapse, giving the appearance of a third segment; and *Kompsonomyumar* Huber, with a single described species from Australia, appears to have only partial divisions separating the claval segments. The hosts and biology of all but one (*Stethynium*) of the above genera are unknown. Among these, *Krokella, Paracmotemnus* and *Polynemoidea* have a fore wing venation longer than half the wing length, as in *Neopolynemoidea*, but none have the extremely long scape in females. Females of the only described species of *Polynemoidea*, however, have a long, exerted ovipositor. Therefore, based wing venation and ovipositor features a close relationship of *Neopolynemoidea* to *Polynemoidea* is proposed as being the most probable.

**Neopolynemoidea chilensis Huber, sp. nov.**
https://zoobank.org/C7A589BC-F6FD-442F-A5CC-AC81E07C0EB9
Figs 2–10

**Material examined.** **Holotype** female (CNC) in Canada balsam on slide (Fig. 5) labelled: 1. “Chile: Cautin, 1150m, Conguillio Nat. Park, Araucaria Nothofagus Feb. 6 1988 18PT L. Masner Chile Exp.” 2. “Neopolynemoidea chilensis # Huber HOLOTYPE”. **Paratypes**: one female (CNC) on card, with same locality data as holotype.

**Diagnosis.** *Neopolynemoidea chilensis* is the only described species in the genus so its diagnosis the same as for the generic description.

**Description.** **Female. Colour.** Uniformly brown; scape, pedicel and legs except coxae and metafemur brownish yellow. Fore wing with brown suffusion except for a small clear area distal to stigma, a larger triangular area along posterior margin, a clear area anterior to retinaculum and a small one posterior to parastigma (Fig. 7). **Body length.** 1000 (paratype, card mount). **Head.** Head width ~226. Face with 6 setae ventral to level of ventral margin of torulus and faint engraved reticulations except for a band of more distinct striations extending between eyes ventral to toruli and a narrow dorsal band extending along preorbital groove (Fig. 2a). Vertex with 2 setae between lateral ocelli and slightly more distinct engraved reticulations. Back of head with faint transverse engraved reticulations dorsally, becoming vertical lateral to foramen, 2 short seta dorsal to foramen, and a few shorter setae laterally along eye (Fig. 2b). **Antenna.** Scape with faint, fine longitudinal sculpture on inner surface and several setae on ventral and dorsal margins (Fig. 3). F$_{u_1}$ with 1 mps, F$_{u_2}$ and F$_{u_6}$ each with 2 mps, clava with 2, 2, and 4 mps on segments 1–3, respectively; funicle with segments enlarging towards apex, each with apex squarely truncate and each with numerous
Three new genera

fairly long setae (Figs 3, 4). Length/width (ratio) (holotype): scape ~320/30 (10.55); pedicel 76/36 (2.11); fu 1 83/26 (3.19); fu 2 72/28 (2.57), clava 185/47 (3.92). **Mesosoma.** Pronotum with 2 minute submedial and 2 longer sublateral setae. Mesocutum with faint engraved reticulate sculpture, 1 adnotaular seta and 1 lateral seta on lateral lobe. Scutellum with faint engraved reticulate sculpture, campaniform sensillum midway between anterior and posterior margins and closer to each other than to scutellar seta, scutellar seta at margin of axilllular carina, a minute seta/pit? anterior to apex of scutellar carina, and fenestra an isosceles triangle with rounded angles; axilla with 1 lateral seta and faint engraved reticulate sculpture; frenum with faint reticulate sculpture becoming longitudinal at lateral margin. Propodeum with 2 minute propodeal setae well separated from spiracle and with reticulate sculpture. **Wings.** Fore wing with a single line of microtrichia separating bare space posterior to parastigma from bare space anterior to retinaculum; hypochaeta close to proximal macrochaeta; wing length (holotype) 1210, width 222, length/width 5.46, longest marginal setae 312, venation length 739. Hind wing with a median row of about 15 microtrichia mostly in apical half beyond venation; wing length 1224, width 36, longest marginal setae 216, venation length 376. **Legs.** Metatibia with setae at least 2× as long as tibial width (Fig. 6). **Metasoma.** Petiole ~0.4× as long as wide, distinctly narrower than gt 1 (Figs 6, 9a). Gaster with segments subequal in length except gt 1 slightly shorter; gt 6 triangular, apically truncate. Gr 1 with 2 sublateral setae, gt 6 and gt 7 each with 1 submedian setae, remaining terga with 3 (sometimes 2) submedian/sublateral setae. Ovipositor length 833, ~1.8× as long as metatibia, and exserted length 400.

**Biology.** Unknown.

**Porcepicus** Huber, gen. nov.

https://zoobank.org/1323C799-1EA3-4CFB-A3E9-046B757377A3

Figs 11–20

**Type species.** *Porcepicus herison* Huber, here designated.

**Diagnosis.** Female with the following combination of features: back of head dorsal to foramen with median vertical occipital groove and transverse occipital groove/trabecula extending from eye to eye (Fig. 12a); mandible a small stub without teeth (Fig. 12a); gastral petiole apparently absent and gaster wider than long; body, legs and antenna with prominent stout spines (Figs 11–20).

**Description. Female.** **Head.** Head slightly narrower than mesosoma (14:17), ~2.0× as wide as long, ~1.7× as wide as high and ~1.15× as high as long, measured laterally; transverse and supraorbital trabeculae with short dark sections alternating with light sections. (Fig. 12a). Face slightly wider than high; torulus ~1.4× its own height from transverse trabecula; preorbital groove bulging laterally ventral to eye. Compound eye ~1.7× as long as malar space and with a few short blunt setae among ommatidia. Vertex posteriorly with sharp, slightly concave margin at junction with occiput (Fig 12b); median ocellus well separated from transverse trabecula; ocelli in a low triangle, with lateral ocelli at posterolateral angle of vertex, and POL ~2× LOL and ~23× OOL. Back of head with vertical occipital
groove, complete transverse occipital groove obtusely angled medially dorsal to occipital foramen, and oral cavity posteriorly almost confluent with occipital foramen (Fig. 12b).

**Antenna.** Scape with radicle barely differentiated; funicle 6-segmented; clava 1-segmented (Figs 14a, b).

**Mouthparts.** Mandibles without teeth, with rounded apex shorter than maxilla, presumably not meeting when closed (Fig. 12a).

**Mesosoma.** Mesosoma ~0.8× as long as wide, ~1.2× as long as high, and ~1.4× as wide as high. Pronotum in lateral view almost vertical, apparently longitudinally divided medially; in dorsal view barely visible except laterally. Prosternum almost 2.0× as wide as long and longitudinally divided medially (Fig. 19).

**Wings.** Fore wing narrow and curved (Fig. 15) with distinct lobe posterior to parastigma; venation ~0.3× as long as wing length; parastigma with distal macrochaeta but without proximal macrochaeta or hypochaeta. Hind wing (Fig. 16) with distinct bend in basal third beyond venation, with anterior margin concave and posterior margin convex.

**Legs.** Legs short; tarsi 5-segmented, with protarsomere 1 the longest segment, and meso-and metatarsomere 1 the shortest segments.

**Metasoma.** Metasoma ~0.8× as long as mesosoma (Figs 18a, 20). Petiole vertical, not visible in dorsal view, ~10× as wide as long (high). Gaster ~1.2× as wide as long, and ~1.1× as wide as high; gt₂ and gt₃ the longest terga, gt₁ planoconvex, the almost straight anterior margin and curved posterior margin meeting laterally to form an acute angle (Fig. 18a); cercus apparently with only 2 cercal setae. Ovipositor arising in apical half of gaster, slightly less than 0.5× gaster length and slightly less than 0.5× metatibia length.

**Male.** Unknown.

**Derivation of genus name.** An arbitrary combination of letters based on the French word for porcupine, porc-épique, referring to the long and strong setae distributed on the antenna, body, and legs.

**Relationships.** Porcepicus belongs to the *Camptoptera* group of genera. It appears to be most similar to *Camptoptera* by the back of the head having a vertical occipital groove, transverse occipital groove, and narrow and curved fore wing and lack of a hypochaeta. The 6-segmented funicle in females, slightly dorsoventrally flattened mesosoma, gaster wider than long, and apparent absence of a petiole distinguishes it from *Camptoptera* Foerster as well as the other genera in the genus group.

**Porcepicus herison** Huber, sp. nov.

https://zoobank.org/6642FF75-B403-4E19-9897-AD8676F847A4

Figs 11–20

**Material examined.** Holotype female (CNC) in Canada balsam on slide (Fig. 17) labelled: 1. “Peru: Loreto 220m Teniente Lopez 2°36′S, 76°07′W, 22.VII.1993, R. Leschen FIT” 2. “Porcepicus herison f# HOLOTYPE.”
Three new genera

**Paratypes:** Four females. PERU. Same locality data as holotype (2 females on cards, CNC); Junín River, NW of San Ramón, Río Oxabamba, San Fernan Farm, 925 m, 11°5’36"S, 75°23’43"W, 30.vi.2010, M. Hoddle, MT [Malaise trap] (1 female on slide, UCRC, UCRC ENT 285052); San Martín, 19 km NE Tarupoto, 950 m, 6–8.vii.2004. B. V. Brown, MT (1 female on point, UCRC, UCRC ENT 457917).

**Diagnosis.** *Porcepicus herison* is the only described species in the genus so its diagnosis is the same as for the generic description.

**Description. Female. Colour.** Body brown (mesoscutum light brown in one paratype) except anterior surface of gt 1 white; legs light brown, pedicel and tarsi almost white; thick setae and their sockets on body, antenna and legs dark brown (Figs 11, 20). **Body length.** 310–330 μm (paratypes). **Head.** Head width 145. Face almost smooth, with 4 fairly long strong setae at or ventral to level of ventral margin of torulus. Vertex with shallow transversely reticulate sculpture and 2 long strong erect setae on each side of lateral ocellus. Gena with 1 strong seta lateral to oral cavity (Fig. 12a, b). Back of head (Fig. 12b) with faint transverse to oblique reticulate sculpture and 2 short setae dorsal to occipital groove. **Antenna.** Scape with faint trace of longitudinal sculpture on inner surface and about 4 long setae on ventral and dorsal margins; pedicel 0.8× as long as scape, with ventral margin strongly indented basally; funicle with segments enlarging towards apex, each with apex obliquely truncate (Figs 13, 14) and with 1 or 2 long, fairly strong setae on ventral margin; fu 5–fu 6 each with 1 (possible 2) mps; clava with 1 (possibly 2) longitudinal mps (Fig. 14). Length/width (ratio) (holotype): scape ~55/23 (~2.30), pedicel ~35/25 (1.40), fu 1 15/9 (1.67), fu 2 11/11 (1.00), fu 3 11/12 (0.92), fu 4 15/13 (1.15), fu 5 16/13 (1.23), fu 6 17/16 (1.06), clava 50/24 (2.08). **Mesosoma.** Pronotum with 1 long strong lateral seta; mesoscutum with transverse reticulate sculpture and 1 long strong seta at lateral angle; scutellum without campaniform sensilla and apparently smooth; axilla smooth, with 1 long strong seta; frenum with faint transverse reticulations medially, becoming longitudinal at lateral margin. Propodeum with long strong seta, its base almost in contact with small circular spiracle. **Wings.** Fore wing with a row of about 9 microtrichia between usual anterior and posterior rows; wing length (holotype) 368, width 32, length/width 11.5, longest marginal setae 157, venation length 114. Hind wing medially with anterior row of about 15 microtrichia and posterior row of 3 microtrichia; wing length 379, width 12, longest marginal setae 114, venation length 103. **Legs.** Meso- and metatibia each with 3 long strong setae on dorsal margin; coxae and femora with shorter, moderately strong setae (Fig. 18a). **Metasoma.** Gaster apparently smooth (Fig. 18a); gt 2–gt 5 each with 1 or 2 long strong sublateral and lateral setae; apical tergum with 1 median seta (Fig. 18b). Ovipositor length 45, its apex distinctly anterior to apex of gaster (Figs 18b, 19).

**Derivation of species name.** The name is an arbitrary combination of letters similar to the French word for hedgehog, hérisson. The name is treated as a noun in apposition.
**Biology.** Unknown. As with most species in the *Camptoptera* group of genera the hosts are unknown. We suggest the hosts are Coleoptera based on at least one record from that order for *Camptoptera* and one for *Litus*.

**Discussion**

The fairyfly fauna of the Neotropical region is one of the most diverse in the world, with about 50 genera, taking into account synonymies and genera added since Huber (1995, 2006); it is about equal to or second to that of the Australian region (Lin et al. 2007). Generically, the fauna is certainly much more diverse than the Nearctic region including Mexico (Guzmán-Larralde et al. 2017; Huber et al. 2020) and the Afrotropical region (Huber et al. 2020). The species described above do not fit in any previously described genus of Mymaridae in the Neotropical region. While one would expect most new genera to be found among the smaller members (less than 0.5 mm in length) of Mymaridae, it is a surprise that the largest member represents a distinct new genus. This shows how little is really known about the Neotropical fauna, especially in relatively uncollected habitats such as tree canopies of equatorial forests or soil.

**Figure 1.** *Megamymar waorani* Huber, holotype female, lateral habitus (ovipositor photoshopped to curve downward to fit page better).
Figures 2–4. *Neopolynemoidea chilensis* Huber, holotype female 2a head, anterior 2b head posterior (seen through head and flipped horizontally) 3 right antenna 4 left antenna.
Figures 5–8. Neopolyomoidea chilensis Huber, holotype female 5 holotype slide 6 habitus without head, dorsal 7 fore wing 8 hind wing.
Three new genera

Figure 9. *Neoplynemoidea chilensis* Huber, holotype female a mesosoma, dorsal b mesosoma, ventral (seen through mesosoma).
Figure 10. Neopolynemoidea chilenis Huber, holotype female a metasoma, dorsal b metasoma, ventral (seen through metasoma and flipped vertically), showing sterna c metasoma, ventral (seen through metasoma and flipped vertically), showing genitalia.
Figure 11. *Porcicus herison* Huber, holotype female on card, before slide mounting.
Figures 12–17. Porcepicus herison Huber, holotype female 12a head, anterior 12b head, posterior (seen through head and flipped horizontally) 13a right antenna (clava and fu5 missing) 13b right antenna (opposite surface seen through antenna and flipped horizontally) 14a left antenna 14b left antanna (opposite surface seen through antenna) 15 fore wing 16 hind wing 17 holotype slide.
Three new genera

Figure 18. Porcopicus herison Huber, holotype female 18a habitus without head, dorsal 18b genitalia (seen through gaster).
Figures 19, 20. *Porcopicus herison* Huber 19 holotype, habitus without head, ventral (seen through body and flipped vertically) 20 paratype, habitus, dorsal, fore wings missing.
Three new genera

Acknowledgements

We thank the late T. Erwin, National Museum of Natural History, Washington, DC, for allowing the senior author to sort through some of the rich canopy fogging material he obtained over many years of collecting in Neotropical forests. Much remains to be sorted for Mymaridae, however, so perhaps more specimens of *M. waorani* may still be found in the collected material. We also thank K. Bolte (retired from Natural Resources Canada) who took the photograph of the holotype of *M. waorani*. We thank S. Triapitsyn (UCRC) for recognizing two specimens of *P. herison* in UCRC and recommending their addition to the type series.

References


Revision of the Palearctic species of *Fidiobia* Ashmead (Hymenoptera, Platygastroidea)

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Abstract

The Palearctic species of the genus *Fidiobia* are revised, seventeen new species are described (*F. bohemica* sp. nov.; *F. brevialis* sp. nov.; *F. communis* sp. nov.; *F. gallica* sp. nov.; *F. hirta* sp. nov.; *F. insooae* sp. nov.; *F. lisenchiae* sp. nov.; *F. longiclava* sp. nov.; *F. nipponica* sp. nov.; *F. platystasioides* sp. nov.; *F. politoides* sp. nov.; *F. pronotatoides* sp. nov.; *F. roatai* sp. nov.; *F. rugosifronsoides* sp. nov.; *F. sashai* sp. nov.; *F. triangularis* sp. nov.; *F. vladlubomiri* sp. nov.), and eleven species (*F. brevinotaula* Veenakumari et al., 2018; *F. filicornis* Buhl, 2014; *F. flaviabdominalis* Veenakumari et al., 2018; *F. hispanica* Popovici & Buhl, 2010; *F. hofferi* Kozlov, 1978; *F. polita* Buhl, 1998; *F. pronotata* Szabó, 1958; *F. rugosifrons* Crawford, 1916; *F. striatitergitis* (Szabó, 1962); *F. synergorum* (Kieffer, 1921); *F. vanharteni* Buhl, 2010) are redescribed. A key for identification of females and distributional data for each species are provided. Brachypterous specimens are reported for *F. rugosifrons* and *F. hofferi*. *Fidiobia gordoni* Popovici & Buhl, 2010 is treated as a junior synonym of *Fidiobia striatitergitis* (Szabó, 1962).

Keywords

α-taxonomy, egg-parasitoids, new species, Platygastroidea, Sceliotrachelinae

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Introduction

Fidiobia Ashmead, 1894 is one of the “classical” genera of Platygastridae, originally described as monotypic, with F. flavipes Ashmead, 1894 as the type species. Masner and Huggert (1989) placed Fidiobia in Sceliotrachelinae and it is presently the largest genus in the subfamily. The earliest records of Fidiobia are from the Eocene, including compression fossils and Baltic amber (Buhl 2002; Talamas and Buffington 2015), and the body plan of this genus has been remarkably conserved. The numerous undescribed species of Fidiobia, combined with many species that have been insufficiently described, have created the need for large-scale revision of the genus on a worldwide scale. Our efforts here represent the largest treatment of Fidiobia to date.

Taxonomic history

Ashmead (1894) included Fidiobia in the Platygastrinae and placed it between Amitus Haldeman and Anopedias Förster, with interesting remarks comparing structure of the metasoma to that of Telenominae (Scelionidae). The diagnosis of Fidiobia in Ashmead (1894) is very general (sculpture of frons, description of notauli) and contains some errors (e.g., number of antennomeres, fore wing venation, propodeum with two foveolae). Because of this, Brues (1909), who was aware of Fidiobia, erected Rosneta Brues, 1909 with the type species R. tritici Brues, 1909, and considered it to be related to Fidiobia and Anopedias. Rosneta was separated from Fidiobia by the 9-merous antenna and the deeply grooved notauli (parapsidal furrows in Brues 1909).

Crawford (1916) amended the diagnosis of Fidiobia, correcting some of Ashmead’s errors: sculpture of frons, number of antennomeres, notauli (mesonotal furrows in Crawford 1916) and the propodeal carinae. Also, Crawford (1916) described the second species in Fidiobia, F. rugosifrons Crawford, 1916. In the same year, Brèthes (1916), apparently unaware of Fidiobia and Rosneta, described a new genus, Triclavus Brèthes 1916, with the type species Triclavus bonariensis Brèthes, 1916, as a genus close to Allotrropa Förster. Kieffer (1921) described a new monotypic genus, Fahringeria, but mentioned no apomorphic character to identify it. Fouts (1924) revisited the diagnosis of Fidiobia and treated Rosneta as a junior synonym of Fidiobia. Fouts (1924) regarded the type species of Rosneta as a junior synonym of F. flavipes. Two years later, apparently unaware of Fouts (1924), Kieffer (1926) treated Fidiobia and Rosneta as distinct genera and considered them to be restricted to the Nearctic region. Concerning Fidiobia, Kieffer followed Ashmead’s perspective and placed it in the identification keys near Amitus, Isolia and Anopedias. In the case of Rosneta, Kieffer placed it near his genus Fahringeria. Szelényi (1938) described the monotypic Platyllotropa with the type species P. gallicola Szelényi, 1938, for which the main distinguishing characteristic was the strongly depressed body. Szelényi (1938) made no mention of possible relationships of Platyllotropa with other platygastrid genera. Muesebeck and Masner (1967) transferred Fidiobia from the Platygastrinae to Inostemminae and synonymized Triclavus with Fidiobia.
The next important step in the taxonomy of *Fidiobia* was made by Masner and Huggert (1989) in their review of the subfamilies Inostemmatinae and Sceliotrichelinae. Here, *Fidiobia* was for the first time well described, keyed, and diagnosed and the relationships between *Fidiobia* and other platygastrid genera were discussed. Masner and Huggert (1989) treated *Fahringeria* and *Platyllotropa* as junior synonyms of *Fidiobia*.

**Table 1.** Species of *Fidiobia* described prior to this study and their distribution.

<table>
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<th>Year</th>
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<td>(Nixon)</td>
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<td>Buhl</td>
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<td>8</td>
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Until 1989, only ten species of _Fidiobia_ had been formally described (Table 1) despite there being numerous undescribed species present in the Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa). Masner and Huggert (1989) incorporated the morphological diversity present in these undescribed species, in addition to those that had been formally characterized, in their description and diagnosis of the genus. The number of _Fidiobia_ species that have been described has since increased to forty-eight (Table 1). This spectacular rise in the number of newly described species of _Fidiobia_ came to support the metaphoric comparison of this genus with the tip of an iceberg by Lubomír Masner in 2010 (Popovici and Buhl 2010).

This paper is only a small part of a large and ambitious project concerning the revision of the world fauna of _Fidiobia_, a genus of beetle egg parasitoids.

**Materials and methods**

**Specimens**

Taxonomic studies are greatly informed by the examination of large numbers of specimens to determine morphological variation and geographic distribution, and to associate conspecific males and females. _Fidiobia_ is not a rare genus, but the number of specimens in European collections is typically very small. We believe this is partly because knowledge about the biology of the genus is lacking, which hinders the development of more efficient collecting strategies. For example, some genera that are now commonly collected (e.g., _Baeoneurella_ Dodd, _Tiphodytes_ Bradley, _Baryconus_ Förster) were once considered rare. Now that the biology of some of their species has been elucidated, they can be easily captured with appropriate methods in certain habitats.

The specimens used in this study are deposited in the following institutions with the abbreviations (in bold) used in the text and the name of curators in parentheses:

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Palearctic species of *Fidiobia*

ZMUC  Zoological Museum, University of Copenhagen, Denmark (Lars Vilhelmsen).

**Primary types**

Images of the primary types of *Fidiobia rugosifrons* Crawford, 1916, were made available via the Museum of Biological Diversity database at The Ohio State University (https://mbd-db.osu.edu/hol/collection_units/0ea5d1c-58ba-3aaa-e053-0100007f2cc9) by Prof. Dr. Norman Johnson. Primary types of *Platyllotropa gallicola* Szélenyi, 1938 (HNHM), *Fidiobia tatracea* Szélenyi, 1941 (HNHM), *Rosneta phryne* Debauche, 1947 (ISNB), *Fidiobia pronotata* Szabó, 1958 (HNHM), *Fidiobia bofferi* Kozlov, 1978 (OPPC), *Fidiobia polita* Buhl, 1998 (ZMUC), *Fidiobia hispanica* Popovici & Buhl, 2010 (ZMUC), *Fidiobia vanharteni* Buhl, 2010 (ZMUC) and *Fidiobia filicornis* Buhl, 2012 (ZMUC) were studied and photographed. In our opinion, the digitisation of the type specimens is essential because it allows the specimens to be accessible to a large number of researchers around the world while minimizing the risk associated with shipping.

**Collecting and preserving methods**

The specimens used in this study were collected using a variety of methods. For each specimen, the collecting method, when known, is placed in parentheses using the following abbreviations:

- **LT** light trap.
- **MT** Malaise trap. For some species this method was very useful in obtaining a series of specimens.
- **SN** sweep net. This method uses an entomological net with a circular or triangular frame. Specimens are extracted individually using an aspirator.
- **SS** screen sweeping. This method uses an entomological net with a triangular frame (Noyes 1982), equipped with a 4–7 mm wire mesh screen across the net opening to exclude debris and large insects (e.g., butterfly, bumblebees, crickets, grasshoppers). A similar net was used by Fusu and Polaszek (2017) and Popovici et al. (2018).
- **TT** conical trunk traps for collecting parasites of xylobionts (Tereshkin 1990, Varga 2017).
- **YPT** yellow pan trap.

Samples were stored in 80% ethanol at -20 °C. The micro-Hymenoptera, including minute species of *Fidiobia*, were sorted in the laboratory using a Kruss MSZ54 stereomicroscope. Specimens for general examination were mounted on white points, and specimens selected for photography were mounted on black points to reduce glare.
during imaging. Prior to mounting, the specimens were dehydrated in a series of increasingly concentrated ethanol (90%, 99.6%) and dried using hexamethyldisilazane (‘HMDS’, Brown 1993) to prevent the collapse of weakly sclerotized individuals. For species with a large series of specimens, the antenna and the wings on one side of the body (usually the left side) were removed. Wing interference patterns (WIP) were illustrated using the method of Shevtsova et al. (2011), Shevtsova and Hansson (2011) and Fusu (2017), then the wings and the antenna were mounted in Canada balsam on a small microscope slide placed on the pin, under the labels of the specimen.

Species descriptions

The descriptions of species were generated using vSysLab (https://vsyslab.osu.edu/), an online database application designed to facilitate the generation of descriptions by character data matrices. The output is in the format of „character: state”.

Imaging

Specimen photographs were produced using a Leica DFC-450C camera on a Leica 205A stereomicroscope (with 0.63× video objective attached) and a Leica LED5000 HDI dome illuminator at the CERNESIM facility of the “Al. I. Cuza” University of Iaşi. Extended-focus images were produced with Zerene Stacker (PMax algorithm). Digital drawings were accomplished with Adobe Illustrator. Scanning electron micrographs were produced with a VEGA TESCAN SEM unit at the facility of the “Al. I. Cuza” University of Iaşi (Faculty of Biology) and with HITACHI SU3500 at the facility of the MNHN. The rendered images were postprocessed in Adobe Photoshop to enhance clarity.

Distribution maps

The distribution maps were produced using QGIS 3.22 (QGIS Development Team 2021). On each map, the red areas and points represent the distribution of the material presented in this paper and the blue areas represent the distribution of species from previously published data.

Terminology

Morphological terms follow Masner and Huggert (1989), Mikó et al. (2007) and Lahey et al. (2019). Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010). Uniform Resource Identifiers (URIs) in the format HAO_XXXXXXX represent concepts in the HAO and are provided to enable readers to confirm their understanding of the concepts being referenced. URI links for morphological terms are provided in Table 2.

The terminology of surface sculpturing is from Eady (1968) and Harris (1979).
### Table 2. Morphological terms used with abbreviations in parentheses, cross-referenced to an ontological (formal) definition (Hymenoptera Anatomy Ontology; URI = Uniform Resource Identifier) and the figures where these structures are emphasized.

<table>
<thead>
<tr>
<th>Terms</th>
<th>definition</th>
<th>URIs</th>
<th>Fig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>HEAD</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>antennomere A1, ..., A10</td>
<td>The anatomical structure that is delimited by the proximal and distal margins of the antennal sclerite.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000107">http://purl.obolibrary.org/obo/HAO_0000107</a></td>
<td>1</td>
</tr>
<tr>
<td>clypeus (cly)</td>
<td>The area that corresponds to the site of origin of the clypeo-epipharyngeal muscle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000212">http://purl.obolibrary.org/obo/HAO_0000212</a></td>
<td>2–3</td>
</tr>
<tr>
<td>malar sulcus (ms)</td>
<td>The sulcus that extends between the ventral margin of the compound eye and the base of the mandible.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000504">http://purl.obolibrary.org/obo/HAO_0000504</a></td>
<td>4</td>
</tr>
<tr>
<td>occiput (oce)</td>
<td>The area that is concave and surrounds the postocciput.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000658">http://purl.obolibrary.org/obo/HAO_0000658</a></td>
<td>8</td>
</tr>
<tr>
<td>OD</td>
<td>The diameter of the ocellus.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0002107">http://purl.obolibrary.org/obo/HAO_0002107</a></td>
<td>5</td>
</tr>
<tr>
<td>ocellar ocellar line (OOL)</td>
<td>The anatomical line that is shortest and connects the compound eye and the lateral ocellus.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000662">http://purl.obolibrary.org/obo/HAO_0000662</a></td>
<td>5</td>
</tr>
<tr>
<td>paraocular depressions (paro)</td>
<td>The depressions that flank the lateral margins of the lateral ocelli.</td>
<td>Lahey et al. 2019 <a href="https://doi.org/10.3897/jhr.73.33876">https://doi.org/10.3897/jhr.73.33876</a></td>
<td>5</td>
</tr>
<tr>
<td>proocellar depression (preo)</td>
<td>The depression that flanks the anterior margin of the anterior ocellus.</td>
<td>Lahey et al. 2019 <a href="https://doi.org/10.3897/jhr.73.33876">https://doi.org/10.3897/jhr.73.33876</a></td>
<td>5</td>
</tr>
<tr>
<td>epitorular carina (sc)</td>
<td>The carina that dorsally surrounds the antennal foramen.</td>
<td>Lahey et al. 2021 <a href="https://doi.org/10.3897/jhr.87.59794">https://doi.org/10.3897/jhr.87.59794</a></td>
<td>2–3</td>
</tr>
<tr>
<td>sensillar formula (ps)</td>
<td>Distribution of papillary sensilla (ps) on the ventral clavomeres of the female.</td>
<td>Lahey et al. 2019 <a href="https://doi.org/10.3897/jhr.73.33876">https://doi.org/10.3897/jhr.73.33876</a></td>
<td>1</td>
</tr>
<tr>
<td>torulus (tor)</td>
<td>The foramen that is located on the head in which the radicle is positioned.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0001022">http://purl.obolibrary.org/obo/HAO_0001022</a></td>
<td>3</td>
</tr>
<tr>
<td>ventral (inner) lamella on A1 (vl)</td>
<td>(Semi)transparent sharp edge on the ventral side of the A1, usually on the apex, but sometimes on the entire length of A1, housing the A2 or A2-A6.</td>
<td>Modified after Masner and Huggert 1989</td>
<td>1</td>
</tr>
<tr>
<td>MESOSOMA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>antero-admedian line (aadl)</td>
<td>The signum that is submedian and located on the anterior margin of the mesoscutum and corresponds to the site of origin of the longitudinal flight muscle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000128">http://purl.obolibrary.org/obo/HAO_0000128</a></td>
<td>12</td>
</tr>
<tr>
<td>axilloxillar carina (aaxc)</td>
<td>Carina that connects the axillar carina to the axillar latar carina. Can be regarded as an extension of the axillar carina.</td>
<td>Present study.</td>
<td>6–8</td>
</tr>
<tr>
<td>axillar carina (axc)</td>
<td>The axillar line that is a carina.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000161">http://purl.obolibrary.org/obo/HAO_0000161</a></td>
<td>9–11</td>
</tr>
<tr>
<td>transverse pronotal sulcus (cps)</td>
<td>The sulcus that corresponds to the anteromedian pronotal ridge.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0001032">http://purl.obolibrary.org/obo/HAO_0001032</a></td>
<td>13</td>
</tr>
<tr>
<td>dorsal axillar area (daa)</td>
<td>The area that is located medially on the axilla and is delimited laterally by the axillar carina and postero-medially by scutocutellar sulcus.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000252">http://purl.obolibrary.org/obo/HAO_0000252</a></td>
<td>14</td>
</tr>
<tr>
<td>dorsal metapleural area (dma)</td>
<td>The area that is delimited posterodorsally by the metapleural carina and anteroventrally by the metapleural sulcus.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000261">http://purl.obolibrary.org/obo/HAO_0000261</a></td>
<td>15</td>
</tr>
<tr>
<td>mesofemoral depression (fd)</td>
<td>The scrobe that is located on the mesopleuron into which the mesofemur fits when pressed against the mesosoma.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000326">http://purl.obolibrary.org/obo/HAO_0000326</a></td>
<td>16</td>
</tr>
<tr>
<td>foamy structure (fs)</td>
<td>Foamy structures are extensions of cuticle that usually emanate from carinae on the propodeum and metapleuron but may also occur on T1 and S1.</td>
<td>Lahey et al. 2019 <a href="https://doi.org/10.3897/jhr.73.33876">https://doi.org/10.3897/jhr.73.33876</a></td>
<td>15, 17</td>
</tr>
<tr>
<td>internotaular area (ina)</td>
<td>The area on the mesoscutum that is delimited laterally by notauli</td>
<td>Mikó et al. 2010 <a href="https://doi.org/10.11646/zootaxa.2708.1.1">https://doi.org/10.11646/zootaxa.2708.1.1</a></td>
<td>18</td>
</tr>
<tr>
<td>lateral pronotal area (lpa)</td>
<td>The area of the pronotum that is lateral and delimited medially by the epiomial carina.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000483">http://purl.obolibrary.org/obo/HAO_0000483</a></td>
<td>19</td>
</tr>
<tr>
<td>Terms</td>
<td>Definition</td>
<td>URIs</td>
<td>Fig.</td>
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<tr>
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</tr>
<tr>
<td>lateral propodeal carina (lpc)</td>
<td>The carina that is oblique and arises submedially from the anterior margin of the metapetal-propodeal complex and extends to the posterior propodeal projection.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000486">http://purl.obolibrary.org/obo/HAO_0000486</a></td>
<td>21–23</td>
</tr>
<tr>
<td>marginal setae of fore wing</td>
<td>The row of setae that is located along the margin of the wing blade in the same plane as the wing blade.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000511">http://purl.obolibrary.org/obo/HAO_0000511</a></td>
<td></td>
</tr>
<tr>
<td>mesocutellum (mes)</td>
<td>The scutellum that is located on the mesonotum.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000574">http://purl.obolibrary.org/obo/HAO_0000574</a></td>
<td>20</td>
</tr>
<tr>
<td>mesopleural carina (mplc – red arrow)</td>
<td>The carina that crosses the mesopleuron and limits ventrally the mesofemoral depression.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000559">http://purl.obolibrary.org/obo/HAO_0000559</a></td>
<td>24</td>
</tr>
<tr>
<td>mesopleuron (mpl – marked with red dots)</td>
<td>The area that is located lateral of the mesodiscrinen.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000621">http://purl.obolibrary.org/obo/HAO_0000621</a></td>
<td>24</td>
</tr>
<tr>
<td>mesoscutum</td>
<td>The scutum that is located on the mesonotum.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000575">http://purl.obolibrary.org/obo/HAO_0000575</a></td>
<td></td>
</tr>
<tr>
<td>metapleural carina (mtpc)</td>
<td>The carina that delimits the metapleuron dorsally from the propodeum, extends from just ventral of the metapleural arm to the metacoxal articulation and passes anteroventral to the propodeal spiracle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000609">http://purl.obolibrary.org/obo/HAO_0000609</a></td>
<td>25, 50</td>
</tr>
<tr>
<td>metapleural sulcus (mtps – red arrow)</td>
<td>The line that corresponds with the metapleural ridge.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000614">http://purl.obolibrary.org/obo/HAO_0000614</a></td>
<td>26</td>
</tr>
<tr>
<td>metapleuron (mtp – marked with red dots)</td>
<td>The area of the metapetal-propodeal complex that is located laterally of the metadiscrinen.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000621">http://purl.obolibrary.org/obo/HAO_0000621</a></td>
<td>26</td>
</tr>
<tr>
<td>metascutellar carina (mtsc)</td>
<td>The carina that delimits laterally the metascutellum.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000624">http://purl.obolibrary.org/obo/HAO_0000624</a></td>
<td>27</td>
</tr>
<tr>
<td>metascutellum (mts)</td>
<td>The area that is located postero medially on the metanotum, is delimited laterally by the metanotal trough and corresponds to the reservoir of the dorsal vessel.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000625">http://purl.obolibrary.org/obo/HAO_0000625</a></td>
<td>27</td>
</tr>
<tr>
<td>metasomal depression (medt)</td>
<td>The acetabulum that is concave, surrounds the nu cha and accommodates the base of the metasoma.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000627">http://purl.obolibrary.org/obo/HAO_0000627</a></td>
<td>28–29</td>
</tr>
<tr>
<td>notauli (nt)</td>
<td>The line that extends submedially along the mesoscutum and corresponds to the median border of the site of origin of the first mesopleuro-mesonal muscle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000647">http://purl.obolibrary.org/obo/HAO_0000647</a></td>
<td>22</td>
</tr>
<tr>
<td>parapsidal lines</td>
<td>The signum that is located between the notaulus and the parascutal carina and corresponds to the site of origin of the dorsoventral indirect flight muscle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000694">http://purl.obolibrary.org/obo/HAO_0000694</a></td>
<td></td>
</tr>
<tr>
<td>plica (pl)</td>
<td>The carina that arises from the anterior margin of the abdominal tergum 1 medially of the propodeal spiracle extends to the posterior propodeal projection.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000735">http://purl.obolibrary.org/obo/HAO_0000735</a></td>
<td>30</td>
</tr>
<tr>
<td>posterior mesoscudellar sulcus (pms)</td>
<td>The line that extends along the posterior margin of the mesocutellum and corresponds to the posterior mesocutellar ridge.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000757">http://purl.obolibrary.org/obo/HAO_0000757</a></td>
<td>31</td>
</tr>
<tr>
<td>prespecular sulcus</td>
<td>The sulcus that delimits anteriorly the speculum and corresponds to the anterior margin of the speculum.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000816">http://purl.obolibrary.org/obo/HAO_0000816</a></td>
<td>42</td>
</tr>
<tr>
<td>pronotum (pr)</td>
<td>The notum that is located in the prothorax.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000853">http://purl.obolibrary.org/obo/HAO_0000853</a></td>
<td>32</td>
</tr>
<tr>
<td>scuto-scutellar sulcus (ss)</td>
<td>The sulcus that extends along the scutoscutellar suture.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0000919">http://purl.obolibrary.org/obo/HAO_0000919</a></td>
<td>33</td>
</tr>
<tr>
<td>transepisternal line (tspl)</td>
<td>The line that is longitudinal, extends ventrolaterally on the mesopleuron and corresponds with the site of origin of the second and third mesopleuro-third axillary sclerite of fore wing muscle and the second mesopleuro-mesonal muscle.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0001205">http://purl.obolibrary.org/obo/HAO_0001205</a></td>
<td>34</td>
</tr>
<tr>
<td>transscutal articulation (tsc)</td>
<td>The line of separation that extends along the transscutal line.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0001204">http://purl.obolibrary.org/obo/HAO_0001204</a></td>
<td>35</td>
</tr>
<tr>
<td>METASOMA</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>metasomal tergite 1, 2, ... n. (T1–Tn)</td>
<td>The abdominal tergum that is located in the metasoma.</td>
<td><a href="http://purl.obolibrary.org/obo/HAO_0001349">http://purl.obolibrary.org/obo/HAO_0001349</a></td>
<td>36–37</td>
</tr>
<tr>
<td>anterior pits of T2 (apT2)</td>
<td>Paired, oval or circular depressions situated anterolaterally on T2, often filled with dense pilosity.</td>
<td><a href="https://doi.org/10.4039/entm121147fv">https://doi.org/10.4039/entm121147fv</a></td>
<td>36–37</td>
</tr>
</tbody>
</table>
Figures 1–14. Morphological structures: 1 F. gallica  2 F. communis  3 Fidiobia sp.  4 F. tripotini  5 F. nipponica  6, 14 F. roatai  7 F. pronotata  8, 11 F. hofferi  9, 10, 13 F. striatitergitis  12 F. rugosifrons.
Results

Here, we follow the generic concept of *Fidiobia* presented in Masner and Huggert (1989). Males of many species of *Fidiobia* are unknown, rare, or morphologically similar to their female conspecifics. For this reason, we present a key to females; however, given the similarity between males and females of many species, the identification of males may be possible using this key.

Key to Palearctic *Fidiobia* (females)

1. Antenna 10-merous (Figs 232, 237); plica converging with lateral propodeal carina (Fig. 239); T1 subrectangular (Figs 36, 228) ........................................ 2

2. Antenna 9-merous (Figs 199, 191, 219); plica converging with metapleural carina (Figs 285, 292); T1 usually trapezoidal (Fig. 37), in few cases subrectangular ................................. 7

1. Notauli present, incised; junction of T1 and T2 covered by a transverse row of long, strong setae (Fig. 228).

2. Notauli absent (Figs 125, 127, 259) or indicated only by change in sculpture or setation (Figs 90, 135); junction of T1 and T2 not covered by setae.

3. Mesoscutellum with reticulate-rugose to longitudinally strigose microsculpture, smooth anteromedially (Figs 30, 33); T2 strigose (Figs 36a, 228, 282); lateral propodeal carina without foamy structures (Figs 30, 33); median carina present between lateral propodeal carinae; metapleural carina prolonged posterodorsally into a long and strong tooth.

4. OOL 5× diameter of lateral ocellus (Figs 142, 143); distance between notauli at least twice the maximum width of notaulus; posterior mesoscutellar sulcus present (Fig. 140); metascutellum visible; transepisternal line visible as a ridge on the anteroventral mesopleuron (Fig. 141); mesopleuron with a mesofemoral depression with a mesopleural carina along ventral margin; dorsal metapleural area glabrous.

5. Body flattened; marginal setae of fore wing long (Fig. 97); posterior side of hind coxa simple, without a setose furrow; transepisternal line absent; prespecular sulcus present.

6. Malar sulcus absent (Fig. 136); T2 wider than long; A9 longer than wide (Fig. 133); transverse pronotal sulcus covered by dense, short, silver setae; transepisternal line almost complete, straight (Fig. 136); notauli not incised, but visible as a change in setation (Fig. 135); hind coxa with a depression surrounded by two rows of setae, internal row higher than external one, forming a crease that continues to foamy structure of metapleural carina; anterior pits of T2 strongly transverse, medially very close to each other (Fig. 129), or merging together.

7. Malar sulcus present (Fig. 257); T2 longer than wide (1.2 times as long as maximum width); A9 wider than long (Fig. 258); transverse pronotal sulcus with few, sparse, short setae; transepisternal line short (Fig. 260); notauli totally absent (Fig. 259); hind coxa with a depression surround-
ed by two rows of almost equal, short setae; anterior pits of T2 ovate, space between anterior pits of T2 larger than the transverse diameter of pits ................................................................. *F. tripotini* sp. nov.

| 7 | Notauli present, incised ................................................................. 8 |
|   | – Notauli absent ............................................................................. 23 |
| 8 | Sculpture of frons areolate-rugulose (Figs 85, 174, 184, 185, 189, 218) ... 9 |
|   | – Sculpture of frons reticulate-coriaceous or alutaceous (Figs 51, 122, 149) ... 15 |
| 9 | A1 strongly widened with lamella well developed along the entire ventral margin (Figs 85, 86); A3 long, at least 0.75 times as long as A2; lateral propodeal carinae converging and rising up posteriorly (Fig. 81b); disc of fore wing with reticulate sculpture (Fig. 87) ....................................... *F. gallica* sp. nov. |
|   | – A1 moderately widened with lamella present only in the apical third (Figs 175, 191, 199, 219); A3 short, at most 0.5 times as long as A2; lateral propodeal carinae usually parallel and not rising up posteriorly (Figs 181, 192); disc of fore wing without reticulate sculpture (Figs 176, 194, 222) ...................... 10 |
| 10 | Brachypterous (Figs 170, 181, 197) ..................................................... 11 |
|   | – Macropterous (Figs 187, 195, 202, 213, 215) .................................... 13 |
| 11 | Apex of fore wing tapering to a point (Fig. 176); dorsal pronotum well-developed, length along midline almost 0.5× length of mesoscutum (Figs 170, 172); median prominence of T1 setose (Fig. 170) ................................................. *F. pronotata* Szabó, 1958 |
|   | – Apex of fore wing rounded (Figs 181, 197); dorsal pronotum weakly developed, hardly visible in dorsal view (Figs 181, 183, 197); median prominence of T1 glabrous (Fig. 181) ............................................. 12 |
| 12 | Apex of fore wing not reaching the middle of T2 (Fig. 181); area between notauli smooth in posterior half (Fig. 181); lateral pronotal area smooth in ventral half (Fig. 182); transverse carina between lateral propodeal carinae absent (Fig. 181) ...................................................... *F. pronotatoides* sp. nov. |
|   | – Apex of fore wing surpassing the middle of T2 (Fig. 197); area between notauli entirely sculptured (Fig. 197); lateral pronotal area entirely sculptured (Fig. 198); transverse carina between lateral propodeal carinae present (Fig. 197) ................................................................. *F. rugosifrons* Crawford, 1916 |
| 13 | Area between notauli entirely sculptured (Figs 195, 202, 213, 286); lateral pronotal area entirely sculptured (Fig. 196); scutoscutellar sulcus continuous with a large sulcus along the internal side of axillular carina (Figs 195, 197); dorsal axillar area large ................................................................. *F. rugosifrons* Crawford, 1916 |
|   | – Area between notauli smooth at least posteriorly (Figs 192, 285, 288, 289); lateral pronotal area smooth in ventral half (Figs 193, 221); narrow sulcus along the axillular carina (Figs 220, 285, 288, 289); dorsal axillar area very small ......................................................................................... 14 |
| 14 | Area between notauli entirely smooth (Figs 192, 285); lateral margin of notaulus and axillular carina forming a continuous line; submarginal vein shorter than the length of tegula or absent (Fig. 194); dorsal propodeum
with no foamy structures; epitorular carina absent (Fig. 189).................
.............................................................................................................
...**F. roatai sp. nov.**
– Area between notaui smooth in posterior half (Figs 220, 288, 289); lateral
margin of notaulus disjunct from axilllar carina; apex of submarginal vein
reaching the posterior margin of propodeum (Fig. 216); dorsal propodeum
with foamy structures; epitorular carina present (Fig. 218)...........................
.............................................................................................................
...**F. rugosifronsoides sp. nov.**
15 Brachypterous species; fore wing reduced, hardly visible (Fig. 105), or ex-
tending to T2 (Figs 104).................................................................**F. hofferi Kozlov, 1978**
– Macropterous species, fore wings extending to or surpassing apex of meta-
soma (Figs 103, 109) .............................................................................6
16 Metascutellum not visible in dorsal view, covered by posterior margin of mes-
oscutellum (Figs 117, 153) .......................................................................17
– Metascutellum visible in dorsal view as a narrow strip bordered by meta-
scutellar carinae (Figs 56, 123, 268, 291, 292) .............................................8
17 Marginal setae of fore wings short (Fig. 55) .................................................
.............................................................................................................
...**F. brevinotaula Veenakumari et al., 2018**
– Marginal setae of fore wings long (Fig. 119) .......................**F. insoonae sp. nov.**
18 Epitorular carina present on frons..........................................................19
– Epitorular carina absent on frons ...........................................................21
19 Metapleuron with posteroventral third entirely covered with short, dense,
white setae (Fig. 59); fore wing with visible marginal fringe (Fig. 60)............
.............................................................................................................
...**F. communis sp. nov.**
– Metapleuron with posteroventral third not entirely covered by setae (Figs
106, 112, 265); fore wings with short, hardly visible marginal fringe (Figs
107, 114, 267).........................................................................................20
20 Metapleuron with a line of stout setae along the dorsal and posterior margins;
fore wing dark medially; OOL equal to or less than OD..........................
.............................................................................................................
...**F. vanharteni Buhl, 2010**
– Metapleuron with only sparse setae, not arranged in a continuous line; fore
wings uniformly hyaline; OOL equal to about 2 OD .................................
.............................................................................................................
...**F. hofferi Kozlov, 1978**
21 Fore wings with long, visible marginal fringe; T1 with three pairs of sublateral
setae (Fig. 38); metapleural carina with a broad flange of foamy structure;
metapleural epicoxal area with a flange of foamy structure over the base of
hind coxa.................................................................................................**F. bohemica sp. nov.**
– Fore wings with hardly visible marginal fringe; T1 with two pairs of sublateral
setae; metapleural carina with a very narrow crease of foamy structure; meta-
pleural epicoxal area without a flange of foamy structure over the base of hind
coxa.................................................................................................22
22 T2 square or nearly so, at least 4 times as long as T1; notaui parallel; dorsal
mesopleuron with numerous delicate, transverse and dense striae; lateral pro-
notal area sculptured in dorsal two thirds; tibia and scape dark brown .........
...........................................................................................................  F. platystasioides sp. nov.
– T2 transverse, at most 3 times as long as T1; notauli diverging anteriorly; dor-
sal mesopleuron with two transverse striae bordering a smooth space; lateral
pronotal area sculptured in dorsal third; tibia and scape yellow ....................
...........................................................................................................  F. lisenchiae sp. nov.
23 Transscutal articulation incomplete (Fig. 293), visible only laterally; wings
micropterous, only about twice as long as tegula .................... F. sashai sp. nov.
– Transscutal articulation complete; wings macropterous or brachypterous, ex-
tending posteriorly beyond propodeum ................................................. 4
24 Lateral propodeal carinae not connected by a transverse carina (Figs 88a, 294,
295); metasomal depression square or longer than wide ....................... 25
– Lateral propodeal carinae sometimes connected by a transverse carina
(Figs 43, 66); metasomal depression strongly transverse .......................... 26
25 Body flat, strongly depressed dorsoventrally; width of mesosoma at least 2.7
times its height; metascutellum not visible dorsally, covered by posterior mar-
gin of mesoscutellum; mesopleuron without large circular depression; tran-
sepisternal line complete (Fig. 244); notaulus entirely absent; dorsal axillar
area small, hardly visible ..............................................  F. synergorum (Kieffer, 1921)
– Body not depressed dorsoventrally; width and height of mesosoma nearly
equal; metascutellum visible dorsally; mesopleuron with a large circular de-
pression (Fig. 91); transepisternal line absent; notaulus indicated by the ab-
sence of setation; dorsal axillar area, large, conspicuous .....................  F. birta sp. nov.
26 Transepisternal line present (Fig. 67); anterior pits of T2 strongly transverse,
medially contiguous or nearly so; median carina present between lateral propo-
deal carinae .................................................................  F. filicornis Buhl, 2014
– Transepisternal line absent; anterior pits of T2 ovate, distinct separated; me-
dian carina between lateral propodeal carinae variable ......................... 27
27 T2 distinctly longer than wide (Fig. 43); OOL around 2 times as long as
OD ...................................................................................... 28
– T2 about as long as wide (Fig. 165), or wider than long; OOL 0.8–1.2 times
as long as OD ............................................................................. 29
28 Apex of fore wing not extending beyond the middle of T2; ventral third of
mesopleuron without longitudinal striae; metapleural sulcus present; metas-
cutellum visible dorsally .......................................................  F. brevialis sp. nov.
– Apex of fore wings surpassing end of metasoma; ventral third of mesopleuron
longitudinally striate; metapleural sulcus absent; metascutellum not visible
dorsally, covered by posterior margin of mesoscryptellum ......................  F. flaviabdominalis Veenakumari et al., 2018
29 Fore wing with long marginal fringe (Figs 153, 158, 160) ........................
...........................................................................................................  F. polita Buhl, 1998
– Fore wing with short marginal fringe (Fig. 165, 169) ...........................  F. politoides sp. nov.
Species descriptions

1. *Fidiobia bohemica* Popovici, Masner & Lahey, sp. nov.
https://zoobank.org/1AE01224-E095-4058-88D3-CB4A651636A3
Figs 38–42, 298

**Description. Female.** Body length: 0.7 mm. Colour of body: melanic (Figs 38, 39).


Palearctic species of *Fidiobia*


**Figures 38–42.** *Fidiobia bohemica* 38 habitus, dorsal view (Holotype) 39 habitus, lateral view 40 head and toruli 41 antenna 42 head and mesosoma, lateral view.

Male. unknown.

Etymology. Named after the country where the type material was collected. Noun in apposition.


Distribution. Czech Republic (Fig. 298).

Diagnosis. Fidiobia bohemica is close to F. communis and F. hofferi because of the presence of notauli, the visible metasternum and the reticulate-coriaceous to alutaceous sculpture of the frons. Fidiobia bohemica differs from these species by the presence of three pairs of sublateral setae on T1 (only two in F. communis and F. hofferi) and the absence of epitorular carinae on the frons (present in F. communis and F. hofferi).

2. Fidiobia brevialis Popovici, Masner & Lahey, sp. nov.

https://zoobank.org/BE867A1A-C8FE-45BC-A4F6-AFCB8443E0E9

Figs 43–47, 299

Description. Female. Body length: 0.8 mm. Colour of body: xanthic (Figs 43, 44).


Palearctic species of Fidiobia

Figures 43–47. Fidiobia brevialis: 43 habitus, dorsal view (Holotype) 44 habitus, lateral view 45 head, dorsal view 46 head, frontal view 47 antenna (♀).


**Male.** unknown.

**Etymology.** The species name is derived from Latin words “brevis” and “alis”, meaning "short wings".


**Distribution.** Japan (Fig. 299).

**Biology.** unknown.

**Diagnosis.** *Fidiobia brevialis* and *F. sashai* are the only Palearctic species of the genus that are brachypterous and lack notauli. These species can be separated by the length of the fore wings (hardly longer than the tegula in *F. sashai* and surpassing the middle of T2 in *F. brevialis*) and the length of the transscutal articulation (incomplete in *F. sashai* and complete in *F. brevialis*).

### 3. *Fidiobia brevinotaula* Veenakumari, Popovici & Buhl, 2018

Figs 48–55, 300


**Description. Female** (Figs 48, 49). Body length: 0.6 mm. Colour of body: melanic, T1 lighter than the rest of body (Fig. 48).

Palearctic species of *Fidiobia*


Figures 48–55. *Fidiobia brevinotaula*: 48 habitus, dorsal view (OPPC0073) 49 habitus, lateral view 50 head, dorsal view 51 head, frontal view 52 antenna (♀) 53 mesosoma, dorsal view 54 head and mesosoma, lateral view 55a wings 55b WIP.

**Metasoma** (Fig. 48): Posterior of T2 some or all tergites may be under T2. Shape of T1: trapezoidal. Colour of T1: light brown. Lateral setae of T1: 2 pairs. Colour of T2: dark-brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** unknown.


South Korea: 1♀, Gyeongsan-si, Dachak-ro 280, Yeungnam University, 35.82119°N, 128.7634°E, 14.viii.2016, Fusu L. (YPT) (OPPC0073).

**Distribution.** India (Veenakumari et al. 2018), Russia, South Korea (Fig. 300).

**Diagnosis.** *Fidiobia brevinotaula* is a distinct species based on the abbreviated notauli; the transaxillar carina and horizontal part of the dorsal axillar area that are not visible; the presence of foamy structures on the lateral propodeal carinae; the long, strong, white, dense setae on the metapleuron; and the minute size of specimens. It is close habitually to *F. insoonae*, but these species can be separated by the marginal setae of fore wings (short in *F. brevinotaula* and long in *F. insoonae*) and by the setation of metapleuron (there are long, strong, dense setae in *F. brevinotaula* and short, tiny, sparse setae in *F. insoonae*).

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**4. Fidiobia communis** Popovici, Masner & Talamas, sp. nov.

https://zoobank.org/CF0AA5FE-1EFE-4EDA-A166-46B3487E21DD

Figs 56–60, 301

**Description. Female.** Body length: 0.8–0.9 mm. Colour of body: melanis (Figs 56a, 58).


Male (Fig. 57a): similar to the female, differing in the structure of the antenna (Fig. 57b).

Etymology. This species is named “communis” because of the absence of any peculiar or striking characters.

Figures 56–60. *Fidiobia communis*: 56a female, habitus, dorsal view (Holotype) 56b antenna (♀) 57a male, habitus, dorsal view (OPPC0578) 57b antenna (♂) 58 female, habitus, lateral view 59 female, mesosoma, lateral view 60a wings 60b WIP.


Estonia: 2♀, 1.5 km NE Sööru, 58.66111°N, 26.88531°E, 4–11.vii.2011, leg. Soon V. (SN) (OPPC0664, 0665).


Ukraine: 1♀, Transcarpathia, Svydovets, 2–3 km NW of Kvasy, 48.15247°N, 24.26621°E, 7.v–5.vi.2014, leg. Varga O. (TT) (OPPC0230); 1♀, Transcarpathia,

**Distribution.** Czech Republic, Estonia, Romania, Ukraine (Fig. 301).

**Diagnosis.** *Fidiobia communis* is close to *F. hofferi* because of its general habitus, the metascutellum that is visible in dorsal view and the presence of epitorular carinae. These two species differ mainly by the sculpture of the dorsal mesopleuron (reduced in *F. hofferi* and extending to the middle of the mesopleuron in *F. communis*), setation of the ventral metapleural area (few, sparse setae in *F. hofferi* and dense, long setae in *F. communis*) and the length of the marginal setae on the fore wings (very short, hardly visible in *F. hofferi* and clearly visible in *F. communis*).

5. *Fidiobia filicornis* Buhl, 2014
Figs 61–68, 296, 302


**Description.** Female. Body length: 0.7–0.8 mm. Colour of body: bicoloured, head and mesosoma dark brown to brown, metasoma brown to reddish brown with T1 and the apex of T6 lighter (Figs 61, 62).


Figures 61–68. *Fidiobia filicornis*: 61 female, habitus, dorsal view (OPPC0074) 62 female, habitus, lateral view 63 male, habitus, dorsal view (OPPC0045) 64 antenna (♀) (OPPC0517) 65 antenna (♂) (OPPC0818) 66 head and mesosoma, dorsal view 67 head and mesosoma, lateral view 68a wings (OPPC0517) 68b WIP.

Palearctic species of Fidiobia


Distribution. Togo (Buhl 2014), China, South Korea (Fig. 302).

Biology. unknown.

Diagnosis. Fidiobia filicornis is the only known Palearctic species with 9-merous antenna in the female and 10-merous antenna in the male. As is typical for Fidiobia, the female antenna is clavate and the male antenna is clubbed, but in the male of F. filicornis the antenna is almost filiform as in F. longiclava or F. vladlubomiri (both species with 10-merous antenna in male and female). Another distinctive character among the Palearctic species with 9-merous antennae is the presence of the transepisternal line, which is narrow, deeply incised, transverse and nearly complete in F. filicornis. This species is not known from the Oriental region (Veenakumari et al. 2018), but a new species, Fidiobia setosa was recently described from India and is considered a close relative of F. filicornis. These two species can be easily separated because of the presence of a hyperoccipital carina and 10-merous antennae in F. setosa.

Comments. Fidiobia filicornis was described from the Afrotropical region (Togo) by Buhl (2014). It was described from a singleton male specimen with distinctive filiform antenna with 10-antennomeres and without notauli. At the moment, there are no data concerning the distribution or the abundance of this species in the Afrotropical region, but it is one of the best represented species in our Palearctic material. The specimens from China are from the Sino-Japanese region but do not differ morphologically from South Korean specimens. The difference between our material and the type specimen is in the sculpture of mesoscutum, which is smoother in the latter.
6. *Fidiobia flaviabdominalis* Veenakumari, Popovici & Buhl, 2018
Figs 74–79, 303


**Description.** Female. Body length: 0.5 mm. Colour of body: xanthic, head and metasoma brown, metasoma light brown to yellow (Figs 74, 75).


**Metasoma** (Fig. 74): Posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: light brown. Lateral setae of T1: 2 pairs. Colour of T2: light brown apically and darker basally. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: darker than T2.


**SOUTH KOREA:** 25♀, Jeollabuk-do, Buan-gun Samae-myeon Yuyu village, 35.4191°N, 127.2755°E, 5.vii–14.viii.2007, leg. Tripotin P. (MT) (OPPC0785, 0786, 0787, 0788, 0793, 0792, 0789, 0784, 0790, 0791, 0805, 0809, 0810, 0811, 0806,
Figures 74–79. *Fidiobia flaviabdominalis*: 74 habitus, dorsal view (OPPC0405) 75 habitus, lateral view (OPPC0786) 76 antenna (♀) (OPPC0647) 77 mesosoma, dorsal view 78 mesosoma, lateral view 79a wings (OPPC0647) 79b WIP.

Palearctic species of *Fidiobia*

55

**Distribution.** India (Veenakumari et al. 2018), Japan, South Korea (Fig. 303).

**Biology.** unknown.

**Diagnosis.** *Fidiobia flaviabdominalis* is superficially similar in size and general habitus to *F. insooanae*, *F. polita* and *F. politoides*. It differs from *F. insooanae* mainly by the absence of notauli (present in *F. insooanae*) and to *F. polita* and *F. politoides* because of the length of T2 (T2 is longer than wide in *F. flaviabdominalis* and wider than long in *F. polita* and *F. politoides*).

**Comments.** *Fidiobia flaviabdominalis* is one of the smallest species of the genus in the Palearctic region. It is peculiar among Palearctic *Fidiobia* because of its reduced size and the light color. Our specimens differ from the original description by the presence of longitudinal striae on the lower third of the mesopleuron and A4 longer than A3 in females.

7. *Fidiobia gallica* Masner, Popovici & Talamas, sp. nov.
https://zoobank.org/A403E05B-AAEA-4C91-AD59-F11214D6DF6B
Figs 80–87, 304

**Description.** Female. Body length: 1.1 mm. Colour of body: bicoloured, head and mesosoma black, metasoma brown with T1 lighter (T1 light brown to reddish) (Figs 80–82).


**Mesosoma** (Figs 81b, 84). Colour of mesosoma: black. Mesosoma: weakly compressed dorsoventrally. Pronotum in dorsal view: present mostly as lateral shoulders. Transverse pronotal sulcus: present as a wide groove along the anterior rim of prono-

Figures 80–87. *Fidiobia gallica*: 80, 81a habitus, dorsal view (Holotype) 81b mesosoma, dorsal view 82 habitus, lateral view 83 head, dorsal view 84 mesosoma, lateral view 85 head and antenna 86 antenna 87 wings.
Male. unknown.

Etymology. This species is named “gallica”, meaning “French”, for the country where the specimen was collected. This species was named after the ancient name of France.


Distribution. France (Fig. 304).

Biology. unknown.

Diagnosis. *Fidiobia gallica* is one of the most peculiar species of the genus because of the lamellate scape, elongate A3, reticulate pattern on the disc of the fore wing and a narrow metasomal depression (width of metasomal depression is less than the length of the lateral propodeal carina) bordered by lateral propodeal carinae that are nearly parallel and are elevated posteriorly. The combination of these four characters differentiates this species from the remainder of the Palearctic fauna.

Comments. The development of the ventral lamella of A1 is found in other Palearctic platygastrids, including *Iphitrachelus* Walker and *Amblyaspis* Förster. In other regions, this can be found in *Sacespalus* Kieffer, *Platygastoides* Dodd, *Plutomerus* Masner and Huggert, and *Pulchrisolia* Szabó. The reticulate fore wing can also be found in an undescribed species from Madagascar (Z. Lahey, unpublished data).

8. *Fidiobia hirta* Popovici, Masner & Talamas, sp. nov.

https://zoobank.org/7379AD45-4FD4-42E9-B7D9-73E8C11D63DF

Fig. 88–91, 305

Description. Female. Body length: 1.1 mm. Colour of body: melanic (Figs 88a, 89).


**Metasoma** (Fig. 88a): posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 3 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.
Male. unknown.

Etymology. This species is named for the Latin term for hairy, “hirta”.


Distribution. This species was encountered only in Far East Russia and South Korea (Fig. 305).

Biology. unknown.

Diagnosis. Fidiobia hirta differs from other species in the genus because the body is not flattened dorsoventrally, the mesoscutum and mesoscutellum are convex in lateral view, the metasomal depression is large, the lateral propodeal carinae diverge posteriorly, and T3 is at least as long as its maximum width.

Figures 88–91. Fidiobia hirta: 88a habitus, dorsal view (Holotype) 88b antenna 89 habitus, lateral view 90 head, dorsal view 91 head and mesosoma, lateral view.
9. *Fidiobia hispanica* Popovici & Buhl, 2010
Figs 92–102, 306


**Description. Female.** Body length: 0.7–0.9 mm. Colour of body: melanic (Fig. 92).


Metasoma (Fig. 92): Tergites posterior of T2 may be retracted under T2. Shape of T1: subrectangular. Colour of T1: brown. Lateral setae of T1: 3 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T6: T3–T5 the same as T2, T6 lighter than T2.

Male (Fig. 101): Similar to female, differing in the structure of the antenna and in some metasomal characters (see Popovici and Buhl 2010).
Palearctic species of *Fidiobia*

**Material examined.** 22♀ and 3♂. **Spain:** *Holotype* (Fig. 99): 1♀, Pina de Ebro, Pine / Juniper forest, leg. J. Blasco Zumeta (Fig. 77) (ZMUC). **Paratypes:** 1♀, Pina de Ebro, UTM30TYL2894 (41.5207°N, -0.5055°E), 9.iii.1991, leg. Zumeta B. (OPPC 0801); 1♀, Pina de Ebro, UTM30TYL2894 (41.5207°N, -0.5055°E), 9.iii.1991, leg. Zumeta B. (Fig. 75) (ZMUC); 1♂, Pina de Ebro, UTM30TYL2894 (41.5207°N, -0.5055°E), 9.iii.1991, leg. Zumeta B. (Fig. 101) (ZMUC).

**Non-type material.** **England:** 16♀ and 3♂, London, Greenwich, Vanbrugh Pits, reared from a batch of beetle eggs in vacated *Andricus lignicola* (Hartig, 1840) gall on *Quercus robur* Linnaeus, 1753, (gall collected 17.i.2010, Notton D.G.) (BMNH); 5♀, London, Greenwich, Vanbrugh Pits, TQ397771 (51.4758°N, 0.0111°E), reared from a batch of beetle eggs in a vacated cell of *Synergus umbraculus* (Olivier, 1791) in an old *Andricus kollari* (Hartig, 1843) gall on *Quercus robur*, (gall collected 14.iii.2010, Notton D.G.) (BMNH).

**Distribution.** Spain, Ireland, England (Popovici and Buhl 2010; Notton et al. 2014) (Fig. 306).

**Biology.** Popovici and Buhl (2010) reported *Andricus lignicola* (Hartig) (Hymenoptera: Cynipidae) on *Quercus* as the host of *F. hispanica*, as it was in O’Connor et al. (2004). Notton et al. (2014) observed that, in fact, *F. hispanica*, was reared from beetle eggs found in a vacated gall of *Andricus lignicola* (Fig. 98) on *Quercus robur* and from beetle eggs found in a vacated *Synergus umbraculus* (Olivier) cell in a vacated

**Figures 99–102.** Types of *Fidiobia hispanica*: 99 Holotype ♀ 100 Paratype ♀ 101 Paratype ♂ 102 labels of the holotype.
Andricus kollari (Hartig) gall. For this reason, we consider it likely that the true host is a beetle and not a cynipoid as mentioned in Popovici and Buhl (2010).

**Diagnosis.** The small size and delicate exoskeleton of *F. hispanica* make this species unmistakable among the Palearctic species with 10-merous antennae. The habitus is somewhat similar to that of *F. synergorum* and these species have been previously confused (Buhl 1999b; O’Connor et al. 2004). The main differences between them are the number of antennomeres (10 in *F. hispanica* and 9 in *F. synergorum*) and the ratio between the width and height of the mesosoma in females (1.6 in *F. hispanica* and 2.7 in *F. synergorum*), the transverse carina between the lateral propodeal carinae (present in *F. hispanica* and absent in *F. synergorum*) and the structure of the metasoma in males (present in Popovici and Buhl 2010). The 1:1:1 sensillar formula (Fig. 95b) is unique among the Palearctic species of *Fidiobia* in which this character has been observed.

10. **Fidiobia hofferi** Kozlov, 1978


**Description. Female.** Body length: 0.5–0.6 mm. Colour of body: melanic (Figs 103a, 104a, 105, 106).


Male. unknown.


Romania: 8♀ (brachypterous) and 8♀ (full winged), Iași, Bărnova forest near Slobozia, 47.01139°N, 27.60306°E, 4.vii.2011, leg. Noyes JS. (SS) (OPPC0660, 0659, 0658, 0657, 0662, 0656, 0826, 0661 and OPPC0635, 0636, 0637, 0655, 0633, 0663, 0638, 0634).


Distribution. Finland, Sweden, Iran (Koponen and Huggert 1982; Asadi-Farfar et al. 2020), Czech Republic, Romania, Ukraine (Fig. 307).

Biology. The host is unknown, but Lemarie (1958, 1959, 1960, 1961) reported that the specimens from the type series were reared from an ichneumonid parasitoid
Figures 103–108. *Fidiobia hofferi*: 103a fully winged specimen, habitus, dorsal view (OPPC0635) 103b antenna in fully winged specimen (♀) (OPPC0638) 104a brachypterous specimen, habitus, dorsal view (OPPC0826) 104b antenna in brachypterous specimen (♀) 105 specimen with extremely brachiptery (OPPC0823) 106 brachypterous specimen, lateral view 107a fully developed wings 107b WIP in fully developed wings 108a brachypterous wings (OPPC0656) 108b WIP in brachypterous wings.
of *Exoteleia dodecella* (Linnaeus) (Lepidoptera: Gelechiidae). We consider this assumption to have no support. The habitat of this species in Romania is represented by glades with shrubby vegetation.

**Diagnosis.** This species can be diagnosed by the visible metascutellum and nearly glabrous metapleuron. It is relatively close to *F. vanharteni* and *F. polita* based on its general habitus. *Fidiobia hofferi* is most likely to be confused with *F. polita*, a species with which it is sympatric. The main difference is the presence of notaulli in *F. hofferi* and the absence of these structures in *F. polita*. Another difference between these two species is the OOL:OD ratio (OOL is 2 times as long as OD in *F. hofferi* and OOL is equal to OD in *F. polita*).
**Fidiobia hofferi** can be separated from *F. vanharteni* because the fore wings are uniformly hyaline in *F. hofferi* and dark medially in *F. vanharteni*. Also, the OOL is equal to about 2 OD in *F. hofferi* and the OOL is equal to or less than OD in *F. vanharteni*. *Fidiobia hofferi* is a polymorphic species and contains brachypterous females among the Romanian material.

**Comments.** In specimens from the type series, the median prominence of T1 is smooth and without carinae. In the Romanian material, the median prominence of T1 has two carinae. Also, the specimens from Romania are more gracile than the specimens from the type series. The specimen from Ukraine has the wings more reduced than the brachypterous specimens from Romania, which are about half the length of the notauli, and the medial prominence of T1 with three carinae. The Ukrainian specimen otherwise matches our concept of *F. hofferi*.

11. **Fidiobia insoonae** Popovici, Talamas & Lahey, sp. nov.
https://zoobank.org/331C571D-68E6-4FBA-A734-4B5112018278
Figs 115–119, 308

**Description. Female.** Body length: 0.5 mm. Colour of body: melanic (Figs 115a, 116).


**Metasoma.** Posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** unknown.

**Etymology.** This species is named in honor of Insoon Tripotin.


**Distribution.** South Korea (Fig. 308).

**Diagnosis.** *Fidiobia insoonae* is superficially similar to *F. polita*, *F. politoides*, *F. flaviabdominalis*, and *F. hofferi* because of the almost similar size and the general habitus. It most obviously differs from *F. polita*, *F. politoides*, and *F. flaviabdominalis*...
(it is sympatric with the latter two) by the presence of notauli. *Fidiobia insoonaee* and *F. hofferi* are allopatric and differ from each other mainly by the metascutellum, which is covered by the posterior margin of mesoscutellum and not visible in *F. insoonaee*, and because of the setation of the metapleuron is sparse in *F. hofferi* and dense in *F. insoonaee*. Also, the marginal fringe of the fore wing is short and barely noticeable in *F. hofferi* but it is long in *F. insoonaee*.

12. *Fidiobia lisenchiae* Popovici, Lahey & Talamas, sp. nov.  
https://zoobank.org/9DFB135B-F9D7-4CDC-85B9-0E1C03F6703B  
Figs 120–124, 309

**Description. Female.** Body length: 0.7 mm. Colour of body: melanic (Fig. 120).


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**Figures 120–124.** *Fidiobia lisenchiae.* 120 habitus, dorsal view (Holotype) 121 head, dorsal view 122 head (frontal view) and antenna 123 mesosoma, dorsal view 124 head and mesosoma, lateral view.

**Metasoma** (Fig. 120): Posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: transverse. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** unknown.

**Etymology.** This species is named after Camelia Lisenchi because of her great support during a collecting trip in Cyprus.

**Material examined.** 1 ♀. Cyprus: **Holotype** 1 ♀, 6 km N of Lemessos, 34.727°N, 33.05°E, 24.v.2009, leg. Popovici O. and Fusu L. (SN) (OPPC0813).

**Distribution.** Cyprus (Fig. 309).

**Diagnosis.** *Fidiobia lisenchiae* is similar to *F. platystasioides* because of the absence of epitorular carinae, the fore wings with very short marginal setae and the notaulli slightly dilated posteriorly. These two species are easily separated because the mesosoma is slightly flattened in *F. lisenchiae* and visibly flattened in *F. platystasioides*. Also, T2 is transverse in *F. lisenchiae* and square or nearly so in *F. platystasioides*. The difference between these two states of T2 is reflected in the ratio of T2:T1. T2 is at most 3 times as long as T1 in *F. lisenchiae* and at least 4 times as long as T1 in *F. platystasioides*. The submarginal vein is shorter in *F. lisenchiae* than in *F. platystasioides*, with the apex of the submarginal vein hardly surpassing the posterior edge of the propodeum in *F. lisenchiae* and surpassing the middle of T1 in *F. platystasioides*. Other subtle differences between these species are the color of the scape and tibia (yellow in *F. lisenchiae* and dark brown in *F. platystasioides*), the sculpture of the dorsal mesopleuron (with few striae and a smooth area in *F. lisenchiae* and with numerous, dense striae in *F. platystasioides*) and in the sculpture of the lateral pronotal area (sculptured only in dorsal third in *F. lisenchiae* and in dorsal two thirds in *F. platystasioides*).

13. *Fidiobia longiclava* Popovici, Masner & Talamas, sp. nov.
https://zoobank.org/97F07876-1F41-408C-88A2-362489490758
Figs 125–137, 310

**Description. Female.** Body length: 0.8–1.0 mm. Colour of body: Variable, melanic specimens are brown with hardly lighter T1; xanthic specimens are light brown to yellow with darker head (Figs 125–128).


together in a deep and transverse anterior depression. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male** (Figs 129, 130). Similar to the female, but differing in the structure of the antenna (Fig. 134).

**Etymology.** This species is named for the elongate shape of the clavomeres.


**Distribution.** South Korea (Fig. 310).

**Biology.** unknown.

**Diagnosis.** The most diagnostic feature is the elongated shape of the clavomeres, which are unique among the Palearctic species of *Fidiobia* with 10-merous antennae. Non-sexually dimorphic characters that can be used to identify males are the notaular lines that are visible as a change in the setation of the mesoscutum and the nearly straight transepisternal line. The transverse anterior pits of T2 that nearly merge medi ally is unique among Palearctic *Fidiobia* that have a 10-merous antenna, lack notauli and have the junction of T1–T2 not covered by a row of setae. The color of the body in this species is highly variable, ranging from almost entirely yellow to completely brown.

14. *Fidiobia nipponica* Popovici, Masner & Lahey, sp. nov.

https://zoobank.org/61A1FCC4-6124-4DED-9FD0-2F11081700F1

Figs 138–144, 311

**Description. Females.** Length of body: 1.1 mm. Colour of body: melanic species (Figs 138, 139).


**Metasoma** (Figs 138, 139): Tergites posterior of T2 exposed and clearly visible. Shape of T1: subrectangular. Colour of T1: reddish-brown. Lateral setae of T1: absent. Colour of T2: brown. Shape of T2: transverse. Anterior pits of T2: merging together in a deep and
Figures 138–144. *Fidiobia nipponica*: 138 habitus, dorsal view (Holotype) 139 habitus, lateral view 140 mesosoma, dorsal view 141 mesosoma, lateral view 142 head, dorsal view 143 head, frontal view 144a head and antenna (♀) 144b antenna (♀).

transverse anterior depression. Sculpture of T2, lateral to anterior pits of T2: subtrigulate on 1/2 of T2 length. Colour of T3–T6: T3 the same with T2, T4–T6 lighter than T2. **Male.** unknown.
Etymology. This species is named after the country where the type material was collected.


Distribution. Japan (Fig. 311).

Biology. unknown.

Diagnosis. We consider *F. nipponica* to be close to *F. striatitergitis* based on the presence of a metascutellar carina with a tooth, a posterior mesoscutellar sulcus and the very short marginal fringe of the fore wing. Although most of T2 in this species is smooth and shining, some very fine longitudinal striae can be observed laterally, but this sculpture is distinctly different than the extensive striaion on T2 that is found in *F. striatitergitis*. The metasomal depression is completely covered with foamy structures and the large distance between the posterior ocellus and compound eye make this species easy to recognize among the Palearctic species of *Fidiobia* with 10-merous antennae.

15. *Fidiobia platystasioides* Masner, Popovici & Talamas, sp. nov.
https://zoobank.org/67CB2934-4D11-4933-8552-D0F944F70E26
Figs 145–152, 312

Description. Female. Body length: 0.7 mm. Colour of body: melanic (Figs 145, 146).


**Metasoma** (Fig. 145): posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: dark brown. Lateral setae of T1: 2 pairs. Colour of T2: dark brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** Unknown.

**Etymology.** This species is named for its similarity with species of *Platystasius* Nixon, 1937.


**Distribution.** China (Fig. 312).

**Biology.** Unknown.

**Diagnosis.** *Fidiobia platystasioides* is similar to *F. lisenchiae* because of the absence of epitorular carinae, the fore wings with very short marginal setae and notauli slightly dilated posteriorly. The main differences between these two species is the ratio T2:T1 (in *F.*
Platystasioides T2 is at least 4 times as long as T1 and in F. lisenchiae T2 is at most 3 times as long as T1) and the length of the submarginal vein (the apex of the submarginal vein surpassing the middle of T1 in F. platystasioides and hardly surpassing the propodeum in F. lisenchiae). Other subtle differences between these species are the color of the scape and tibia (dark brown in F. platystasioides and yellow in F. lisenchiae), the sculpture of the
dorsal mesopleuron (with numerous dense striae in *F. platystasioides* and with few striae and a smooth area in *F. lisenchiae*) and the sculpture of the lateral pronotal area (sculptured in dorsal two thirds in *F. platystasioides* and only in dorsal third in *F. lisenchiae*).

**Comments.** *Fidiobia platystasioides* is a distinct species because the notauli are slightly dilated posteriorly and almost parallel, and the body is flattened. These characteristics closely resemble those seen in the genus *Platystasius* Nixon.

Figs 153–164, 297, 313


**Description. Female.** Body length: 0.5–0.6 mm. Colour of body: melanic (Figs 153, 154, 159).


**Metasoma** (Figs 153; 159): posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: transverse. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** unknown.


Sweden: Holotype ♀, (Figs 159–164) (ZMUC).


**Distribution.** Estonia, Greece, Hungary, Romania, Sweden, Ukraine (Fig. 313).

**Biology.** unknown.

**Diagnosis.** *Fidiobia polita* is distinct among the Palearctic species of this genus with 9-merous antennae and without notauli because T2 is transverse or about as long as wide and the OOL is about as long as an OD (OOL 0.8–1.2 times as long as OD). Of the Palearctic fauna, *F. polita* is most similar to *F. politoides* and differs in the length
of the fore wing marginal setae (long marginal setae in *F. polita* and very short marginal setae in *F. politoides*). According to the studied material these species are allopatric.

In the European fauna, *F. polita* is similar to *F. hofferi* but differs by the notauli (which are present in *F. hofferi* and absent in *F. polita*) and by the ratio OOL:OD.
(OOL = 2OD in F. hofferi and OOL = OD in F. polita). Because of the small size of both species, and because in some specimens of F. hofferi the notauli are superficial, the presence of notauli can be difficult to observe. Minor differences can also be observed in the structure of the antenna: A3 is shorter than A4 and the junction between A2 and A3 is narrow in F. polita, but in F. hofferi A3 is almost as long as A4 and the junction between A2 and A3 is large. In F. polita, A5 has the same shape as A4 (globular or moniliform), but in F. hofferi A5 it is more transverse than A4. The study of these characters requires examination of the antenna on a microscopic slide.

**Figures 159–164.** Holotype of Fidiobia polita: 159 habitus, dorsal view 160 habitus, lateral view 161 mesosoma, dorsal view 162 mesosoma, lateral view 163 head and antenna 164 labels.
Comments. In our material, the specimens from Sweden (type locality) are very similar to the specimen from Estonia. The specimen from Greece is the smallest, relatively weakly sclerotized and, in connection with this, the color of body is lighter than in the rest of the specimens. However, there are no characters to reliably separate it. Also, the Romanian specimen is slightly larger than the rest of the specimens examined.

17. *Fidiobia politoides* Popovici, Talamas & Lahey, sp. nov.
https://zoobank.org/CE22B92E-FBC4-4274-9C35-98EF3D147992
Figs 165–169, 314

Description. Female. Body length: 0.5 mm. Colour of body: melanic (Figs 165–166).


**Figures 165–169.** Fidiobia politoides: 165 habitus, dorsal view (OPPC0475) 166 habitus, lateral view 167 head (frontal view) and antenna 168 antenna (♀) 169a wings 169b WIP.

**Metasoma** (Figs 165, 166): Posterior of T2 some or all tergites may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T5: the same as T2.

**Male.** Unknown.

**Etymology.** This species is named for its similarity to *F. polita.*


**Distribution.** South Korea (Fig. 314).

**Biology.** Unknown.

**Diagnosis.** *Fidiobia politoides* is close to *F. polita* because T2 is transverse or about as long as wide and the OOL is about as long as an OD (OOL 0.8–1.2 times as long as OD) and they differ in the length of the fore wing marginal setae (long marginal setae in *F. polita* and very short marginal setae in *F. politoides*). In the structure of antenna, the clava in *F. politoides* is larger than in *F. polita*, and A5 and A6 are more transverse in *F. politoides* than in *F. polita*. According to the studied material these species are allopatric.

18. *Fidiobia pronotata* Szabó, 1958

Figs 170–180, 284, 315


**Description. Female.** Body length: 0.9–1.0 mm. Colour of body: bicoloured, head and mesosoma black, metasoma brown (Figs 170, 171).

striking different from the rest of the antenna (clava brown, rest of antenna yellow). Number of antennomeres: nine. Shape of A1: more or less cylindrical. Ventral (inner) lamella on A1: present as a trace in the apical part of A1. Length of A3 of female: distinctly shorter than A2. Sensillar formula (A7:A8:A9): 2:2:1 (Fig. 175b).


**Metasoma** (Figs 170, 178): Tergites posterior of T2 may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: reddish brown. Lateral setae of T1: 2 pairs. Colour of

**Male.** unknown.

**Material examined.** 11♀. FRANCE: 1♀, Côte-d’Or, Esbarres, 47.102°N, 5.229°E, 1.ix.1948, leg. Barbier J. (MNHP); 1♀, Côte-d’Or, Esbarres, 47.102°N, 5.229°E, 22.ix.1955, leg. Barbier J. (MNHP); 1♀, Côte-d’Or, Gevrolles, 47.985°N, 4.772°E, 4.ix.1957, leg. Barbier J. (MNHP); 1♀, Côte-d’Or, Esbarres, 47.102°N, 5.229°E, 16.vii.1958, leg. Barbier J. (CNCI); 1♀, Côte-d’Or, Esbarres, 47.102°N, 5.229°E, 27.viii.1959, leg. Barbier J. (CNCI).

**Hungary:** **Holotype:** ♀, Pesta, Szentendrei-sziget, 47.643°N, 19.099°E, 2.vii.1957, leg. Szabó JB. (HNHM) (Figs 177–180); **Paratype:** 1♀, Siófok, Zamárdi, 46.861°N, 17.953°E, 29.x.1953, leg. Balogh J. (HNHM).

**Romania:** 1♀, Iași, Botanical Garden, 47.186°N, 27.5512°E, 17.ix.2003, leg. Popovici O. (sweep net) (OPPC0692); 1♀, Constanța, Vadu, 44.47265°N, 28.8064°E, 26.viii.2004, leg. Popovici O. (sweep net) (OPPC0693); 1♀, Iași, Ciric lake, 47.18778°N,

**Figures 170–176. Fidiobia pronotata: 170** habitus, dorsal view (OPPC0693) 171 habitus, lateral view 172 head, dorsal view 173 head, frontal view 174 head and antenna 175a antenna (♀) (OPPC0692) 175b sensillar formula 176 fore wing (OPPC0692).
Figures 177–180. Holotype of Fidiobia pronotata. 177, 178 habitus, dorsal view 179 habitus, lateral view 180 data labels.


**Distribution.** Germany (Buhl et al. 2016); Republic of Moldova (Kozlov 1987); France, Hungary, Romania (Fig. 315).

**Biology.** unknown.

**Diagnosis.** Fidiobia pronotata can be easily identified by the elongate pronotum, shortened wings and large, non-foveate mesoscutal humeral and suprahumeral sulci. The epomial carina is absent, or very short and weakly indicated. This combination of characters is unique among Palearctic Fidiobia.

**Comments.** In the original description of this species, Szabó (1958) designated the holotype and one paratype. Both specimens were located in HNHM. In the case of the holotype, near the original labels there is one label that indicates the specimen as the lectotype (Fig. 180). We do not understand the significance of this label.

It is a relatively rare species not often collected with sweep nets or Malaise traps.

19. **Fidiobia pronotatoides** Popovici, Lahey & Talamas, sp. nov.
https://zoobank.org/77B46AEB-73ED-4B95-8DA3-251EE57E739B
Figs 181–185, 316

**Description. Female.** Body length: 0.84 mm. Colour of body: melanic (Figs 181, 182).

Palearctic species of Fidiobia

93


**Male.** unknown.

**Etymology.** This species is named for its similarity to *F. pronotata*.


**Distribution.** Romania (Fig. 316).

**Biology.** unknown.

**Diagnosis.** There are three brachypterous species of *Fidiobia* with notauli and areolate-rugulose sculpture on the frons: *F. pronotanoides*, *F. pronotata*, and *F. rugosifrons*. Between these species, brachyptery is always observed in *F. pronotata* and *F. pronotatoides*, but it is a rarity for *F. rugosifrons*.

*Fidiobia pronotatoides* is very close to *F. pronotata*, differing by the pronotum of typical length, the narrow mesoscutal humeral and suprahumeral sulci, the well developed

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**Figures 181–186.** *Fidiobia pronotatoides*: 181 habitus, dorsal view (Holotype) 182 habitus, lateral view 183 head, dorsal view 184 head, frontal view 185 head and antenna 186 antenna (♀).
epomial carina (longer than half the length of the pronotum measured along midline), fore wings apically rounded (acuminate in *F. pronotata*), legs light brown with brown coxae (legs entirely yellow in *F. pronotata*) and a glabrous median prominence of T1 (setose in *F. pronotata*). *Fidiobia pronotatoides* can be separated from *F. rugosifrons* by the length of the fore wing (not reaching the middle of T2), the internotaular sculpture (smooth in posterior half), and the lateral pronotal area (smooth in ventral half).

20. *Fidiobia roatai* Popovici, Talamas & Lahey, sp. nov.
https://zoobank.org/62BC0958-38CC-42B5-B83C-6221396A6DA8
Figs 187–194, 285, 317

**Description. Female.** Body length: 0.9–1.0 mm. Colour of body: melanic (Figs 187, 188).


Metasoma (Fig. 187): Tergites posterior of T2 may be retracted under T2. Shape of T1: trapezoidal. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T6: the same as T2.

Male. unknown.


Etymology. This species is named after Dr. Cristian Roată, a well-known surgeon from Iași (Romania).

Distribution. Romania (Fig. 317).

Biology. The host is unknown. The specimens were collected from a typically steppe habitat.

Diagnosis. Fidiobia roatai is distinct among species with an areolate-rugulose frons because of its dark body, absence of sculpture between the notauli, absence of foamy structures on the propodeum, the ratio between A2 and A3 (A2 1.3–1.5 times as long as A3 in F. roatai and 2.4–2.6 times as long as A3 in F. rugosifronsoides), the ratio between A3 and A4 (A3 1.8–2.0 times as long as A4 in F. roatai and 1.2–1.3 times
Figures 187–194. *Fidiobia roatai*: 187. habitus, dorsal view (Holotype) 188 habitus, lateral view 189 head, frontal view 190 head, dorsal view 191 antenna (♀) (OPPC0548) 192 mesosoma, dorsal view 193 mesosoma, lateral view 194a wings (OPPC0548) 194b WIP.
as long as A4 in *F. rugosifronsoides*) and the rudimentary or absent submarginal vein of fore wing. Also, the fore wings in *F. roatai* have a peculiar pattern in color and in the distribution of setae. The basal 1/5 of the fore wing is light brown and the setae are absent or punctiform on this area. The apical 3/5 of fore wing is also light brown but covered with short setae. Between basal and apical brown areas of the fore wing there is a lighter almost triangular area. The anterior margin of the fore wings is also peculiar with an expanded costal lobe.

Figs 195–214, 286, 287, 318


**Description. Female.** Body length: 0.7–1.0 mm. Colour of body: melanic (Figs 195–198).


**Male.** similar to the female, but differs in the structure of the antenna (Fig. 200).


**Belgium:** **Holotype** of *Rosneta phryne* Debauche (Figs 209–211): 1♀, Heverlé, 1.vi.1941. **Paratypes** of *Rosneta phryne* Debauche (Figs 212–214): 3♀, the same data as the holotype; 1♀, Heverlé, 9.vii.1942; 1♀, Kessel-Loo, 27.viii.1945.

**Hungary:** Type of *F. tatnae* Szelényi (Figs 206–208): ♀ Magas Tátra, 22.viii.1934 (HNHM).

**Non-type material.** Hungary: 2♀, Örseg, Nemzeti Park, Lugosy Valley, 46.9°N, 16.45°E, 28.vi.2010, leg. Noyes JS. (SS) (OPPC0582, 0583); 7♀, Vas Co, Köseg, 47.36633°N, 16.52173°E, 26.vi.2010, leg. Hansson C. (SS) (OPPC0707, 0700, 0698,
Figures 195–201. *Fidiobia rugosifrons*: 195 habitus, dorsal view (OPPC0703) 196 habitus, lateral view 197 habitus, dorsal view (brachypterous form OPPC0474) 198 habitus, lateral view (brachypterous form) 199 antenna (♀) (OPPC0699) 200 antenna (♂) (OPPC0691) 201a wings (OPPC0576) 201b WIP.
Palearctic species of *Fidiobia*


**France:** 1♂, Puy de Dôme, Gergovie Plant., 45.71°N, 3.01°E, 16.vii.1977, leg. de V. Graham MWR (BMNH).

**Germany:** 2♀, Kiel, leg. Boness M. (BMNH).


**Biology.** reared from the eggs of *Hypera punctata* (F) (Coleoptera: Curculionidae) on *Triticum* sp. (Vlug 1995). This species prefers grassland habitats, e.g., meadows and glades.

**Distribution.** Asia: Central Altai, Kazakhstan, Central Asia (Kozlov 1978); Mongolia (Buhl 2004); North America: Canada (Evans and Peña 2005); USA [Pennsylv-ania (Crawford 1916); Indianapolis (Evans and Peña 2005)]; Central America: Panama (Evans and Peña 2005); Europe: Sweden, Norway (Buhl 1999a); Romania (Fabritius 1974); Moldavia (Kozlov 1978); Spain (Buhl 2000); Slovacia, Czech Republic (Popo-vicci and Buhl 2010). In our material we identify *F rugosifrons* from: Belgium, Estonia, France, Germany, Hungary and Romania (Fig. 318).

**Diagnosis.** *Fidiobia rugosifrons* is very close to *F rugosifronsoides* and *F roatai* because of the general habitus and the sculpture of the head, especially the frons. Based on this revision, the main characteristics of *F rugosifrons* are the totally sculptured internotaular area (unsculptured in *F roatai*, or partially sculptured in *F rugosifronsoides*), totally sculptured lateral pronotal area (sculptured only on the dorsal half in *F rugosifronsoides* and only in the dorsal third in *F roatai*) and A3 1.5 times as long as A4 (A3 1.8–2.0 times as long as A4 in *F roatai* and 1.2–1.3 times in *F rugosifronsoides*).
Comments. The sculptured internotaular area was mentioned by Crawford (1916) in the original description, “the head completely covered with sculpture as is mesonotum except for broad furrows”, and also by Kozlov (1978, 1987), Buhl (1999a) and

Palearctic species of *Fidiobia*

Popovici and Buhl (2010). Fouts (1924) added to the sculpture of mesonotum a new character, the ratio of A3/A4, mentioning “fourth antennal joint distinctly shorter than the third”. This antennal character was used later by Kieffer (1926) and Evans and Peña (2005). Fabritius (1974) considered that in *F. rugosifrons* A3 is two times as long as A4, but in his drawing (p. 294, Abb. 2) A3 appears to be longer. Szélényi (1941) described his new *Fidiobia tatrae* and separated it from *F. rugosifrons* based on the shape of antennomeres, but without details concerning this difference. Regarding the sculpture of the mesoscutum from the description of Szélényi, it is clear that the type of sculpture is the same as that of *F. rugosifrons*, but it is not clear if the internotaular space is entirely sculptured.

We located the type of *F. tatrae* in HNHM, but the specimen is essentially lost. On the card remain only the right antenna, clava of the left antenna, legs on the right side, and middle and hind legs from the left side (Figs 206, 207). Studying the antenna on the card and the drawing of Szélényi (1941), it can be observed that A3 is longer than A4, so we find no reason to consider *F. tatrae* different from *F. rugosifrons*. Based on this, we agree with Jansson (1956) who treated these two species as synonyms.

Debauche (1947), apparently unaware of *F. rugosifrons*, described a new species, *Rosneta phyrine*. Jansson (1956) presented informative drawings of the habitus and antenna (here can be observed the ratio between A3 and A4) in *Rosneta phyrine* and considered it a junior synonym of *F. rugosifrons*. By studying the type material of *Rosneta phyrine* stored in Institut royal des Sciences naturelles de Belgique, Bruxelles, we observed that the holotype was destroyed; on the points remain only the femora, tibiae and the tarsi from the middle and hind legs (left side), and from the middle leg (right side) and hind wing from the right side. The paratypes (some of them topotypic with the holotype) perfectly match our concept of *F. rugosifrons*.

Prior to this study, we believe that the name “rugosifrons” was used for a complex of species including *F. rugosifrons*, *F. rugosifronsoides* and *F. roatai*. Although *F. rugosifrons* was considered as a species with a wide distribution (Fig. 318), we found it only in Estonia, France, Germany, Hungary and Romania. For the first time, a specimen in the Romanian material was identified as a female with reduced wings and this reduction appears not to be a teratology, as it otherwise conforms to our concept of *F. rugosifrons*.

22. *Fidiobia rugosifronsoides* Popovici, Lahey & Talamas, sp. nov.
https://zoobank.org/071D11EE-A8C7-46A2-B6CB-78D53497B13F
Figs 215–222, 288, 289, 319

**Description. Female.** Body length: 0.9–1.0 mm. Colour of body (Figs 215, 216): bicoloured, head and mesosoma black to dark brown, metasoma brown with T1 and sometimes the proximal half of T2 lighter, almost pale in the Asian material.


Figures 215–222. *Fidiobia rugosifronsoides*: 215 habitus, dorsal view (OPPC0681) 216 habitus, lateral view (OPPC0593) 217 head, dorsal view 218 head, frontal view 219 antenna (♀) (OPPC0040) 220 mesosoma, dorsal view 221 mesosoma, lateral view 222a wings (OPPC0040) 222b WIP.


**Male.** unknown.

**Etymology.** This species is named for its similarity to *F. rugosifrons*.


**Distribution.** Estonia, Finland, Sweden, China, South Korea (Fig. 319).

**Biology.** unknown.

**Diagnosis.** *Fidiobia rugosifronsoides* is close to *F. rugosifrons*. The main differences between these two species consist of the sculpture of the area between the notauli (smooth in the posterior half in *F. rugosifronsoides* and totally sculptured in *F. rugosifrons*), in the ratio of A3 to A4 (A3 1.2 times as long as A4 in *F. rugosifronsoides* and A3 1.5 times as long as A4 in *rugosifrons*) and in the sculpture of the lateral pronotal area (entirely sculptured in *F. rugosifrons* and sculptured only in the dorsal half in *F. rugosifronsoides*).

**Comments.** In our material we found this species in Europe in Estonia (here, it is sympatric with *F. rugosifrons*), Finland and Sweden and in Asia in China and South Korea. Striation below the tegula and longitudinal sculpture below the mesofemoral depression are more evident in specimens from Europe than in the Asian material; the striae of T1 are longer and coarser in the European material; T1 and sometimes the proximal half
of T2 is lighter, almost pale in the Asian material and brown in the European material; notauli are broader, and the distance between the medial margin of the notaulus near the transscutal articulation is greater in the European material than in the Asian material.

23. *Fidiobia sashai* Popovici, Talamas & Lahey, sp. nov.
https://zoobank.org/CAA5728C-E3DE-4AF2-A884-08C407F8BBD8
Figs 223–227, 293, 320

**Description. Female.** Body length: 0.6 mm. Colour of body: xanthic, brown head and light brown mesosoma and metasoma (Figs 223, 224).


**Etymology.** This species is named after Oleksandr “Sasha” Varga, who collected the holotype specimen.

**Male.** unknown.


**Distribution.** Ukraine (Fig. 320).
Biology. unknown.

Diagnosis. *Fidiobia sashai* is the only Palearctic species of the genus with an incomplete transscutal articulation, which is visible only laterally. It is superficially similar to some brachypterous specimens of *F. hofferi*, but it differs by the incomplete transscutal articulation and the absence of notauli. In *F. hofferi* the transscutal articulation is complete and the notauli are present.

24. *Fidiobia striatitergitis* (Szabó, 1962)
Figs 9, 10, 13, 16, 19, 21, 25, 29, 30, 33, 36, 228–240, 282, 321


*Fidiobia gordoni* Popovici and Buhl 2010: 1137.

*Fidiobia striatitergitis*: Kamalanathan et al. 2019: 471, 472 (type information, generic transfer)

Description. Females (Figs 228, 229). Length of body: 1.1–1.3 mm. Colour of body: bicoloured, head and mesosoma dark brown, T1 light brown, T2–T5 brown, T6 brown becoming lighter brown at apex (Fig. 228).


Metasoma (Figs 36a, b, 228): Tergites posterior of T2 exposed and clearly visible. Shape of T1: subrectangular. Colour of T1: reddish-brown. Lateral setae of T1: absent. Colour of T2: brown. Shape of T2: transverse or at most as long as wide. Anterior pits of T2: distinctly separated (Fig. 36a). Sculpture of T2, lateral to anterior pits of T2: strigose on most the length of T2. Colour of T3–T6: T3–T5 the same as T2, apex of T6 lighter.

Male. We did not study the male of this species, the only known male being the type of this species described under the name of *Isolia striatitergitis* Szabó. High quality photos of the male are presented in Veenakumari et al. (2019). It is similar to the female, except the antenna is almost filiform.

Figures 228–234. *Fidiobia striatitergitis*: 228 habitus, dorsal view (OPPC0710) 229 habitus, lateral view 230 head, frontal view 231 head, dorsal view 232a antenna 232b sensillar formula 233 head and mesosoma, lateral view 234a wings (OPPC0725) 234b WIP.

Distribution. Hungary (Szabó 1962), Greece (Fig. 321).

Biology. The host is unknown. Based on the collection data, this species prefers wet habitats with lush vegetation beside rivers.

Diagnosis. *Fidiobia striatitergis* may be recognized by the reticulate-rugose mesocutellar disc, strigose T2, metapleural carina posterodorsally prolonged into a strong tooth, lateral propodeal carina and metasomal depression with no foamy structures.

Comments. *Fidiobia striatitergis* was originally described in *Isolia* Förster based on a single male specimen (Szabó 1962). Veenakumari et al. (2019) transferred *Isolia*
striatitergitis to *Fidiobia*. Popovici and Buhl (2010) described this species as *F. gordoni*, which we here recognize as a junior synonym of *F. striatitergitis*. Although Szabó’s material is represented by a single male and the material of Popovici and Buhl (2010) consists only of females, the main apomorphies of this species (reticulate-rugose mesoscutellar disc, substriate T2, metapleural carina posterodorsally prolonged into a strong tooth, lateral propodeal carina and metasomal depression with no foamy structure) are not sexually dimorphic. Therefore, we have confidence that these specimens are conspecific.

25. *Fidiobia synergorum* (Kieffer, 1921)
Figs 241–252, 294, 295, 322

* Fahringeria synergorum* Kieffer, 1921: 69; Kieffer 1926: 844; Maneval 1940: 117; Masner and Huggert 1989: 69.


**Description. Female.** Body length: 0.8–0.9 mm. Colour of body: melanic (Figs 241, 242).


**Metasoma** (Figs 241, 251): posterior of T2 some or all tergites may be retracted under T2. Shape of T1: subrectangular. Colour of T1: brown. Lateral setae of T1: 2 pairs. Colour of T2: brown. Shape of T2: longer than wide. Anterior pits of T2: distinctly separated. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T6: T3–T5 the same as T2, T6 lighter.

**Male.** similar to female, but different in the structure of the antenna (Fig. 246).


UKRAINE: 8♀, Transcarpathia reg., Tyachiv distr., 6.5 km N of Mala Ugolka, 48.2609°N, 23.6169°E, 12–31.v.2015, beech forest, leg. Varga O. (MT),
Palearctic species of *Fidiobia*

Figures 241–247. *Fidiobia synergorum*: 241 habitus, dorsal view (OPPC0217) 242 habitus, lateral view 243 head and mesosoma, dorsal view 244 mesosoma, lateral view 245 antenna (♀) (OPPC0800) 246 antenna (♂) (OPPC0798) 247 wings (OPPC0824) 247b WIR
Figures 248–252. Holotype of *Platyllotropa gallicola* Szelényi: 248 habitus, dorsal view 249 habitus, lateral view 250 head and mesosoma, dorsal view 251 body without wings 252 data labels.

Distribution. Austria (Kieffer 1926), Greece, Hungary, Norway, Slovakia, Ukraine (Fig. 322).

Biology. This species was reportedly reared from *Synergus gallepomiformis* Fonscolombe (Hymenoptera: Cynipidae) on *Quercus* sp., *Biorhiza pallida* Olivier (Hyme-
noptera: Cynipidae) on *Quercus* sp., and *Aphelonyx cerricola* Gir. (Hymenoptera: Cynipidae) (Vlug 1995), but a direct connection among *F. synergorum* and these cynipids was not established through dissections. This species seems to prefer forested habitats rather than grassland. In Ukraine it was collected in beech and mixed forests and the most effective methods were the trunk mounted trap and Malaise trap.

**Diagnosis.** *Fidiobia synergorum* is conspicuous because the body is strongly depressed dorsoventrally, the transepisternal line is straight and almost complete (Fig. 244), T1 is strongly transverse, almost rectangular and the median carina between the lateral propodeal carinae is absent (Fig. 295). *Fidiobia synergorum* may be confused with *F. hispanica* but can be easily separated from that species by the different number of antennomeres (nine in *F. synergorum* and ten in *F. hispanica*), transepisternal line (absent, or at most as a trace in *F. hispanica*) and by the median carina between the lateral propodeal carinae (present in *F. hispanica*).

**Comments.** In most *Fidiobia* with a 9-merous antenna, T1 is trapezoidal, whereas a transverse and almost rectangular T1 is characteristic for species of *Fidiobia* with 10-merous antennae. The knob of the submarginal vein of the fore wing is visibly curved downward as in species of *Acerotella* Masner. Specimens belong to this species were observed with the 8-merous teratological antennae (symphysis – A3–A4) (Popovici and Buhl 2010). In the Palearctic region, a similarly depressed body can be found in *Allotropa helenae* (Kozlov).

### 26. *Fidiobia tripotini* Popovici & Masner, sp. nov.

https://zoobank.org/A8A57C94-6441-4F45-969F-7A4EED9E4FB3
Figs 253–261, 323

**Description. Female.** Body length: 0.9–1.1 mm. Colour of body: bicoloured, head and mesosoma medium to dark brown, metasoma light to medium brown with T1 and sometimes apex of T6 lighter (Figs 253–255).


**Mesosoma** (Figs 259, 260). Colour of mesosoma: dark brown. Mesosoma: weakly compressed dorsoventrally. Pronotum in dorsal view: present mostly as lat-


**Etymology.** This species is named after Pierre Tripotin, collector of the holotype specimen and a tremendous friend of Popovici OA. Noun in the genitive case.

**Male.** unknown.
Figures 253–261. *Fidiobia tripotini*: 253, 254 habitus, dorsal view (Holotype) 255 habitus, lateral view 256 head, dorsal view 257 head, lateroventral view 258a antenna (♀) (OPPC0735) 258b sensillar formula 259 mesosoma, dorsal view 260 mesosoma, lateral view 261a wings (OPPC0735) 261b WIP.


Distribution. South Korea (Fig. 323).

Biology. unknown.

Diagnosis. This species can be recognized by the presence of a malar sulcus, the short transepisternal line and T2 which is elongate and longer than wide. All other Palearctic Fidiobia with 10-merous antennae have T2 wider than long and the malar sulcus absent.

Comments. Fidiobia tripotini is the only known species of the genus with a malar sulcus. The malar sulcus is not flanked by striation, a state that is found only in Orwellium Johnson, Masner and Musetti among extant Platygastridae. Other extant platygastrids with a malar sulcus, e.g. Metaclisis Förster, have facial and malar striae.

27. Fidiobia vanharteni Buhl, 2010
Figs 262–272, 324


Description. Female. Body length: 0.7–0.8 mm. Colour of body: melanic (Figs 262–264, 268, 269).


Male, unknown.

Material examined. 18♀. UAE: Holotype ♀, (Figs 263–267) (ZMUC).


Distribution. Yemen, UAE (Fig. 324).
Diagnosis. *Fidiobia vanharteni* is relative morphologically similar to *F. hofferi* because of fore wings with short, hardly visible marginal fringe, presence of epito- rular carina and metascutellum visible in dorsal view, but it can be recognized by its light coloration, faintly banded fore wing (uniformly hyaline in *F. hofferi*), and OOL slightly shorter or equal to the ocellar diameter (OOL is equal to about 2 OD in *F. hofferi*).

28. *Fidiobia vladlubomiri* Popovici & Masner, sp. nov.
https://zoobank.org/4C7658D5-B4E8-4ECE-9B50-6AFC1661EFA1
Figs 273–281, 283, 325

Description. Female. Body length: 0.8–1.0 mm. Colour of body: melanic (Fig. 273).

Palearctic species of *Fidiobia*

Figures 273–281. *Fidiobia vladlubomiri*: 273 ♀, habitus, dorsal view (OPPC0331) 274 ♂, habitus, dorsal view (OPPC0502) 275 head, dorsal view 276 head, frontal view 277a antenna (♀) (OPPC0313) 277b sensillar formula 278 antenna (♂) (OPPC0502) 279 mesosoma, dorsal view 280 mesosoma, lateral view 281a wings (OPPC0313) 281b WIP.

Metasoma (Fig. 273): Tergites posterior of T2 exposed and clearly visible. Shape of T1: subrectangular. Colour of T1: brown. Lateral setae of T1: numerous. Colour of T2: brown. Shape of T2: transverse. Anterior pits of T2: merging together in a deep and transverse anterior depression. Sculpture of T2, lateral to anterior pits of T2: absent. Colour of T3–T6: the same as T2.

Male (Fig. 274). Similar to female; differing in the structure of the antenna (Fig. 278).

Etymology. Patronym, named for the son of Ovidiu Popovici – Vlad Lubomir.


Distribution. Japan, Laos, South Korea (Fig. 325).

Biology. unknown.

Diagnosis. Fidiobia vladlubomiri is a distinct species that can be recognized by wide, deeply incised notauli with the lateral margins located medial to the axillular
Palearctic species of Fidiobia

carina, meeting the scutoscutellar sulcus. The transepisternal line is nearly complete and sigmoid in shape. The dorsal mesopleural area has some transverse striae, and between these striae and the transepisternal line there is a large unsculptured area (in F. striatitergitis and F. nipponica this area is transversely striate). The dorsal metapleural area is covered with dense silvery setae that easily distinguish F. vladlubomiri from F. striatitergitis and F. nipponica. The papillary sensillum located at the apex of the distal clavomere (Fig. 277b) makes F. vladlubomiri unique among the known Palaearctic species of Fidiobia.

Figures 298–300. Geographical distribution of: 298 F. bohemia 299 F. brevialis 300 F. brevinotaula
(Blue area—data from Veenakumari et al. 2018. Red area—our data).
(Blue area–data from Szabó 1962. Red area–our data).
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References

Palearctic species of *Fidiobia* 139


Buhl PN (1999b) Platygastridae (Hymenoptera) species of a *Juniperus thurifera* L. forest of Los Monegros region (Zaragoza, Spain). Zapateri, Revista aragonesa de Entomologia 8: 11–42.


Description of a Neotropical gall inducer on Araceae: 
*Arastichus*, gen. nov. (Hymenoptera, Eulophidae) 
and two new species

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Abstract

A new genus of a Neotropical gall inducing tetrastichine eulophid on Araceae is described and confirmed using Ultraconserved Elements (UCE) phylogenomic data. *Arastichus* Gates, Hanson, Jansen-González & Zhang, *gen. nov.*, includes two new species and one species transferred from *Aprostocetus* Westwood: *A. capipunctata* Gates, Hanson, Jansen-González & Zhang, *sp. nov.*, *A. gallicola* (Ferrière), *comb. nov.*, and *A. gibernau*, Gates, Hanson, Jansen-González & Zhang, *sp. nov.*

Keywords

Chalcidoidea, *Philodendron*, Phytophagy, Tetrastichinae, *Thaumatophyllum*
Introduction

The Chalcidoidea is a large and diverse superfamily with broad biological diversity (Heraty et al. 2013), and with estimates of over 500,000 species (Noyes 2019) on Earth. Although primarily entomophagous, many phytophagous forms are known, among these the gall inducers that deform plant tissue in order to complete their development. The biology of gall inducers and the evolution of gall induction in Chalcidoidea have been reviewed recently (LaSalle 2005). Gall induction has evolved in seven different families of Chalcidoidea, with at least 16 independent origins both from entomophagous and phytophagous ancestors (LaSalle 2005; Böhmová et al. 2022). This includes the Eulophidae, the largest and most diverse chalcidoid family including over 4,300 species in 332 genera (Noyes 2019; Rasplus et al. 2020). The diversity of gall inducing eulophids is highest in the Australian Opheliminae and the cosmopolitan Tetrastichinae, the latter is a large and diverse subfamily with 15 genera recorded as phytophagous species (Kim et al. 2004, 2005; Mendel et al. 2004; LaSalle 2005; Kim and LaSalle 2008; Rasplus et al. 2011; Fisher et al. 2014). Overall, knowledge of the specific biology of gall associated tetrastichines is minimal but falls into three categories: parasitoid of gall inducer, inquiline, or gall inducer. LaSalle (2005) divides gall-associated tetrastichines into two groups: (1) the Australian inducers that gall Myrtaceae, and (2) mostly Neotropical groups that are often larger and more heavily sclerotized.

LaSalle (1994) records seven plant families serving as hosts for gall inducing Tetrastichinae: Araceae, Chenopodiaceae, Euphorbiaceae, Fabaceae, Myrtaceae, Myrsinaceae, and Solanaceae. Additionally, tetrastichines have also been recorded as gall inducers from Casuarinaceae (Fisher et al. 2014), Sapotaceae (Singh et al 2022), and Smilacaceae (Gates et al. 2020). In evaluating the gall-inducers associated with the Araceae (Alismatales) in general, focusing specifically on Hymenoptera, we note that very few taxa are known to be associated with this family, particularly as suspected phytophages (Table 1).

Here we describe a new genus of Neotropical tetrastichines inducing galls on Thaumatophyllum and Philodendron (Araceae), Arastichus Gates, Hanson, Jansen-González & Zhang, gen. nov. (Fig. 1). We describe two new species: A. capipunctata Gates, Hanson, Jansen-González & Zhang, sp. nov., and A. gibernau, Gates, Hanson, Jansen-González & Zhang, sp. nov. Additionally, we transfer Trichaporus gallicola Ferrière to Arastichus, comb. nov., from its current placement in Aprostocetus Westwood, and provide a redescription along with designation of lectotype.

Materials and methods

Collection and identification

Mature infrutescences of Thaumatophyllum bipinnatifidum and Philodendron radiatum were cut from the plant in the laboratory, or mass reared in bags hung on clothes-
Description of Arastichus (Eulophidae) and two new species

As the spathe was still closed in most of the infructescences, careful incisions with a knife were used to expose the fruits beneath. A few fruits were dissected under a stereomicroscope to ensure they had galls with pupae or adults inside. The selected infructescences were then put in individual organdy bags (40 cm × 30 cm) for wasp emergence. Emerging wasps were collected and stored in 70% EtOH.

Ethanol-preserved specimens were dehydrated through increasing concentrations of ethanol and transferred to hexamethyldisilazane (HMDS) (Heraty and Hawks 1998) before point-mounting. A Nikon SMZ1500 stereomicroscope with 10× oculars (Nikon C-W10X/22) and a Chiu Technical Corporation Lumina 1 FO-150 fiber optic light source were used for point-mounted specimen observation. Mylar film was placed over the ends of the light source to reduce glare from the specimen. Scanning electron microscope (SEM) images were taken with a Hitachi TM3000 (Tungsten source). Body parts of a disarticulated specimen were affixed to 0.1 mm minuten pins with Loctite Ultra Gel super glue. These were then adhered to a 12.7×3.2 mm Leica/Cambridge aluminum SEM stub by a carbon adhesive tab (Electron Microscopy Sciences, #77825-12). Stub-mounted specimens were sputter coated with gold-palladium using a Cressington Scientific 108 Auto from at least three different angles to ensure complete coverage (~20–30 nm coating). One set of wings was removed and slide-mounted in polyvinyl alcohol prior to imaging; wings were photographed with a Olympus SC-100 digital camera attached to a Olympus BX43 light microscope and processed using

Table 1. Hymenoptera associated with Araceae.

<table>
<thead>
<tr>
<th>Family (Subfamily)</th>
<th>Species</th>
<th>Plant</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eulophidae (Tetrastichinae)</td>
<td>Arastichus gallicola (Ferrière)</td>
<td>Philodendron sp. Schott</td>
<td>DeSantis 1979</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. undulatum Engler</td>
<td>Ferrière 1924</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. tweedieanum Schott (as P. dubium (Chodat and Vischer))</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Thaumatophyllum bipinnatifidum (Schott ex Endl.) (as P. petraea Chodat and Vischer)</td>
<td>This study</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. solimosoense (A.C.Sm.) Sakar., Calazans &amp; Mayo</td>
<td>This study</td>
</tr>
<tr>
<td>Eulophidae (Tetrastichinae)</td>
<td>Arastichus capipunctata sp. n.</td>
<td>Philodendron radiatum (Schott)</td>
<td>This study</td>
</tr>
<tr>
<td>Eulophidae (Tetrastichinae)</td>
<td>Arastichus gibernau sp. n.</td>
<td>Philodendron hederaceum var. oxycardis Schott</td>
<td>This study</td>
</tr>
<tr>
<td>Eurytomidae (Eurytominae)</td>
<td>Prodecotoma philodendri Ferrière</td>
<td>Philodendron hederaceum (Jacq.) (as P. oxycardis (Schott))</td>
<td>DeSantis 1979</td>
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<tr>
<td></td>
<td></td>
<td>P. tweedieanum (as P. dubium)</td>
<td>DeSantis and Fidalgo 1994 Ferrière 1924 Gibernau 2002</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T. solimosoense (A. C. Sm.) (as P. solimosoense)</td>
<td>Lotfalizadeh et al. 2007 Perioto and Lara 2019</td>
</tr>
<tr>
<td>Eurytomidae (Eurytominae)</td>
<td>Aranedra millsi Burks</td>
<td>Philodendron sp.</td>
<td>Burks 1971 DeSantis 1979</td>
</tr>
<tr>
<td>Braconidae (Doryctinae)</td>
<td>Monitoriella elongata Hedqvist</td>
<td>P. radiatum</td>
<td>Infante et al. 1995 Shimbori et al. 2011</td>
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</tbody>
</table>
analySIS getIT 5.2 (Olympus Soft Imaging Solutions). The habitus image was captured using an EntoVision Imaging Suite, which includes a firewire JVC KY-75 3CCD digital camera mounted on a Leica M16 zoom lens via a Leica z-step microscope stand.

**Figure 1.** Illustration of the lifecycle of *Arastichus gallicola* with its host plant, *Thaumatophyllum solimo-sense* (Areaceae). Illustrated by Taina Litwak.
The program Cartograph 5.6.0 (Microvision Instruments, France) was used to merge an image series into a single in-focus, composite image. Lighting was achieved using techniques summarized in Buffington et al. (2005), Kerr et al. (2008), and Buffington and Gates (2008). When possible, male and female genitalia were extracted, cleared with KOH 10% and temporarily mounted in glycerin for imaging. Genitalia were photographed using the same setup as for wings (indicated above). These and SEM images were used for the elaboration of schemes of each genitalia using GIMP 2.8.10.

Morphological terminology follows Gibson (1997), while the surface sculpture follows Harris (1979). Several measurements were taken, including: body length, in lateral view from the anterior projection of the face to the tip of the metasoma; head width through an imaginary line connecting the farthest lateral projection of the eyes; head height through an imaginary line from the vertex to the clypeal margin bisecting both the median ocellus and the distance between the toruli; malar space, in lateral view between the ventral margin of the eye and lateral margin of the oral fossa; eye height in anterior view; vertex bristle in anterior view; mesoscutum and scutellum, in dorsal view through imaginary, median transverse and longitudinal lines; marginal vein, the length coincident with the leading fore wing edge to the base of the stigmal vein; stigmal vein, the length between its base on the marginal vein (M) and its apex; postmarginal vein (PMV), the length from the base of the stigmal vein (S) to its apex on the leading fore wing edge. Metasomal sclerites were measured dorsally along the midline. Abbreviations used: A1–n (anellus), F1–n (funicular segment), LOL (lateral ocellar line), OOL (ocellar ocellar line), POL (posterior ocellar line), SMV (submarginal vein), A (anellus), C (clava), F (funicle), MPS (multiporous mlate sensilla), Gt1–n (gastral tergites), Gs1–n (gastral sternites). The antennal formula consists of: scape, pedicel, anelli, funiculars, clava.

Specimens are deposited in the following collections: ANIC (Australia National Insect Collection, Canberra, Australia), BMNH (The Natural History Museum, London, England), CNCI (Canadian National Collection, Ottawa, Canada), CNIN (National Collection of Insects – The National Autonomous University of Mexico, Mexico City, Mexico), MNHN (The National Museum of Natural History, Paris, France), MZUCR (Museum of Zoology – University of Costa Rica, San José, Costa Rica), MZUSP (Museum of Zoology – University of São Paulo, São Paulo, Brazil), USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA).

Molecular analysis

One specimen each of A. gallicola and A. capipunctata were extracted, amplified, and sequenced at the Laboratories of Analytical Biology (LAB) at the Smithsonian Institution’s National Museum of Natural History (NMNH, Washington, DC, USA). A modified Ultraconserved Elements (UCE) protocol was used (Faircloth et al. 2012; Branstetter et al. 2017) along with the HymV2P probe set to enrich the UCE loci, (Branstetter et al. 2017). The library was sent to Admera Health (South Plainfield, NJ) and sequenced on an Illumina HiSeq 4000 (150-bp paired-end, Illumina Inc., San Diego, CA, USA). Additional eulophid UCE sequences were supplemented from Cruaud et al. (2019) and Rasplus et al. (2020).
PHYLUCE v1.7.0 (Faircloth, 2015) was used for UCE processing. SPAdes v3.14.0 (Bankevich et al. 2012) was used to align the contigs, sequences were aligned using MAFFT v7.490 (Katoh and Toh 2008), and trimmed using Gblocks v0.91b (Castresana 2000) with the following settings: b1 = 0.5, b2 = 0.5, b3 = 12, b4 = 7. A 50% complete matrix was used for downstream phylogenomic analysis. Additionally, fragments of legacy markers (COI, 28S, and CytB) were extracted from the UCE contigs using PHYLUCE. Trimmed reads for the newly generated sequences in this study are available from the National Center for Biotechnology Sequence Read Archive (SRA; BioProject ID PRJNA827143), and Sanger markers are available on GenBank (Suppl. material 1).

Phylogenomic analysis was conducted under the maximum likelihood (ML) criterion with IQ-TREE v2.1.1 (Minh et al. 2020), partitioning based on loci and with the best models of nucleotide substitution selected in ModelFinder with “-m MFP” (Kalyaanamoorthy et al. 2017). To assess nodal support, we performed a Shimodaira-Hasegawa approximate likelihood-rate test (SH-aLRT, Guindon et al. 2010) with 1000 replicates using the “-alrt” flag, and 1000 ultrafast bootstrap replicates (UFBoot2; Hoang et al. 2017) using “-bb”. Only nodes with support values of SH-aLRT ≥ 80 and UFBoot2 ≥ 95 were considered robust.

Results

The 50% UCE matrix consisted of 567 loci, with *A. capipunctata* and *A. gallicola* having 1715 and 1802 UCE loci recovered, respectively. The topology recovered was largely identical to that of Rasplus et al. (2020). The new genus *Arastichus* was recovered within the subfamily Tetrastichinae with strong support (Fig. 2). *Arastichus* is within the *Aprostocetus* group sensu Rasplus et al. (2020), and the sister to *Neohyperteles* DeSantis with strong support (Fig. 2).

**Arastichus** Gates, Hanson, Jansen-González & Zhang, gen. nov.
https://zoobank.org/6DB405D8-4660-4698-A9B6-1950816E86DF
Figs 3–25

**Type species.** *Arastichus gallicola* (Ferrière).

**Diagnosis.** Vertex with single erect seta mesad to eye margin, ~0.5× eye height (Fig. 10); vertex depressed posteriad and laterad lateral ocelli (Figs 12, 22); toruli positioned above middle of face, 1–1.5× torular diameters from median ocellus (Figs 10, 21, 24); intrascrobal carina step like in lateral view with V-like carinae diverging to lateral margins of median ocellus (Figs 12, 22); antennal formula 11242 (Fig. 14) or 11342 in *A. capiculata*. A1 ~1.5× wider at apex rather than base (note: often appears subdivided, representing fusion of two segments) wedge-like in lateral view, longest ventrally; ventral plaque present in male scape (Figs 5, 7, 9); clypeus bilobed, lobes apically truncate; gena ventrally extended beyond oral fossa/base of mandible (Figs 10, 21, 24); mesosoma shiny dorsally (Fig. 23); scutellum lacking submedian grooves (Figs 16, 23); petiole
membranous ventrally; a tuft or sometimes one seta(e) anterad mesocoxa (Fig. 9); propodeal spiracles large, ~0.3× length propodeum; distinct, suberect setation on mesal surface of procoxa and metacoxa (Figs 8, 9), Gt 6 with spiracular rim elevated (Fig. 19).

*Arastichus gallicola* was first described by Ferrière (1924) as *Trichaporus gallicola*, which was then transferred to *Exurus* Philippi by Costa Lima (1959a). LaSalle (1994) synonymized *Exurus* with *Aprostocetus*, through its type species *E. colliguayae* Philippi. He was hesitant about the status of *A. gallicola* (Fig. 3) as he was not able to examine any type specimens, but commented that it is quite distinct and warranted its own genus. As Ferrière did not designate a holotype, we hereby designate the top left specimen (female) on the pin with three other specimens as the lectotype (Fig. 3). The degree of morphological variation seen in *Aprostocetus* makes it difficult to characterize consistently using few characters; however, according to LaSalle (1994), most species have the SMV with ≥ 3 seta, propodeal spiracle partially covered by overhanging lobe of callus, and one cercal setae distinctly longest and sinuate or curved. Although *Arastichus* shares these diagnostics, several additional apomorphies set it apart from *Aprostocetus* (as noted in the diagnosis above).

**Description. Coloration:** Female. Length 3.8–5.2 mm. Head, antennae, body, coxae, and legs yellow or brown (Figs 3–9). Tegula pale golden. Pronotum either completely brown, or yellow except for the anterolateral panel. Ventral mouthparts and tarsomeres pale yellow. Female fore wing with soft opaque area at basal and cubital

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**Figure 2.** Maximum likelihood reconstruction of Eulophidae phylogeny inferred from 50% complete matrix of 567 Ultraconserved Elements (UCE) loci. Support values shown as SH-aLRT/UFBoot2. All nodes except for Tetrastichinae collapsed, with the two major genus groups (*Aprostocetus* group and *Tetrastichus* group) highlighted, and *Arastichus* in red.
folds, disc hyaline (Fig. 4). Male fore wing with opaque base of cubital and basal folds; disc with soft opaque pattern (Fig. 5).

**Head:** Surface rugulose or umbilicately punctate dorsally, laterally, and anteriorly, 1.3–1.6× as broad as high. Supraclypeal area concave, glabrous, asetose (Figs 10, 21, 24), extending to toruli; lower tentorial pits minute. Genal carina present, extending to lower third of eye posteriorly (Figs 10, 13). Torulus with dorsal margin positioned at lower ocular line; intertorular space punctate, obtusely pointed; scrobal depression margined laterally, margin fading dorsally, reticulate with fine irregular rugae and with median carina between depressions in ventral half (Fig. 10). Eyes setose, seta sparsely distributed and very short. Mandible tridentate with apical and middle teeth acute, basal tooth broad and rounded (Fig. 21). Clypeus emarginate in step-like manner (Fig. 21), medially produced. Posterior surface of head without postgenal lamina, postgenal grooves slightly ridged, slightly convergent ventrally, extending to upper margin of hypostomal bridge; dorsal margin of lateral foraminal plate obliterated; subforaminal plate absent; postgenal sulci distinct; postgenal bridge glabrous (Fig. 11). Antenna (Figs 14, 15) with scape broadest medially, coarsely imbricate. Pedicel triangular in
lateral view, narrowed ventrally; anelli (two in all species except *A. capipunctata*, which has three) transverse, glabrous; F1 chalice-shaped, imbricate in basal half (Fig. 14); funicle with each segment fusiform, longer than broad, apically truncate with two rows.
of MPS and sparse, semi-erect setation; F5–6 fused, apex with radially asymmetric sensillar area (Fig. 14).

**Mesosoma:** Surface smooth, rugulose or umbilicate with interstices alveolate. Pronotum in dorsal view 2.2–3.3× as broad as long. Mesoscutal midlobe 1.0–1.1× as broad as long; notaules complete, clearly indicated (Fig. 16). Scutellum 1.2–1.3× as long as broad at its widest; broadly convex dorsally. Scutellum distinctly overhanging dorsellum. Sub-lateral prepectal concavity shallow; epicnemium flattened, with superficial submedial, shallow depressions to receive procoxa, these separated by low carina connecting to epinomial carina ventrally. Procoxa imbricate anterobasally and medially, flat, low diagonal carina separating this area from umbilicately punctate anteroventral and lateral portion of procoxa; mesocoxa rugulose to imbricate; mesocoxal foramina narrowly open posteriorly; metacoxa rugulose to imbricate. Metapleuron and lateral areas of propodeum shallowly umbilicate, propodeum vaguely rounded laterally (Fig. 20), bordered laterally by reticulate sculpture overlain with umbilicate punctuation; spiracle situated about 1/3 its greatest diameter from dorsellum, median channel with series of distinct transverse carinae (Fig. 20). Fore wing hyaline, venation whitish, setae pale brown, evenly distributed; PMV 1.0–1.1× of V and S 0.7–0.8× of M. Basal cell delimited by cubital and basal folds; speculum present; disc uniformly setose; number of dorsal setae on submarginal vein: female: 2–3, male: 1–4. Parastigma not swollen; marginal vein constricted near its base after parastigma and three times as long as stigmal vein. Stigmal vein at an angle of 20°–30° in relation to marginal vein. Uncus small, not extending far from stigma. Postmarginal vein reduced, less than 1/4 of stigmal vein (Figs 4, 5). Hind wing disc evenly setose. with apex of vein (at hamuli) not swollen or knobbed but darkened, with three hamuli.

**Metasoma:** Petiole 0.3–0.4× as long as broad in dorsal view, laterally protuberant, connected by dorsal transverse carina. Gaster ovate in lateral view; all terga with finely imbricate sculpture, evenly setose, setae fine and erect; Gt1 depressed behind petiole, setose; Gs1 fused with petiole (Fig. 19); syntergum short, setose; third valvula setose apically, arranged radially and curved.

**Genitalia:** Female: First valvifer falcate 1/4–1/8 of ovipositor total length, articulates with T9 and the second valvifer very near each other, on its proximal end; second valvifer broad, sickle-shaped; second valvula 3/4 of ovipositor length, with row of 3–4 spaced setae at apical half; third valvula 1/3–1/5 of total ovipositor length (Fig. 26). Male: Phallobase cylindrical, 1.5–2.0× as long as wide, paramere pointed with one apical seta, 1/5× the length of phallobase. Volsella 1/2–1/3 of paramere length. Digitus dorsoventrally flattened, bean-shaped in either ventral or dorsal view, 2–3× as long as wide, bearing a single apical digital spine. Aedeagus cylindrical, dorsoventrally flattened, pointed or round at apex (Fig. 27).

**Etymology.** Name from the host plant family, Araceae. Gender masculine.

**Biology.** Ferrière (1924) first described *Arastichus gallicola* (as *Trichoporus gallicola*) and defined the species as gall inducer on pistilate flowers of *Philodendron selloum* (now a synonym of *Thaumatophyllum (Philodendron) bipinnatifidum* (Mayo 1991) (Fig. 3). Gibernau et al. (2002) described the galls of *A. gallicola* on flowers of *T. solimoesense* and reported it as a seed predator. Recently, a more detailed study of the developmental biology of *A. gallicola* discards seed predation and supports the idea that this species is a gall inducer specialized on ovaries of *T. bipinnatifidum* (SJG, unpublished).
Female wasps of *A. gallicola* oviposit during the period of anthesis which lasts 24–48 hours, when the inflorescence spathe is open and leaves the hundreds of pistilate flowers accessible to pollinators and female *Arastichus* (Gibernau et al. 2002). Once anthesis ends the spathe closes and the space between the spathe and the inflorescence fills with a liquid, often trapping and killing the female wasps inside.

Time of development can vary from one to four months in *Arastichus gallicola*. Once the infrutescence attains maturity, the spathe develops an encircling dehiscent line at its base and falls, uncovering the orange fruits and galls. Exposure of galls to light and outer atmosphere might trigger adult wasp emergence from the galls, which is done by chewing through each gall wall. A single wasp develops per gall with up to six galls developing in a single fruit. It is possible to find infrutescences and/or fruits containing only seeds, combinations of seeds and galls, or only galls (Fig. 1).

Although we have detailed information about gall induction only in *A. gallicola*, it is possible that the other two species of *Arastichus* are also gall inducers rather than seed predators. Examination of collected material for *A. gibernau* and *A. capipunctata* indicates that the biology of these species should not be very different from that of *A. gallicola*.

The eurytomid *Prodecatoma philodendri* is associated with the galls of *Arastichus gallicola* and *A. gibernau*. Ferrière (1924) reported that *Prodecatoma* were phytophagous, and oviposits from the outside when the spathe is closed and *Arastichus* galls are in the process of formation (Gibernau et al. 2002; SJG pers. obs.). When examining the cavities from which *Prodecatoma* adults emerge, a series of tunnels communicate with adjacent *Arastichus* galls. These attacked galls contained dismembered body parts of *Arastichus* pupae, indicating that *Prodecatoma* larvae might consume several of them along with some gall tissue (Gibernau et al. 2002; SJG pers. obs.); this is in line with the fact that the adult *Prodecatoma* is about 4–5 times larger than the *Arastichus* adult. Thus, taken all together, *P. philodendri* is likely entomophytophagous, a common mode of feeding within Eurytomidae.

It is difficult to estimate the taxonomic breadth of the relationship between *Arastichus* and Araceae. *Philodendron* is traditionally subdivided in three subgenera: *Meconostigma*, *Philodendron* and *Pteromischum*, but members of *Meconostigma* have been recently recognized as a distinct genus *Thaumatophyllum* Schott (Sakuragui et al. 2018). *Arastichus* has been found in species belonging to *Thaumatophyllum* (*T. bipinnatifidum*, *T. solimoesense*), and in the subgenus *Philodendron* (*P. radiatum*). SJG has collected what seem to be female *Arastichus* body parts from inside closed spathes of *P. cordatum* and *P. curvilobum* in Brazil. Further studies and more extensive collecting are needed to determine the degree of species-specificity and to determine whether *Arastichus* is present in the subgenus *Pteromischum* as well.

**Key to Species of *Arastichus***

1. Mesoscutum bilobed at posterior margin (Fig. 23). Face with numerous large punctures (Figs 21, 22). Female body (excluding legs and lower face) completely brown (Fig. 6)………………………………………………………….. *A. capipunctata* sp. nov.

   - Mesoscutum straight or slightly emarginate at posterior margin (Fig. 16). Face with at most a few faint, widely spaced punctures (Figs 10, 24). Female head and thorax extensively yellow (Figs 4, 8)………………………………………………………….. 2
Posterior corner of metapleuron with circular fossa that is at least half as wide as propodeal spiracle (Fig. 25, arrow). Vertexal suture rounded where it curves down along the inner eye margin (Fig. 24)....................A. gibernau sp. nov.

Posterior corner of metapleuron without a noticeable fossa, or with an elongate depression (Fig. 4). Vertexal suture angulate or rounded where it reaches the inner eye margin (Fig. 10)...............................A. gallicola (Ferrière)

Arastichus capipunctata Gates, Hanson, Jansen-González & Zhang, sp. nov.
https://zoobank.org/3F50B966-83A2-456F-9D56-52C800D8C907
Figs 6, 7, 21–23

Diagnosis. Arastichus capipunctata can be distinguished from all other known species through the bilobed mesoscutum at the posterior margin (Fig. 23), and the numerous large punctures on the face (Figs 21, 22). The coloration of both males and females are uniformly brown (Figs 6, 7). Females have three anelli.

Material examined. Holotype COSTA RICA • [1F]; Guanacaste 9km S Santa Cecilia, Estación Biológica Pitilla, 600 m 18.XII.2010. L. Chavarria leg.; USNMENT01788075; deposited in USNM. Paratypes: [44F, 26M]; same information as holotype; USNMENT01829180–250; USNM. [4F, 4M]; same information as holotype; ANIC. [4F, 4M]; same information as holotype; BMNH. [4F, 4M]; same information as holotype; CNCI. [4F, 4M]; same information as holotype; MNHN. Mexico • [3F, 4M]; Veracruz, San Andrés Tuxtla, Est. Biol. Tropical Las Tuxtla, 2.III.2017, 124 m 18°35′22.1″N, 95°5′24.9″W, G. Amancio, A. Aguirre, F. Ozul leg., ex galled fruit Philodendron radiatum; USNMENT01788065–69; USNM. [1F, 1M]; same information as before; CNIN. [46F, 52M]; same information as before; MZUCR.

Description. Holotype female. Body length 2.9 mm. Color: Brown except for the following yellow: scape, pedicel, lower face, prepectus, legs (except metacoxa brown), wing veins white to brown (Fig. 6).

Head. 1.45× as broad as high, with large punctures (Figs 21, 22); anterior tentorial pits with epistomal groove extending ventrally. Supraclypeal area glabrous; clypeus bilobed. Lower margin of eyes slightly sunken; malar suture distinct; malar space 0.37× eye height, asetose beneath eye in elongate microreticulate area; frons protuberant. Preorbitals carina absent; intrascrobal area divergent dorsally to laterad anterior ocellus, delimiting shallow equilateral triangular depression in front of anterior ocellus. Ratio of LOL:OOL:POL as 1:2.1:2.5. Vertexal seta 0.45× eye height; vertexal suture rounded at inner eye margin (Fig. 21); occipital margin without transverse, sinuate carina. Head posteriorly lacking postgenal lamina, postgena with ventral depression near ventral margin.

Antenna. (Fig. 6) ratio of scape (minus radicle): pedicel: A1: A2: A3: F1: F2: F3: F4: F5: club as 74:14:1:1:2:18:18:18:16:16; A1 constricted medially; A2 transverse; one row of MPS on all funicular segments, erect setae at 45° angle to angle to funicular segment, shorter than the funicular segment to which it is attached (Fig. 6).
Mesosoma. 1.27× as long as broad. Pronotum with two sets of setae posterolaterally. Midlobe of mesoscutum 0.88× as long as broad; smooth, with one pair of adnotaular setae; posterior margin of mesoscutum bilobed (Fig. 24, arrow). Notauli

Figure 6–7. Lateral habitus of *Arastichus capipunctata* 6 holotype female 7 paratype male.
complete, shallow. Scutellum 0.90× as long as broad, effaced imbricate, with two pairs of setae; scutellum lacking submedian scutellar grooves, posterior margin rounded. Propodeum raised medially, laterally imbricate, with paraspircular carina complete.

**Figure 8–9.** Lateral habitus of *Arastichus gibernau* 8 holotype female 9 paratype male.
Prepectus triangular, broadly rounded posteriorly, imbricate. Mesepimeron smooth anteriorly. Epicnemium imbricate. Metapleuron without circular fossa that is at least half as wide as propodeal spiracle. Fore wing with ratio of M:PMV:S as 9:1:4 (Fig. 6); SMV with three setae on dorsal surface.

**Metasoma.** Finely imbricate; setose along the posterior edges of each gastral tergite; gastric sternites fused or weakly divided; third valvula extends beyond gaster.

**Male.** Overall morphology and coloration as in female (Fig. 7). Body length 2.9 mm. Antennal ratio of scape (minus radicle):pedicel: A1:F1:F2:F3:F4:F5:F6:club as 25:8:1:2:17:17:17:16:9; scape with distinct ventral plaque in apical ½ (Fig. 7), funicular segments clavate basally, with whorl of setae extending ~1.5x length of the funicular segment to which it is attached. MPS sparse and located at midlength; clava with basal whorl and apical setae, MPS located at apex (Fig. 7). Genitalia: phallobase less than twice as long as broad, digitus with tooth-like projection on anterior margin, aedeagus broad, with apex rounded (Fig. 27).

**Variation.** Both sexes: setation and sculpture variable; sometimes with faint traces of submedian scutellar grooves. Females: length of body 2.9–3.2 mm, SMV with 2–3 setae. Males: length of body 2.4–2.9 mm.

**Etymology.** Named for the distinctive punctate head.

**Biology.** Reared from Philodendron radiatum.

**Distribution.** Costa Rica and Mexico.

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*Arastichus gallicola* (Ferrière), comb. nov.

Figs 3–5, 10–20

*Trichaporus gallicola*, Ferrière, 1924.

*Exurus gallicola* (Ferrière), Costa Lima (1959)

*Aprostocetus gallicola* (Ferrière), LaSalle (1994)

Diagnosis. *Arastichus gallicola* is morphologically similar to *A. gibernau*, but the posterior corner of metapleuron of *A. gallicola* lacks a noticeable fossa, or with an
Description of *Arastichus* (Eulophidae) and two new species

elongate depression (Fig. 4). Additionally, the vertexal suture is angulate or rounded where it reaches the inner eye margin in *A. gallicola* (Fig. 10), whereas in *A. gibernau* this suture is always rounded.

**Description.** *Female holotype.* Body length 3.3mm. **Color:** Yellow: head, mouthparts, scape, pedicel, mesosoma, femoral depression, acropleuron, legs, ovipositor sheaths; dark brown: funicular segments, apices of mandibles, pronotum immediately surrounding spiracle, scutellum, dorsellum, propodeum, mesopleuron, metapleuron, metasoma. Wing veins white to light brown (Figs 3, 4).

**Head.** 1.3× as broad as high, effaced imbricate; anterior tentorial pits with epistomal groove extending ventrally (Fig. 10). Supraclypeal area glabrous; clypeus bilobed. Lower margin of eyes slightly sunken; malar suture distinct; malar space 0.58× eye height, asetose beneath eye in elongate microreticulate area; frons protuberant (Fig. 10). Preorbital carina absent; intrascrobal area divergent dorsally to laterad anterior ocellus, delimiting shallow equilateral triangular depression in front of anterior ocellus. Ratio of LOL:OOL:POL as 1:3.1:3.4. Vertexal suture angulate, or rounded at inner eye margin (Fig. 10); occipital margin with transverse, sinuate carina. Head posteriorly lacking postgenal lamina, postgena without ventral depression near ventral margin.

**Antenna.** Ratio of scape (minus radicle): pedicel: A1: A2: F1: F2: F3: F4: F5: F6: club as 12.5:3.8:1.3:4.5:4.5:4.5:3.8:3.8:5; A1 constricted medially; A2 transverse; two rows of setae on all funicular segments (Fig. 14); erect setae at 45° angle to funicular segment, shorter than the funicular segment to which it is attached to (Fig. 4).

**Mesosoma.** 1.8× as long as broad. Pronotum with two sets of setae posterolaterally. Midlobe of mesoscutum 1.0× as long as broad; with two pairs of adnotaular setae; posterior margin of mesoscutum not bilobed (Fig. 16). Scutellum 1.2× as long as broad; effaced imbricate, with one to two pairs of setae; notauli complete, shallow; scutellum lacking submedian scutellar grooves, posterior margin rounded. Propodeum raised medially, laterally imbricate, with parapsiracular carina complete. Prepectus triangular, broadly rounded posteriorly, imbricate. Mesepimeron striate, becoming smooth anteriorly grading into femoral depression. Epicnemium imbricate. Metapleuron without circular fossa that is at least half as wide as propodeal spiracle. Fore wing with ratio of M:PMV:S as 3:1:1.1 (Fig. 4).

**Metasoma.** Finely imbricate; setose along the posterior edges of each gastral tergite; gastric sternites fused or weakly divided; third valvula does not extend beyond gaster.

**Male.** Overall morphology as in female (Fig. 5). Body length 2.5 mm. **Color:** Dark brown except the following golden: base of scape, ventral mouthparts, acropleuron, coxae apically, legs, metatibia in apical 1/4. Antennal ratio of scape (minus radicle): pedicel: A1: F1: F2: F3: F4: F5: F6: club as 6.9:1.4:1:4.3:4.7:4.7:4.3:4.1:3.6:2.9; scape with distinct, white ventral plaque in apical ½ (Fig. 5), funicular segments wide at base and narrowing off towards apex, with whorl of setae extending ~1.5x length of the funicular segment to which it is attached, MPS sparse and located at midlength; clava with basal whorl and apical setae, MPS located at apex (Fig. 5). Genitalia: phallobase twice as long as broad, digitus slender without projection on anterior margin, aedeagus slender, with apex pointed; digiti with or without a submedian longitudinal suture from the base of the digital tooth but not reaching the base of the digiti (Fig. 27).
Figure 16–20. *Arastichus gallicola* 16 dorsal view of mesosoma 17 ventral view of mesosoma 18 ventral view of female metasoma 19 lateral view of female metasoma 20 propodeum.
**Variation.** Both sexes: setation and sculpture variable; sometimes with faint traces of submedian scutellar grooves; vertexal suture can be rounded or angulate. Females: 2.6–3.8mm, scutellum with brown coloration often incomplete laterally, complete medially and anteriorly/posteriorly on scutellar margins; ocellar triangle sometimes brown; pronotal setation ranges from 1–3 per side, adnotaular setation ranges from 1–3 per side with the occasional odd seta in the notaulus; ocellar triangle often with two small divergent setae. Males: 2.5–3.0mm, may have brownish infuscation of the pro- and mesofemur, meso- and metacoxa may be entirely brown. Specimens from Araras Zoo in Brazil consistently had two setae on the lateral lobes of mesoscutum, whereas other specimens had three. However given the lack of other consistent characteristics, we conservatively group them under *A. gallicola*. Variation in female and male genitalia was found. Females reared from *T. bipinnatifidum* showed two distinct ovipositor morphologies with variation due mostly to larger or smaller first and second valvifers. Females reared from *T. solimoesense* showed an intermediate size ovipositor. Males reared from *T. solimoesense* show a longitudinal submedian suture in the digit that begins at the base of the digital tooth and does not reach the base of the digit.

**Biology.** Reared from *Thaumatophyllum bipinnatifidum* and *T. solimoesense*.

**Distribution.** Brazil and Paraguay.

*Arestichus gibernau* Gates, Hanson, Jansen-González & Zhang, sp. nov.

https://zoobank.org/65576A2E-AFA1-4A26-9C76-675B614EAC82

Figs 8, 9, 24, 25

**Material Examined.** Holotype Panama • [1F]; Barro Colorado Island, Canal Zone, 40-22220, J. Zetek leg., ex. *Philodendron oxycardium* flowers, 8.30'40 1.IX.1940 ; USNMEN01829267; USNM. Paratypes [24F, 25M]; same information as holotype; USNMEN01829268–325; USNM. [3F, 3M]; same information as holotype; ANIC. [4F, 4M]; same information as holotype; BMNH. [4F, 4M]; same information as holotype; CNCI. [4F, 4M]; same information as holotype; MNHN. [4F, 4M]; same information as holotype; MZUCR.

**Diagnosis.** *Arestichus gibernau* is morphologically similar to *A. gallicola*, but the posterior corner of metapleuron of *A. gibernau* has a noticeable fossa, or with an elongate depression ([Figs 8, 9]. Additionally, the vertexal suture is always rounded where it reaches the inner eye margin in *A. gibernau* ([Fig. 24]), whereas in *A. gallicola* this suture is angulate or rounded ([Fig. 10]).

**Description.** Female holotype. Body length 4.4 mm. **Color.** Golden: head, mouthparts, antenna (brownish tint), mesosoma, femoral depression, acropleuron, legs, ovipositor sheaths. Light brown: wing veins, antennae. Dark brown: scutellum, dorsellum, propodeum, metapleuron; wing veins whitish to brownish ([Fig. 8]).

**Head.** 1.36x as broad as high, effaced imbricate; anterior tentorial pits with epistomal groove extending ventrally ([Fig. 24]); supraclypeal area with sparse setae extending from below scrobe to clypeus; clypeus bilobed. Lower margin of eyes slightly sunken;
malar suture distinct; malar space 0.46× eye height, asetose beneath eye in elongate microreticulate area; frons protubertant. Preorbital carina absent; intrascrobal area divergent dorsally to laterad of anterior ocellus, delimiting shallow, equilateral triangular depression anterad to anterior ocellus. Ratio of LOL:OOL:POL as 1:2.4:2.6. Vertexal suture rounded at inner eye margin (Fig. 24); occipital margin with transverse, sinuate

Figure 21–25. *Arastichus capipunctata* 21 frontal view of head 22 dorsal view of head 23 dorsal view of mesosoma, arrow pointing to the bilobed posterior margin of mesoscutum 24–25 *Arastichus gibernau* 24 frontal view of head 25 lateral view of mesosoma, arrow pointing to the circular fossa on the posterior corner of metapleuron.
Description of Arastichus (Eulophidae) and two new species

Carina. Head posteriorly lacking postgenal lamina, postgena without ventral depression near ventral margin. Gena expanded ventrally, giving it a “puffy cheeks” appearance.

**Antenna.** Ratio of scape (minus radicle): pedicel: A1: A2: F1: F2: F3: F4: F5: club as 18:5:1.5:1:8.3:7.3:7:6.3:6.3:2.5 (Fig. 8); A1 constricted medially, A2 transverse, one row of MPS on all funicular segment, two rows of erect setae at 45° angle to funicular segment, shorter than the funicular segment to which it is attached (Fig. 8).

**Mesosoma.** 1.34× as long as broad. Pronotum with three sets of setae posterolaterally. Midlobe of mesoscutum 0.73× as long as broad; with two pairs of adnotaular

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**Figure 26.** Female genitalia of *Arastichus* spp. based on photographs of slide-mounted specimens. Morphological variations are evident among species and within species.
setae; posterior margin of mesoscutum not bilobed. Notauli complete, shallow. Scutellum 1.01x as long as broad; effaced imbricate, with two pairs of setae. Metapleuron with circular fossa that is at least half as wide as propodeal spiracle (Figs 8, 25 arrow). Propodeum raised medially, laterally imbricate, with parapspiracular carina complete. Prepectus triangular, broadly rounded posteriorly, imbricate. Mesepimeron striate, becoming smooth anteriorly grading into femoral depression. Epicnemium imbricate. Fore wing with ratio of M:PMV:S as 2.5:3.3:1.

**Metasoma.** Finely imbricate (Fig. 8); setose along the posterior edges of each gastric tergite; third valvula extends beyond metasoma.

**Male.** Overall morphology as in females (Fig. 9). Body length 3.3 mm. **Color:** Dark brown except the following white: all tibia, procoxa apically, pro- and mesofemur, metatibia in apical 1/4. Antennal ratio of scape (minus radicle):pedicel: A1:F1:F2:F3:F4:F5:F6:club as 10.3:2.5:1:6.8:6.8:6.8:6.5:5.3:4.8:3.5; scape with distinct ventral plaque in apical ½ (Fig. 9), funicular segments clavate basally, with whorl of setae extending ~1.5x length of the funicular segment to which it is attached, MPS sparse and located at midlength; clava with basal whorl and apical setae, MPS located at apex (Fig. 9). Genitalia: phallobase twice as long as broad, digitus slender with a blunt projection on anterior margin, aedeagus slender, with apex pointed (Fig. 27).

**Figure 27.** Male genitalia of *Arastichus* spp. based on photographs of slide-mounted specimens. *Dsp* digital spine; *Aed* aedeagus; *Dgt* digitus; *Dsp* digital spine; *Phl* phallobase; *Prm* paramere; *Vsl* volsella.
Variation. Considerable variation is noted. Females: 3.5–5.2mm, pronotal setation ranges from 1–3 per side, adnotaular setation ranges from 1–2 per side. Males: 2.8–3.5mm, may have brownish infuscation of the pro- and mesofemur.

Etymology. Named in honor of Dr. Marc Gibernau for providing a very large sample of specimens of this species for our research.

Biology. Reared from Philodendron hederaceum var. oxycardium.

Distribution. Panama.

Discussion

Gall induction have evolved multiple times within Tetrastichinae, and to date is known from 10 different host plant families (LaSalle 1994; Fisher et al. 2014; Gates et al. 2020; Singh et al 2022) around the world. However, given the diversity and the lack of taxonomic attention in recent years, the true number of tetrastichine gall inducers is likely much higher. Hopefully with the advances of phylogenomic techniques such as UCEs and broader taxonomic sampling of species-rich regions such as the Neotropics, we can gain a better understanding of the true diversity of gall induction within Eulophidae and Chalcidoidea as a whole.

Acknowledgements

We thank Barry Hammel of the Missouri Botanical Gardens and Christian Trejos of the University of Costa Rica for helping with plant identifications in Costa Rica, and Taina Litwak of USDA SEL for the illustration. We thank Christer Hansson and one anonymous reviewer for providing valuable feedback that have improved the manuscript. SJG was supported by FAPESP (#09/10273-9). The computations in this paper were conducted on the Smithsonian High Performance Cluster (SI/HPC), Smithsonian Institution. https://doi.org/10.25572/SIHPC. YMZ is supported by Oak Ridge Institute for Science and Education (ORISE) fellowship. 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


Description of *Arastichus* (Eulophidae) and two new species


Supplementary material 1

Table S1

Authors: Y. Miles Zhang, Michael W. Gates, Paul E. Hanson, Sergio Jansen-González
Data type: Specimen information.
Explanation note: Locality information and accession numbers for UCE/Sanger loci.
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Link: https://doi.org/10.3897/jhr.92.85967.suppl1
Additions to the genus *Cratospila* Foerster (Hymenoptera, Braconidae, Alysiinae) from South Korea

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Abstract
Two new species of the genus *Cratospila* Foerster, 1863 (Braconidae: Alysiinae), *Cratospila albosignata* sp. nov. and *C. longivena* sp. nov., are described and illustrated. In addition, the DNA barcode region of the mitochondrial *cytochrome c oxidase subunit I* (COI) of both species has been sequenced with three previously described species (*C. albifera*, *C. luteocephala* and *C. syntoma*). *Alysia ponerola* Papp, 2009 which was recorded from North Korea is transferred in *Cratospila* (*C. ponerola* (Papp, 2009) comb. nov.). All species validly recorded from Korea are included in a revised key.

Keywords
Alysiini, COI, Hymenoptera, new combination, new record, new species, taxonomy

Introduction
The subfamily Alysiinae is a large taxon of the family Braconidae, which includes two tribes, Alysiini and Dacnusini with 76 genera and 31 genera, respectively (Yu et al. 2016). Alysiinae contains over 2,440 valid species and the subfamily occurs worldwide.

* These authors contributed equally to this paper.

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(Yu et al. 2016), of which 180 species in 21 genera are listed in the National Species List of South Korea (NIBR 2021). Although, Alysiinae are very similar to members of the subfamily Opiinae both genetically and morphologically, the former can be distinguished from the latter easily by having the exodont (= non-overlapping) mandibles. Alysiinae is known as a group of koinobiont endoparasitoids of cyclorrhaphous dipterous larvae. They use the outward-curved teeth of the mandibles to break open the host puparium (Docavo et al. 2002). Some species are commercially utilized for biological control (Ozawa et al. 2001; Chabert et al. 2012).

The genus *Cratospila* Foerster, 1863, is a small and rather isolated taxon in the subfamily Alysiinae, including 18 species worldwide (Yu et al. 2016; Sohn et al. 2021). This genus is easy to be diagnosed by having the first flagellomere at least 1.5 times longer than the second flagellomere and often with white antennal segments apically. So far, four species have been known in the Oriental region but two species of them are doubtful. Bhat (1980) reported *C. curvabilis* from India and *C. bhutanensis* from Bhutan; considering the original description it is questionable if the first species belongs to *Cratospila*. Tobias (1990) described *C. alboapicalis* from Vietnam. Additionally, Wharton (2002) described six species (*C. confusa*, *C. difficis*, *C. dracula*, *C. elongata*, *C. masneri*, *C. neocirce* and *C. storeyi*) from Australia. *Cratospila circe* (Haliday, 1838) was reported from North Korea by Papp (1994) and also from Malaysia by Yaakop and Aman (2012), but both records are likely to concern one of the very similar local species of the genus (Sohn et al. 2021). So far, *C. circe* has been found only in the Western Palaearctic region. Checking figures of the holotype of *Alysia ponerola* Papp, 2009 (Papp 2009; NIBR 2012) made us aware that likely this species was classified into the wrong genus and should be transferred to *Cratospila* (*C. ponerola* (Papp, 2009) comb. nov.). Fortunately, it is different from the very similar and recently described *C. albifera* Sohn & van Achterberg, 2021 from S. Korea as indicated in the added key.

In this study, we present new morphological characters and the barcoding sequences of the COI region of both new species together with three previously described species (*C. albifera*, *C. luteocephala* and *C. syntoma*). Descriptions, diagnoses, species identification key, and photographs of the diagnostic characters of the new species are provided.

**Materials and methods**

Samples used in this study were collected with Malaise traps in South Korea at the Nebang-ri, Sudong-myeon, Nanyangju-si, Gyeonggi-do and Unilam Banilam, Jucheon-myeon, Jinan-gun, Jeollabuk-do. Sorting and preparation were done at the Animal Systematics Lab. (ASL), Department of Biology, Kunsan National University (KSNU) at Gunsan. For morphological identification, Wharton et al. (1997) and Zhu et al. (2017) were used. Morphological characters were observed with a Leica M205C stereo microscope. The Taxapad database (Yu et al. 2016) was used for references. We
followed the terminology of Wharton (2002) and van Achterberg (1993). The type specimens are deposited KNA (Korea National Arboretum).

A Leica DMC2900 digital camera and a Leica M205 C microscope (Leica Geosystems AG) were used for photography and several pictures being taken for each height using multi-focusing technology. LAS V4.11 (Leica Geosystems AG) and Helicon-Focus 7 (Helicon Soft) software were used for stacking work. After stacking work, illustrations were created using Adobe Photoshop CS6.

Extraction of DNA was done in ASL, KSNU. Whole genomic DNA was extracted from the specimens by using a DNeasy Blood & Tissue kit (QIAGEN Inc., Düsseldorf, Germany) following the manufacturer’s protocol. In order to conserve morphologically complete voucher specimens, DNA extraction method was used slightly modified from ‘non-destructive method’ by Favret (2005) and ‘freezing method’ by Yaakop et al. (2009). In the original protocol, the sample was crushed or wounded, and then soaked with 180 μl of buffer ATL + 20 μl of proteinase, following by three hours over incubation at 55 °C. In the slightly modified DNA extraction methods, samples were soaked with 180 μl of buffer ATL + 20 μl of proteinase K without destroying the sample, followed by 10 minutes incubation at 55 °C and then kept in a freezer at -22 °C overnight. After that the general protocol was used for the remaining steps. The primer set of LCO-1490 (5’-GGTCAACAATCATAAGATATTGG-3’) and HCO-2198 (5’-TAAACTTCAGGGTGACCAAAAAATCA-3’) was used to amplify approximately 658 bp as the partial front region of the COI. The polymerase chain reaction (PCR) products were amplified by using AccuPowerH PCR PreMix (BIONEER, Corp., Daejeon) in 20 μl reaction mixtures containing 0.4 μM of each primer, 20 μM of the dNTPs, 20 μM of the MgCl₂, and 0.05 μg of the genomic DNA template. PCR amplification was performed using a GS1 thermo-cycler (Gene Technologies, Ltd., U.K) according to the following procedure: initial denaturation at 95 °C for 5 min, followed by 34 cycles at 94 °C for 35 sec; an annealing temperature of 48 °C for 25 sec; an extension at 72 °C for 45 sec, and a final extension at 72 °C for 5 min. The PCR products were visualized by electrophoresis on a 1.5% agarose gel. A single band was observed, purified using a QIAquick PCR purification kit (QIAGEN, Inc.), and then sequenced directly using an automated sequencer (ABI Prism 3730 XL DNA Analyzer) at Macrogen Inc. (Seoul, South Korea).

Sequence alignment was performed in MEGA version 7 (Kumar et al. 2016) with ClustalW method. To estimate the pairwise genetic distances, the P-distance model was conducted using MEGA version 7.

**Results**

Total of 630 bp of the COI locus were sequenced for *Cratospila albosignata* sp. nov. (GenBank accession no. ON504323), *Cratospila longivena* sp. nov. (GenBank accession no. ON504322), *C. albifera* Sohn & van Achterberg, 2021 (GenBank accession no. MW376064), *C. luteocephala* Sohn & van Achterberg, 2021 (GenBank accession no.
MW376065) and *C. syntoma* Sohn & van Achterberg, 2021 (GenBank accession no. MW376066). Pairwise genetic distances were calculated by using ‘P-distance’ model with option for pairwise deletion; *C. albosignata* differed by 7% from *C. longivena*, by 7% from *C. albifera*, by 9% from *C. luteocephala* and by 6% from *C. syntoma* (Table 1).

**Taxonomy**

*Cratospila* Foerster, 1863  
Figs 1, 2


**Diagnosis.** First flagellomere 1.5–2.1 times longer than second (Figs 1B, 2B), most species with 8–13 white segments in apical part of antenna (unknown of *C. longivena*, but has reddish brown head, morphologically related to *C. albifera* and has according to the COI analysis a derived position compared to other species), face with setae (Figs 1E, 2E), eye slightly oval, clypeus protruding anteriorly (Figs 1E, 2E), clypeus large, triangularly shaped and ventrally truncate, mandible with three teeth, second tooth narrow and sharp, maxillary palp with six segments, as long as mesosoma; notauli at least present anteriorly, scutellar sulcus distinct, precoxal sulcus medially deeply impressed and coarsely crenulate, more or less reduced anteriorly and posteriorly (Figs 1G, 2G); fore wing (Figs 1C, 2C) vein 2-SR slightly bent, vein 3-SR shorter than vein 2-SR; veins 2-SR+M and r-m not sclerotized, hind wing vein 1-M shorter than vein 1r-m; first tergite longer than second (Figs 1H, 2H).

**Biology.** Rather small genus, of which the biology is unknown.

**Distribution.** Cosmopolitan, except Neotropical region.

**Key to species of Cratospila Foerster from Korea**

1. Mesoscutum medio-posteriorly and scutellum reddish brown; notauli on middle of mesoscutum comparatively coarsely crenulate; pterostigma rather slender and narrowly yellow basally; vein 1-SR+M of fore wing slightly sinuate; mesosoma 1.5–1.6 times longer than high in lateral view and anterior half of propodeum less sloping; propodeum less extensively rugose medially; antennal sockets comparatively close to level of inner side of eyes; [head in dorsal view yellowish brown] .........................................................2

2. Mesoscutum medio-posteriorly and scutellum black; head in dorsal view more transverse and at least posteriorly darkened; notauli on middle of
mesoscutum narrowly crenulate; pterostigma rather robust and brown basally; vein 1-SR+M of fore wing nearly straight; mesosoma 1.4–1.5 times longer than high in lateral view and anterior half of propodeum largely sloping; propodeum more extensively rugose medially; antennal sockets more removed from level of inner side of eyes ........................................ 4

Minimum width of face 0.9 times its height (measured from lower rim of antennal socket to upper medio-dorsal margin of clypeus); vein r of fore wing approx. 3 times longer than wide; first subdiscal cell of fore wing approx. 7.5 times longer than wide; [colour of apical antennal segments unknown] ............

........................................ C. luteocephala Sohn & van Achterberg, 2021

– Minimum width of face 1.2 times its height; vein r of fore wing 4–5 times longer than wide; first subdiscal cell of fore wing 4–5 times longer than wide; [antenna of ♀ with 10–11 white segments] ........................................ 3

First tergite about twice as long as wide apically; eye in dorsal view approx. 2.4 times longer than temple and head in dorsal view more transverse (Fig. 2 in Papp 2009); apical antennal segment dark brown; vein r of fore wing less oblique (Fig. 9 l.c.) ........................................ ..............................

........................................ C. ponerola (Papp, 2009) comb. nov.

– First tergite approx. 2.8 times longer than its apical width; eye in dorsal view approx. 1.9 times longer than temple and head in dorsal view less transverse (Fig. 1D in Sohn et al. 2021); apical antennal segment white; vein r of fore wing more oblique (Fig. 1C l.c.) .......... C. albifera Sohn & van Achterberg, 2021

Vein 2-SR 1.8–1.9 times longer than vein 3-SR; first subdiscal cell approx. 8 times longer than wide; minimum width of face 0.95 times its height; [pedicellus entirely yellow; head (except posteriorly) yellowish brown; antenna of ♀ with 10–11 white or ivory segments and apical segment dark brown, pale part 4.6 times longer than apical dark brown part] ........................................

........................................ C. ejuncida Sohn & van Achterberg, 2021

– Vein 2-SR 1.4–1.5 times longer than vein 3-SR; first subdiscal cell 5–6 times longer than wide; minimum width of face 1.1–1.3 times its height............ 5

Eye in dorsal view approx. 1.6 times longer than temple; vein r of fore wing about as long as wide; head black dorsally; pedicellus partly infuscated; [minimum width of face 1.1 times its height] ........................................ ..............................

........................................ C. syntoma Sohn & van Achterberg, 2021

– Eye in dorsal view 2.3–2.8 times longer than temple; vein r of fore wing about twice as long as wide; head reddish brown or blackish brown dorsally; pedicellus yellow ................................................................. 6

First tergite comparatively slender (Fig. 2F), approx. 3.5 times longer than its apical width; minimum width of face 1.1 times its height; head blackish brown dorsally .............................................. C. longivena sp. nov.

– First tergite comparatively robust (Fig. 1F), approx. 2.9 times longer than its apical width; minimum width of face 1.3 times its height; head reddish brown dorsally .............................................. C. albosignata sp. nov.
**Cratospila albosignata** Sohn & van Achterberg, sp. nov.
https://zoobank.org/DF862519-BCFF-4322-BA83-591378EF63B1
Fig. 1A–I


**Description.** **Holotype**, ♀, length of body 2.8 mm in lateral, length of antenna 4.5 mm and of fore wing 2.7 mm.

**Colour:** Body (Fig. 1A) black, but head (Fig. 1A), first tergite and mesonotum entirely reddish brown; antenna yellowish brown basally, medially dark brown, subapically white (11 flagellomeres); mandible pale orange.

**Head** (Fig. 1D): Width of head 1.6 times its median length in dorsal view. Antenna 1.6 times longer than body, 32 segmented. First flagellomere 2.1 times longer than second and 8.7 times longer than wide. Compounded eye slightly oval, in lateral view 1.2 times as long as wide. Minimum width of face (Fig. 1E) 1.3 times its height (measured from ventral rim of antennal sockets to upper margin of clypeus). Eye in dorsal view 2.3 times as long as temple. Ocello-ocular line (OOL) 3.5 times longer than diameter of anterior ocellus; OOL: antero-posterior ocellar line (AOL) : postero-ocellar line (POL) = 30 : 8 : 13. Stemmaticum concave. Vertex smooth and with polished stripe. Mandible pale yellow with three teeth, first tooth lobe-shape, second tooth narrow and sharp with reddish brown tip. Maxillary palp white and approx. as long as mesosoma.

**Mesosoma:** Mesosoma 1.8 times longer than wide in dorsal view; 0.7 times longer than wide in lateral view. Mesoscutum (Fig. 1G) with medio-posterior depression; notauli distinctly impressed anteriorly, not reaching medio-posterior depression; scutellar sulcus with six carinae; in lateral view, ventral of mesopleuron and metapleuron with setae. metanotum sculptured. Propodeum (Fig. 1H) 0.5 times longer than wide, anterior half of propodeum smooth, posterior of median carina wrinkled; precoxal sulcus (Fig. 1F) deep and distinct, with more than 14 carinae, propodeum not curved dorsally in lateral view. Fore wing (Fig. 1C) 2.4 times as long as wide in maximum length; pterostigma 3.9 times longer than wide; vein r of fore wing 3 times longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; 2-SR: r : 3-SR = 17 : 3 : 12; first discal cell of fore wing approx. 1.3 times longer than wide; first subdiscal cell of fore wing approx. 5 times longer than wide. Hind wing vein M+CU : vein 1-M = 11 : 1

**Leg:** Hind coxa compressed and grooved; hind coxa 1.4 times longer than hind trochanter; hind femur 4.2 times longer than wide and 0.7 times longer than hind tibia; hind tibia as long as hind tarsus.

**Metasoma:** First tergite striate and narrow, 2.9 times longer than its apical width and dark brown, T1:T2 = 52:39. Setose part of ovipositor sheath (Fig. 1I) 0.4 times as long as mesosoma, 0.5 times as long as hind tibia and with long setae.

**Male.** Unknown.

**Distribution.** South Korea.

**Etymology.** Named after the conspicuous white apex of the ♀ antenna: “albo” is derived from “albus” (Latin for white) and “signata” is derived from “signatus” (Latin for marked).
Cratospila longivena Sohn & van Achterberg, sp. nov.
https://zoobank.org/13631339-38B5-4DF1-9C13-A3E03E5E78E2
Fig. 2A–I


Comparative diagnosis. Differ from other South Korean species of *Cratospila* by having the first tergite very long (3.5 times longer than its apical width; 2.5–2.9 times...
in other species). Unfortunately, some apical segments of antenna are missing, but COI analysis apparently showed that it is genetically close to *C. syntoma*.

**Description.** Holotype, ♀, length of body in lateral view 2.9 mm, and of fore wing 2.8 mm.

**Colour:** Body (Fig. 2A) black, head dorsally blackish brown, remainder of head, first tergite and mesonotum entirely reddish brown; antenna yellowish brown basally, medially dark brown (apical part of antenna missing, but according to notes made in Netherlands with at least 7 white segments).

**Head** (Fig. 2D): Width of head 1.5 times its median length in dorsal view. First flagellomere 1.6 times longer than second and 7.3 times longer than wide; most of antenna lost during transport from Netherlands to Korea. Compounded eye slightly oval and glossy, in lateral view 1.2 times as long as wide. Width of face (Fig. 2E) 1.1 times its height (measured from ventral rim of antennal sockets to upper margin of clypeus). Face with long setae and glabrous. Eye in dorsal view 2.8 times as long as temple. Ocello-ocular line (OOL) 3.6 times longer than diameter of anterior ocellus; OOL: antero-posterior ocellar line (AOL) : postero-ocellar line (POL) = 32 : 8 : 13. Stemmaticum concave and with setae. Mandible entirely pale orange, with three teeth, second tooth narrow and sharp with dark brown tip, and separated from first tooth and third tooth. Third tooth with carina in ventral view. Medial length of mandible 1.6 times its maximum width. Labrum 0.7 times longer than maximum width. Maxillary palp 0.8 times longer than mesosoma.

**Mesosoma:** Mesosoma 2.0 times longer than its maximum width in dorsal view and 1.4 times its height in lateral view. Mesoscutum (Fig. 2G) with medio-posterior depression; notauli chain-shaped, nearly complete but not reaching medio-posterior depression; scutellar sulcus with six distinct carinae; in lateral view mesopleuron smooth and glossy, apical parts with setae; metapleuron smooth with setae; metanotum sculptured; small basal bump on hind coxa. Propodeum (Fig. 2H) 0.6 times longer than wide, anterior half of propodeum smooth, posterior of median carina strongly wrinkled; precoxal sulcus (Fig. 2F) deep and distinct, with about eight carinae, propodeum curved in lateral view. Fore wing (Fig. 2C) 2.4 times as long as wide; pterostigma long and narrow, 3.2 times longer than wide; vein r of fore wing 3.5 times longer than wide; vein 2-SR slightly bent; vein 2-SR+M and r-m not sclerotized; 2-SR: r : 3-SR = 11 : 2 : 7; first subdiscal cell of fore wing approx. 5 times longer than wide. Hind wing M+CU : 1-M = 22 : 4.

**Table 1.** COI pairwise genetic distances between the three *Cratospila* spp. from South Korea.

<table>
<thead>
<tr>
<th></th>
<th><em>C. albosignata</em></th>
<th><em>C. longivena</em></th>
<th><em>C. albifera</em></th>
<th><em>C. luteocephala</em></th>
<th><em>C. syntoma</em></th>
</tr>
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<td>0.000</td>
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<tr>
<td><em>C. longivena</em></td>
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<td>0.000</td>
<td></td>
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<td>0.092</td>
<td>0.000</td>
<td></td>
<td></td>
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<tr>
<td><em>C. luteocephala</em></td>
<td>0.094</td>
<td>0.092</td>
<td>0.098</td>
<td>0.000</td>
<td></td>
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<tr>
<td><em>C. syntoma</em></td>
<td>0.059</td>
<td>0.071</td>
<td>0.073</td>
<td>0.089</td>
<td>0.000</td>
</tr>
</tbody>
</table>
Figure 2. (A–I) *Cratospila longivena* sp. nov. ♀ A habitus, lateral view B antennae C wings D head, dorsal view E head, front view F mesosoma, dorsal view G mesosoma, lateral view H anterior half of metasoma, dorsal view I ovipositor sheath, lateral view.

**Leg:** Hind coxa compressed and grooved; hind coxa 1.2 times longer than hind trochanter; hind femur 5.5 times longer than wide and 0.7 times longer than hind tibia; hind tibia as long as hind tarsus.

**Metasoma:** First tergite striate and narrow, 3.5 times longer than apical width, T1:T2= 5:3. Setose part of ovipositor sheath (Fig. 2I) 0.5 times as long as mesosoma, 0.5 times as long as hind tibia and with long setae.

**Male:** Unknown.
**Distribution.** South Korea.

**Etymology.** Named after the comparatively long vein r of the fore wing: “longi” is derived from “longus” (Latin for long) and “vena” is Latin for vein.

**Acknowledgements**

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202203201). And this work was also supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR2022231206). This research was also supported by the Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Education (2018R1D1A3B07044298).

**References**


Toxares koreanus sp. nov. – a new Toxares species from South Korea (Hymenoptera, Braconidae, Aphidiinae)

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Abstract
The genus Toxares Haliday, 1840 is a small taxon of Aphidiinae, consisting four valid species in the world. One Toxares species is recorded as new to science from South Korea, in this study. Descriptions and illustrations of the new species, T. koreanus sp. nov., are provided, together with their mitochondrial cytochrome c oxidase subunit I (COI) and D2 region of the nuclear gene for 28S rRNA (28S) sequences. The phylogenetic tree reconstructed using a combination of COI and 28S revealed the phylogenetic position of the genus Toxares within Aphidiinae.

Keywords
DNA barcoding, parasitoid wasps, phylogenetics, systematics, taxonomy

Introduction
The genus Toxares Haliday, 1840 is a small genus of Aphidiinae with four known species from the Holarctic. Toxares deltiger (Haliday, 1833) was the first species to be described from the genus. For a long time, it was only known in Europe, but it has

* These authors contributed equally to this work.

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been recorded from the USA (Pike et al. 2000), Turkey (Tomanović et al. 2008) and several Asian countries (Korea, Kazakhstan, Pakistan, China, India) (Choi et al. 2017; Davidian 2018, 2020). Takada (1965) described Toxares shigai Takada, 1965 from Japan, and later Shuja-Udin (1974) described two additional species, Toxares zakai Shuja-Udin, 1974 and Toxares macrosiphobagum Shuja-Udin, 1974 from India. All known Toxares species were rarely sampled, and most records came from traps and net sweeping, and consequently without evidence about its aphid hosts. Nevertheless, a part of the records came from reared aphid colonies and available literature data, and it is confirmed that aphid hosts of Toxares species belong to the tribes Macrosiphini and Aphidini including some pest aphids (e.g. Metopolophium dirhodum (Walker) (Powell 1980, 1982; Dean et al. 1981; Starý et al. 1981; Höller et al. 1993), Sitobion avenae (Fabricius) (Dean et al. 1981; Powell 1982; Cameron et al. 1984), Acyrthosiphon pisum (Harris) (Cameron et al. 1984), Myzus persicae (Sulzer) (Mackauer 1968; Starý and Ghosh 1975, 1983; Marsh 1979; Hofsvang and Hågvar 1983), Aphis craccivora (Koch) (Raychaudfuri et al. 1990), Schizaphis rotundiventris (Signoret) (Starý and Ghosh 1983) and Rhopalosiphum nymphaeae (L.) (Starý and Ghosh 1983).

Based on the forewing venation being related to braconid ancestors, the genus Toxares is classified within the Ephedrini tribe (Mackauer 1961), which has sometimes been considered basal within Aphidiinae (Belshaw and Quicke 1997; Sanchis et al. 2000; Derocles et al. 2012). Some other studies showed that the tribe Praini is basal (Smith et al. 1999). However, there is very little evidence about molecular data of Toxares species, and its phylogenetic position is still unknown. Derocles et al. (2012) determined that the phylogenetic position of Toxares deltiger is between Ephedrini and Praini based on sequences of the Cytochrome c Oxidase subunit I (COI) gene. Ye et al. (2017) analysed molecular markers for identification of primary parasitoids of cereal aphids. Within their analysis, T. deltiger clustered as a sister group of the Trioxini tribe based on COI sequences and as a sister group of Aphidiini based on 16S ribosomal RNA (Ye et al. 2017).

The aim of this study is to present additional knowledge about the diversity of Toxares species. After initial research of Korean aphid parasitoid fauna, we recognized a new Toxares species which is herein described and diagnostified using morphological and molecular characters. We also analysed phylogenetic relationships among genera Toxares, Ephedrus Haliday, 1833 and Praon Haliday, 1833 and discussed the phylogenetic position of the genus Toxares within Aphidiinae.

Material and methods
Specimen collection and morphological analysis

Specimens were collected by Malaise trap in a deciduous forest habitat (mostly Quercus spp.) in Mt. Beophwa which is about 450 m.a.s.l. Rosa multiflora, Cirsium japonicum, and Urtica thunbergiana were the dominant plant species. Two specimens were slide-mounted with Hoyer medium and one preserved in 70% ethanol. External structure
was studied and measurements taken with a LEICA DM LS phase-contrast microscope. Morphological terminology used in this paper regarding diagnostic characters is based on that of Sharkey and Wharton (1997).

**Molecular analysis**

DNA extraction was performed using a LaboPass Tissue Kit (COSMOgenetech, Korea) following the manufacturer’s protocol. In order to conserve morphologically complete voucher specimens, the DNA extraction method was slightly modified from the ‘non-destructive method’ by Favret (2005) and ‘freezing method’ by Yaakop et al. (2009). In the original protocol, the sample was crushed and then soaked in 180 μl of TL buffer + 20 μl of proteinase-K, followed by three hours of incubation at 55 °C. In the slightly modified DNA extraction methods, samples with all specimens were soaked in 180 μl of TL buffer + 20 μl of proteinase-K without destroying the sample, followed by 10 minutes incubation at 55 °C and kept in a freezer at -22 °C overnight. After that the general protocol was used for the remaining steps. The target site for molecular identification was the front partial region of mitochondrial COI, amplified using the primers LCO1490 (forward) 5’-GGTCAACAAAATCATAAAGATAT-TGG-3’ and HCO2198 (reverse) 5’-TAAACTTCAGGGGTAGACAAAAATCA-3’ (Folmer et al. 1994). The molecular marker used for comparing with other *Toxares* species and species of *Ephedrus* and *Praon* was the D2 region of the nuclear gene for 28S rRNA (28SrDNA), amplified using primers 28SD2f (forward) 5’-AGAGAGAGTTCAAGAGATCGT-3’ (Belshaw and Quicke 1997) and 28SD2r (reverse) 5’-TTGGTCCGTGTTTCAAGACGGG-3’ (Campbell et al. 1993). We used heterogenous F/R primers as referred to by Tomanović et al. (2018).

Polymerase chain reaction (PCR) amplification of COI and 28S was conducted by using AccuPower PCR PreMix (Bioneer Corp., Daejeon, Korea) in 20 μl of a reaction mixture consisting of 3 μl of DNA extract, 2 μl of primer, and 15 μl of H2O. Thermal profile for COI was as follows: denaturation for 5 min at 95 °C; 38 cycles of 20 s at 95 °C, 30 s at 45 °C, and 40 s at 72 °C; and final extension at 72 °C for 5 min. Thermal profile for 28S was as follows: denaturation for 3 min at 95 °C; 32 cycles of 30 s at 95 °C, 30 s at 48 °C, and 30 s at 72 °C; and final extension at 72 °C for 10 min. The PCR products were tested by electrophoresis on agar gel and if a band existed, we commissioned Bionocs (Korea) for sequencing and purification.

Sequences were edited with FinchTV ver. 1.4.0 (www.geospiza.com), aligned with CLUSTAL W integrated in MEGA X (Kumar et al. 2018), and trimmed to lengths of 642 bp (COI), and 476 bp (28S). Sequences are deposited in GenBank under accession numbers: ON007269–ON007271 (COI), ON003419–ON003421 (28S). Additional sequences from GenBank (Fig. 3) were used for phylogenetic analysis.

Average genetic distances were calculated using MEGA X and Kimura’s two-parameter method of base substitution (K2P, Kimura 1980) (Table 1).

MEGA X was used to construct phylogenetic trees based on each gene used in the study, as well as a combined tree employing concatenated sequences of both genes.

Phylogenetic relationships were reconstructed using Maximum Likelihood (ML) and Maximum Parsimony (MP) methods.
Results

Description of the new species

*Toxares koreanus* Tomanović, Kim & Petrović, sp. nov.
https://zoobank.org/82B185A3-71D2-4E6B-B84B-AC887FC14140

**Table 1.** Genetic distances (K2P) between analysed Aphidiinae species based on COI (bold) and 28S (upper right) and on both genes combined (lower left).

<table>
<thead>
<tr>
<th></th>
<th><em>T. koreanus</em> (JS1)</th>
<th><em>T. koreanus</em> (JS1-1)</th>
<th><em>T. koreanus</em> (JS1-2)</th>
<th><em>T. deltiger</em></th>
<th><em>E. belleni</em></th>
<th><em>E. nacheri</em></th>
<th><em>E. persicae</em></th>
<th><em>E. plagiator</em></th>
<th><em>P. abjectum</em></th>
<th><em>P. bicolor</em></th>
<th><em>P. dorsale</em></th>
<th><em>P. yomenae</em></th>
<th><em>V. canescens</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><em>T. koreanus</em> (JS1)</td>
<td>0.00 0.00 0.14 0.21 0.21 0.22 0.21 0.16 0.16 0.17 0.19 0.29</td>
<td>0.00 0.00 0.05 0.20 0.22 0.20 0.23 0.19 0.19 0.19 0.19 0.38</td>
<td>0.00 0.00 0.14 0.21 0.22 0.21 0.21 0.16 0.16 0.17 0.19 0.29</td>
<td>0.05 0.20 0.22 0.20 0.23 0.19 0.19 0.19 0.19 0.19 0.19 0.38</td>
<td>0.09 0.10 0.10 0.23 0.22 0.20 0.23 0.18 0.19 0.18 0.20 0.31</td>
<td>0.21 0.21 0.21 0.21 0.22 0.21 0.22 0.22 0.21 0.21 0.27</td>
<td>0.21 0.21 0.21 0.21 0.20 0.13 0.16 0.22 0.22 0.21 0.22 0.32</td>
<td>0.21 0.21 0.21 0.22 0.08 0.02 0.16 0.22 0.22 0.21 0.22 0.27</td>
<td>0.21 0.21 0.21 0.22 0.08 0.20 0.20 0.20 0.21 0.21 0.26 0.36</td>
<td>0.17 0.17 0.17 0.17 0.22 0.23 0.21 0.23 0.24 0.21 0.22 0.21 0.27</td>
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<td>0.17 0.17 0.17 0.18 0.22 0.22 0.21 0.22 0.22 0.22 0.22 0.22 0.22 0.28</td>
<td>0.18 0.18 0.18 0.19 0.22 0.22 0.22 0.22 0.06 0.05 0.05 0.06 0.08 0.28</td>
</tr>
</tbody>
</table>

**Table 1**. Genetic distances (K2P) between analysed Aphidiinae species based on COI (bold) and 28S (upper right) and on both genes combined (lower left).

**Results**

**Description of the new species**

*Toxares koreanus* Tomanović, Kim & Petrović, sp. nov.
https://zoobank.org/82B185A3-71D2-4E6B-B84B-AC887FC14140

**Diagnosis.** *Toxares koreanus* sp. nov. morphologically resembles *T. shigai* in having elongated flagellomere 1 (F₁), which is clearly longer than flagellomere 2 (F₂) and elongated petiole at the spiracles level. However, *T. koreanus* sp. nov. is easily distinguished from *T. shigai* in the shape of petiole (petiole with parallel sides in *T. koreanus* sp. nov., while laterally expanded and longitudinally striated in *T. shigai*), yellow colored F₁–F₃ and even a yellowish base of F₄ in *T. koreanus* sp. nov., while light brown colored F₁–F₃ in *T. shigai*. Also, *T. koreanus* sp. nov. morphologically resembles *T. macrosiphophagum*, but differs in more elongated F₁ which is clearly longer than F₂, more elongated
Description. Female (Fig. 1, Suppl. material 1: Fig. S1): Head (Fig. 1A) rounded, bearing sparse setae. Eyes large and oval. Tentorial index (tentoriocular line/intertentorial line) 0.30–0.36. Clypeus with about 10 long setae. Malar space equal to 0.20 of longitudinal eye diameter. Mandible bidentate, with 6–7 setae on the outer surface. Maxillary palps with four palpomeres, labial palps with three palpomeres. Antenna 17–18 segmented (17, 2♀; 18, 1♀), flagellate (Fig. 1B). Flagellomere 1 (F₁) (Fig. 1C) clearly longer than F₂ (F₁/F₂ length 1.1–1.2) and 3.75–4.00 times as long as its maximum width at the middle. F₁ with 2–3 and F₂ with 3–5 longitudinal placodes (Fig. 1C). Flagellomeres covered uniformly with semi-erect setae subequal to antennal segments diameter.

Mesosoma. Mesoscutum smooth, rounded, with mid pit in the middle posterior part. Notaulices distinct in very short ascendent portion of anterolateral margin, with two rows of long setae along the dorsolateral part of mesoscutum (Fig. 1D). Scutellum elongated, bearing 6–7 long setae in the central part. Scutellar sulcus divided into equal halves. Propodeum (Fig. 1E) areolated with large central areola. Upper propodeal areolas with 5–7 long setae and lower areolas with 1–4 long setae on each. Forewing (Fig. 1F) densely pubescent, with long marginal setae. Pterostigma elongated, 6.35–6.7 times as long as its width, subequal to R₁ vein (Fig. 1F). Forewing 2RS vein shorter than 3RSa vein (2RS/3RSa = 0.55) and 3RSa shorter than 3RSb vein (3RSa/3RSb = 0.73).

Metasoma. Petiole (Fig. 1G) slightly rugose and convex dorsally, with lateral depression at level of prominent spiracular tubercles. Petiole length 2.80–2.86 times its width at the base of spiracles, with 5–6 long setae along each side (Fig. 1G). Ovipositor sheath deltoid shaped (Fig. 1H).

Body length: about 1.70–2.20 mm.


Male (Fig. 2): Antenna 19-segmented with shorter flagellomeres (Fig. 2A). F₁ about 2.60 times as long as wide and longer than F₂ (Fig. 2B). Number of longitudinal placodes on F₁ and F₂, 3 and 5, respectively. Maxillary palps with four palpomeres, labial palps with three palpomeres. Pterostigma shorter than in female and about 4.7 times as long as wide. Mesosoma with small mid pit. Petiole shorter than in female and about 2.55 times longer than width at spiracles level. Male genitalia (Fig. 2C). Body generally darker than in female. Scapus and pedicel light brown. F₁ yellow, remaining antennal parts brown. Legs yellow to light brown with dark apices. Petiole and first half of metasomal terga light brown, remaining part of metasoma brown. Legs and mouthparts light brown.

Etymology. The name of the new species is derived from Republic of Korea where it was found.
Specimens examined. **Holotype**: Korea • 1 ♀; Mt. Beophwa, San 128-1, Wolgok-ri, Cheoncheon-myeon, Jasnsu-gun, Jeollabuk-do; 35°42’07.6”N, 127°31’54.7”E; collected by Malaise trap: 06.V–24.V.2021; leg. Yeonghyeok Yu, Sangjin Kim, JuHyeong Sohn, Yunjong Han, Gyeongyeon Lee. Holotype deposited in National Institute of Biological Resources, Incheon, Republic of Korea slide mounted.

**Figure 1.** *Toxaeris koreanus* sp. nov., female A head B antennae C flagellomere F1–F4 D mesoscutum E propodeum F petiole G ovipositor H forewing.
A new *Toxares* species from South Korea

**Paratypes:** Korea • 1 ♂; Mt. Beophwa, San 128-1, Wolgok-ri, Cheoncheon-myeon, Jasnsu-gun, Jeollabuk-do; 35°42’07.6”N, 127°31’54.7”E; collected by Malaise trap: 06.V–24.V.2021; leg. Yeonghyeok Yu, Sangjin Kim, JuHyeong Sohn, Yunjong Han, Gyeongyeon Lee. Paratype slide mounted and deposited in National Institute of Biological Resources, Incheon, Republic of Korea.

**Figure 2.** *Toxares koreanus* sp. nov., male 
A antennae B flagellomere F₁ and F₂ C mesoscutum D propodeum E petiole F ovipositor G forewing.
**Additional material.** Korea • 2 ♀; 1 ♀, Mt. Beophwa, San 128-1, Wolgok-ri, Cheoncheon-myeon, Jasnsu-gun, Jeollabuk-do; 35°42′07.6″N, 127°31′54.7″E; collected by Malaise trap: 06.V–24.V.2021; leg. Yeonghyeok Yu, Sangjin Kim, JuHyeong Sohn, Yunjong Han, Gyeongyeon Lee • 1 ♀, same locality; collected by Malaise trap: 24.V–02.VI.2021; leg. Yeonghyeok Yu, Sangjin Kim, JuHyeong Sohn, Yunjong Han, Gyeongyeon Lee. Specimens deposited dry and immersion-mounted in Kunsan National University, Jeollabuk-do, Republic of Korea.

**Molecular analysis.** Obtained phylogenetic trees reconstructed based on COI, 28S and the combination of both genes showed identical topology, and the tree based on the combination of both genes is shown on Fig. 3. *Toxares koreanus* sp. nov. groups with the only other *Toxares* species used in the analysis, while this clade is sister to the clade of *Praon* species. *Ephedrus* species basally form a separate clade on the tree.

Calculated genetic distances (Tables 1, 2) also indicate closer relatedness between *Toxares* and *Praon* than between *Toxares* and *Ephedrus*.

**Discussion**

The genus *Toxares* is considered as one of the most basal within the subfamily Aphidiinae, classified within the tribe Ephedrini (Mackauer 1961), and sharing a braconid ancestral wing venation pattern with species of the genus *Ephedrus*. Except for the fore-wing venation pattern as a clear plesiomorphy, the newly described species, along with other congeners (e.g. *T. deltiger*), shares additional plesiomorphic character states, such as a large number of placodes on F₁ and F₂, areolated propodeum, and 4-maxillary and 3-labial palpomeres. On the other hand, the elongated flagellomeres and petiole represent apomorphic characters (Tomanović et al. 2006). *Toxares koreanus* sp. nov. also possesses a small mid pit on the mesoscutum. This is a unique character present only in some *Ephedrus* species from the subgenus *Fovephedrus* (Chen 1986; Kocić et al. 2019), as well as in all known *Toxares* species. *Toxares koreanus* sp. nov. along with other congeners (e.g. *T. deltiger*) possesses a divided scutellar sulcus (Fig. 1D), a character state present in the subgenus *Breviephedrus* (e.g. *E. brevis*) (Kocić et al. 2019), which supports the phylogenetic position of the genus *Toxares* within the tribe Ephedrini.

**Table 2.** Genetic distances (K2P) between genera *Toxares*, *Ephedrus* and *Praon*.

<table>
<thead>
<tr>
<th></th>
<th>Within group mean distances</th>
<th>Between group mean distances (COI/ 28S/ combined)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>COI</td>
<td>28S</td>
</tr>
<tr>
<td><em>Toxares</em></td>
<td>0.07</td>
<td>0.02</td>
</tr>
<tr>
<td><em>Ephedrus</em></td>
<td>0.14</td>
<td>0.06</td>
</tr>
<tr>
<td><em>Praon</em></td>
<td>0.07</td>
<td>0.01</td>
</tr>
</tbody>
</table>

Calculated genetic distances (Tables 1, 2) also indicate closer relatedness between *Toxares* and *Praon* than between *Toxares* and *Ephedrus*. **Table 2.** Genetic distances (K2P) between genera *Toxares*, *Ephedrus* and *Praon*.
A new *Toxares* species from South Korea

*Toxares koreanus* sp. nov. is the fifth known member of the genus *Toxares* and fourth species described from Asia. Based on the currently available data about the distribution of described species, we can assume that the origin of this genus should be Far Eastern Asia. Considering the habitat and plant diversity in Far Eastern Asia, we can expect to discover additional species of the genus *Toxares*.

**Figure 3.** Phylogenetic relationships between *Toxares*, *Ephedrus* and *Praon* species based on combined sequences of COI and 28S RNA genes. Species name is followed by code or GenBank accession numbers in brackets. Bootstrap values are indicated above/below branches in order ML/MP.
Molecular analysis using COI and 28S supports the description of the new species. *Toxares koreanus* sp. nov. is clearly separated from *T. deltiger* by both genes (Fig. 3, Table 1), in addition to morphological differences.

Molecular markers employed in this study show some incongruence with morphological characters. While *Toxares* is morphologically most similar to *Ephedrus*, molecular data suggests the genus is closer to *Praon* (Fig. 3, Tables 1, 2). Calculated genetic distances between all three genera are very high, based on both genes used in the analysis (Table 2). Although those between *Toxares* and *Ephedrus* are slightly higher than those between *Toxares* and *Praon*, it is still advisable to interpret these results carefully, and use an integrative approach including biological and ecological traits when making conclusions about the relatedness of groups. The discrepancy between morphological and molecular data is a fairly common occurrence in Aphidiinae research and numerous studies have shown that molecular and morphological analyses often give somewhat conflicting results (Tomanović et al. 2013, 2018; Petrović et al. 2015; Jamhour et al. 2016; Čkrkić et al. 2020). One possible solution to this ongoing dilemma could be the use of more molecular markers or increasing the number of molecular operational taxonomic units, in an effort to uncover the mechanisms underlying the differences in multi-locus determined morphological traits (Zimmerman et al. 2000; Mezey et al. 2005; Čkrkić et al. 2020) and more emphasis on functions and adaptation of morphological characters.

Although the genus *Toxares*, as a member of Ephedrini tribe, is already considered as basal within Aphidiinae (Mackauer 1961), our molecular data do not confirm it. We believe that discoveries of more species of this poorly known genus, along with appropriate molecular studies (which will include “ancient” genera *Pseudephedrus* and *Choreopraon*) should allow us to determine the exact phylogenetic position of *Toxares*.

**Acknowledgements**

This work was supported by a grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR202102204). This research was also supported by the Basic Science Research Program through the National Research Foundation of Korea funded by the Ministry of Education (2018R1D1A3B07044298). The contribution of ŽT, AP and JČ is supported by the Serbian Ministry of Science and Education (451-03-68/2022-14/200178).

**References**

A new *Toxares* species from South Korea


Jamhour A, Mitrović M, Petrović A, Starý P, Tomanović Ž (2016) Re-visiting the *Aphidius urticae* s. str. group: Re-description of *Aphidius rubi* Starý and *A. silvaticus* Starý (Hymenoptera: ...


A new *Toxares* species from South Korea


**Supplementary material 1**

**Figure S1**
Authors: Sangjin Kim, Željko Tomanović, Andjeljko Petrović, Jelisaveta Čkrkić, Gyeonghyoen Lee, Jongok Lim, Hyojoong Kim
Data type: Image (tif file)
Explanation note: Figure S1. Habitus of *Toxares koreanus* sp. nov., female.
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Link: https://doi.org/10.3897/jhr.92.84146.suppl1
A new genus and species of Ctenopelmatinae (Hymenoptera, Ichneumonidae) from China

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https://zoobank.org/1AD18B71-B687-4500-B896-DCD27C57A4C7


Abstract
A new genus, Unicarinata Sheng, Li & Sun, gen. nov., of the ichneumonid subfamily Ctenopelmatinae, is described for one new species, Unicarinata ventrialis Sheng, Li & Sun, sp. nov. The new genus is similar to Syntactus Förster, 1869 or Pion Schiodte, 1839, and different in having the propodeum with only one median transverse carina, areas and lateromedian longitudinal carinae entirely absent, tergite 1 straight, tergite 2 shagreened, impunctate, ovipositor straight. Types were collected from Mts Emei, Laojun, and Wawu in the Giant Panda National Park, Sichuan Province, Mts Fanjing and Leigong, Guizhou Province, and Mt Dayao, Guangxi Zhuang Autonomous Region, China.

Keywords
Darwin wasp, Giant Panda National Park, new species, Pionini, Unicarinata

Introduction
The Ctenopelmatinae are a large subfamily of ichneumonid wasps currently comprising 110 genera and 1617 described species, most of which are koinobiont endoparasitoids of sawflies of the superfamilies Pamphilioidea and Tenthredinoidea (Aubert 2000; Yu...
et al. 2016; Khalaim et al. 2019; Kasparyan 2020a, b, 2021; Sheng et al. 2020, 2022; Sun et al. 2021a, b; Watanabe 2021; Li and Sun 2022). The subfamily is subdivided into nine tribes, eight of which have been reported in China (Townes 1970; Yu et al. 2016; Sheng et al. 2020).

The tribe Pionini Smith & Shenefelt, 1955, comprises 20 genera (Townes 1970; Gauld 1984; Aubert 1993; Wang and Yan 1998; Kasparyan 2020a), eight of which have been reported in China (Hinz 1986; Wang and Yan 1998; Sun and Sheng 2012; Sheng et al. 2013, 2020; Sheng and Sun 2014; Yu et al. 2016). Hitherto, one endemic genus, *Celata* Wang, 1998, and 50 species have been reported in China (Yu et al. 2016; Sheng et al. 2020).

In the last three years the authors have been studying the ichneumonids of Mts Emei, Guanwu, Jiuzhaigou, Laojun, Qionglai, and Wawu (Giant Panda National Park), Sichuan Province, situated along the upper reaches of the Yangtze River, which belongs to the southern border of the Palaearctic part of China; Mts Fanjing and Leigong, Guizhou Province, and Mt Dayao, Guangxi Zhuang Autonomous Region, which belongs to the northern border of the Oriental part of China.

One species is a distinctive pionine, but proved very difficult to place in any genus, with a combination of character states that could almost feasibly place it in *Syntactus* Förster, 1869 or *Pion* Schiødte, 1839. For example, both genera have the outer face of the mandible without a basal transverse impression, lower tooth of mandible longer than upper tooth, upper end of epicnemial carina reaching the front edge of the mesopleuron, glymma absent, areolet absent. But propodeum of the new species (Fig. 8) has only one distinct median transverse carina, lack areas, the lateromedian longitudinal carinae are entirely absent, tergite 1 (Figs 13, 14) is very long and slender, straight, tergite 2 (Fig. 15) is shagreened, impunctate, and the ovipositor is straight. We hypothesized that this species represents a new genus.

### Materials and methods

Specimens of the new species were collected by interception traps (IT) (Li et al. 2012) in the National Natural Reserves of Mts Emei (29°33’N, 103°19’E, 2390 m), Laojun (28°42’N, 104°01’E, 1500 m), and National Forest Park, Mt Wawu (29°40’N, 102°59’E, 1180 m), Giant Panda National Park, Sichuan Province, National Natural Reserves of Mts Fanjing (27°53’N, 108°38’E, 1250 m) and Leigong (26°22’N, 108°12’E, 1760 m), Guizhou Province, and Mt Dayao (23°57’N, 110°06’E, 1520 m), Guangxi Zhuang Autonomous Region, China.

Images were taken using a Leica M205A stereo microscope with LAS Montage MultiFocus. The final images were edited in Adobe Photoshop CC. Morphological terminology follows Gauld (1991) and Broad et al. (2018).

The type specimens are deposited in the Insect Museum, Center for Biological Disaster Prevention and Control (CBDPC), National Forestry and Grassland Administration, Shenyang, Liaoning Province, China.
A new genus and species of Ctenopelmatinae from China

Results

Taxonomy

Unicarinata Sheng, Li & Sun, gen. nov.
https://zoobank.org/C13F7A99-67D9-4CFD-A451-73CD1CC21B70

Type species. Unicarinata ventrialis Sheng, Li & Sun, sp. nov. Monotypic.

Diagnosis. Mandible (Fig. 3) large and long, lower tooth distinctly longer than upper tooth. Occipital carina complete, genal carina joining hypostomal carina above base of mandible. Dorsal end of epiconemial carina (Fig. 4) almost reaching front edge of mesopleuron. Areolet absent (Fig. 11). Vein 2rs-m basal to vein 2m-cu. Hind vein 2-cu absent. Propodeum (Fig. 8) with one strong transverse carina level with posterior edge of spiracle. Tergite 1 (Fig. 13) very long and slender; latero-median carina absent, dorso-lateral carina present after spiracle; spiracle located slightly anterior to middle; tergite and sternite fused; glymma absent. Ovipositor sheath (Fig. 12) almost extending to apex of metasoma. Ovipositor slender and straight.

Etymology. The name of the new genus is derived from the propodeum having one strong transverse carina. The gender is feminine.

Remarks. The new genus is similar to Syntactus Förster, 1869 in having the apical margin of the clypeus blunt; base of the mandible without a transverse impression; dorsal end of epiconemial carina almost reaching the front edge of the mesopleuron; glymma absent; areolet absent; however, it can easily be distinguished from Syntactus by the following characters in combination: apical margin of clypeus medially almost truncate (Fig. 3); propodeum with only one strong transverse carina (Fig. 8); area superomedia entirely absent; hind vein 1-cu opposite cu-a; vein 2-cu absent; tergite 1 (Figs 12–14) very slender, straight; tergite 2 (Fig. 15) granulate; and ovipositor (Fig. 12) straight. In Syntactus the apical margin of the clypeus is almost evenly arcuate; propodeum is completely areolated, area superomedia at least partly present; tergite 1 relatively slender, decurved; tergite 2 smooth; and ovipositor upcurved.

In Townes’ (1970) key to Pionini genera, the new genus can be inserted as follows:

2 Outer face of mandible without a basal transverse impression. Subbasal part of lower edge of mandible sharp. Areolet absent.................................3

– Outer face of mandible with a basal transverse impression. Subbasal part of lower edge of mandible rounded. Areolet present or absent......................4

3 Propodeum (Fig. 8) with only one distinct median transverse carina, latero-median longitudinal carinae entirely absent. Tergite 1 very slender, straight (Figs 12–14). Tergite 2 (Fig. 15) shagreened, without punctures. Ovipositor (Fig. 12) straight.............................. Unicarinata Sheng, Li & Sun, gen. nov.

– Propodeum at least with posterior transverse carina, lateromedian longitudinal carinae present. Tergite I decurved. Tergite II smooth, punctate. Ovipositor upcurved.........................................................3'
**Unicarinata ventrialis** Sheng, Li & Sun, sp. nov.

https://zoobank.org/E7315381-2D50-4762-892C-19C04EABBF21

Figs 1–23

Material examined. **Holotype**, ♀ (CBDPC), CHINA: Ernianping, National Natural Reserves of Mt Laojun, Sichuan Province, 28°42’N, 104°01’E, 1500 m, 25. VIII. 2019, leg. Tao Li (IT). **Paratypes**, 1♂ (CBDPC), CHINA: Lingjue Temple, National Natural Reserves of Mt Emei, Sichuan Province, 29°33’N, 103°19’E, 2390 m, 22. VIII. 2019, leg. Peng-Suo Luo (IT); 1♀ 2♂ (CBDPC), CHINA: Lingjue Temple, National Natural Reserves of Mt Emei, Sichuan Province, 29°32’N, 103°19’E, 2310 m, 10. VIII. 2020, leg. Peng-Suo Luo (IT); 1♂ (CBDPC), CHINA: Lingjue Temple, National Natural Reserves of Mt Emei, Sichuan Province, 29°33’N, 103°19’E, 2390 m, 30. VIII. 2020, leg. Peng-Suo Luo (IT); 1♀ (CBDPC), CHINA: National Natural Reserves of Mt Leigong, Guizhou Province, 26°22’N, 108°12’E, 1760 m, 18. V. 2019, leg. Wan-Xin Pan (IT); 1♂ (CBDPC), CHINA: Yapanlin, National Natural Reserves of Mt Fanjing, Guizhou Province, 27°53’N, 108°38’E, 1250 m, 13. IX. 2019, leg. Mao-Fei Tian (IT); 1♀ (CBDPC), CHINA: National Forest Park of Mt Wawu, Giant Panda National Park, Sichuan Province, 29°40’N, 102°59’E, 1180 m, 15. VI. 2020, leg. Gui-Ru Kang (IT); 1♀ 2♂ (CBDPC), CHINA: National Forest Park of Mt Wawu, Giant Panda National Park, Sichuan Province, 29°40’N, 102°59’E, 1180 m, 13. IX. 2020, leg. Gui-Ru Kang (IT); 1♂ (CBDPC), same data as holotype, except 1. VI. 2021; 1♂ (CBDPC), same data as holotype, except 21. VI. 2021; 2♀ 3♂ (CBDPC), same data as holotype except 17. IX. 2021; 2♀ 10♂ (CBDPC), CHINA: Shengtangshan, National Natural Reserves of Mt Dayao, Guangxi Zhuang Autonomous Region, 23°57’N, 110°06’E, 1520 m, 15. X. 2021, leg. Tao Li (IT); 1♀ 4♂ (CBDPC), CHINA: Shengtangshan, National Natural Reserves of Mt Dayao, Guangxi Zhuang Autonomous Region, 23°57’N, 110°06’E, 1520 m, 21. X. 2021, leg. Tao Li (IT); 1♀ 6♂ (CBDPC), CHINA: Shengtangshan, National Natural Reserves of Mt Dayao, Guangxi Zhuang Autonomous Region, 23°57’N, 110°06’E, 1520 m, 15. X. 2021, leg. Tao Li (IT).

**Description. Female.** Body (Fig. 1) length 6.4 to 7.8 mm. Fore wing length 5.7 to 6.8 mm. Ovipositor sheath length 0.4 to 0.5 mm.

**Head.** Inner margins of eyes (Fig. 3) slightly convergent ventrally. Face (Fig. 3) approximately 1.2× as wide as long, shining with fine granular microsculpture and dense yellowish brown setae, median portion evenly longitudinal convex with rough punctures. Clypeus (Fig. 3) 2.5× as wide as long, convex from basal to apical portions; apical margin arced and truncate. Mandible (Fig. 3) large and long, with dense setae medially; lower tooth distinctly longer than upper tooth. Malar space shiny, about 0.4× as long as basal width of mandible. Maxillary palp (Fig. 4) with five segments, extending to mid coxa. Gena (Fig. 4) evenly convergent backward, shiny, with dense yellowish brown setae. Vertex (Fig. 5) with the same texture as gena; posteromedian portion distinctly oblique. Postocellar line approximately 0.8× as long as ocular-ocellar line. Frons almost flat, slightly concave above antennal socket. Antenna with 42 to 46 flagellom-
Figure 1–2. *Unicarinata ventralis* Sheng, Li & Sun, sp. nov. Holotype, ♀ (CBDPC) 1 habitus, lateral view 2 habitus, lateral view. Paratype, ♂. Scale bars: 2 mm (1, 2).
eres; ratio of length from first to fifth flagellomeres (Fig. 6): 1.8:1.4:1.2:1.1:1.0. Occipital carina complete, genal carina joining hypostomal carina above base of mandible.

**Mesosoma.** Pronotum (Fig. 4) shiny, dorsal half of concavity with fine oblique wrinkles; dorsal margin with dense yellowish setae. Epomia absent. Mesoscutum (Fig. 7) convex, shiny, with dense yellowish setae; median portion slightly longitudinally concave, with coarse texture. Notaulus distinct on anterior portion of mesoscutum. Scuto-scutellar groove deep, shiny, with fine longitudinal wrinkles. Scutellum (Fig. 7) distinctly convex, shiny, with sparse setae; lateral carina distinct, extending to median portion. Posteromedian part distinctly convex, with finely granulate; anterior portion concave. Mesopleuron (Fig. 4) almost flat, shiny, lower half with evenly dense yellowish-brown setae; upper portion under subtegular ridge with sparse setae. Speculum relatively large, slightly convex, shiny. Episternal scrobe as shallow transverse

Figure 3–11. *Unicarinata ventralis* Sheng, Li & Sun, sp. nov. Holotype, ♀ (CBDPC) 3 head, anterior view 4 head and mesosoma, lateral view 5 head, dorsal view 6 basal of flagellomeres, ventral view 7 mesoscutum and scutellum, dorsal view 8 propodeum, dorsal view 9 fore tibia, lateral view 10 hind tarsus, lateral view 11 wings. Scale bars: 0.2 mm (3–7); 0.1 mm (8, 9); 0.4 mm (10, 11).
A new genus and species of Ctenopelmatinae from China

groove. Dorsal end of epicnemial carina almost reaching front edge of mesopleuron, about 0.8 of distance to subtegular ridge. Mesosternum (Figs 4, 18) relatively short and evenly convex. Metapleurum (Fig. 4) slight convex, dorsal and median parts shiny, lower part finely granulate; ventro-posterior corner with oblique wrinkles. Juxtacoxal carina complete. Legs slender; claws simple. Fore tibia (Fig. 9) with distinct apical tooth; anterior and apical part with spines. Hind coxa (Fig. 1) conical, dorsally longitudinally concave with fine granular texture; inner spur (Fig. 10) 0.6× as long as first tarsomere. Ratio of length from first to fifth hind tarsomeres (Fig. 10): 4.2:2.2:1.7:1.0:1.0. Wings (Fig. 11) slightly infuscate. Fore wing with vein 1cu-a opposite M&RS. Areolet absent. Vein 3rs-m absent. Vein 2rs-m basal to vein 2m-cu by 0.5× length of vein 2rs-m. Vein CU slightly shorter than 2cu-a. Hind vein M+CU strongly curved. Vein 1-cu opposite cu-a. Vein 2-CU absent. Propodeum (Fig. 8) slightly convex, shiny, with fine granular texture, with one strong transverse carina at level of posterior edge of spiracle; basal median part with one arched transverse carina or irregular wrinkles (Figs 19, 21); lateromedian longitudinal carinae present anteriorly, weak, strongly diverging posteriorly; lateral longitudinal carina interrupted under transverse carina; pleural carina complete; propodeal spiracle reniform, 3.1× as long as width.

**Metasoma** (Fig. 12). Tergite 1 (Fig. 13) 7.3× as long as anterior width, 3.5× as long as posterior width; margins parallel, evenly widened posteriorly; anterior half shiny, posterior half with fine granular texture; posterior part with dense yellowish setae; latero-median carina absent, dorso-lateral carina present posterior to spiracle, ventro-lateral carina complete; spiracle small, circular, located slightly anterior to middle; glymma absent; anterior sclerotized section (Fig. 14) strongly convex; tergite and sternite fused;
sternite 1 extending to posterior 0.3 of tergite 1. Tergite 2 (Fig. 15) trapezoidal, 1.3× as long as anterior width, 0.8× as long as posterior width, with evenly spaced fine yellowish-brown setae. Tergite 3 (Fig. 15) almost rectangular, 0.7× as long as anterior width, with the same microsculpture as tergite 2. Tergites 4–8 shiny, with evenly spaced fine yellowish-brown setae; posterior half of tergite 4–8 compressed. Ovipositor sheath (Fig. 12) almost extending to apex of metasoma. Ovipositor slender and straight.

**Coloration.** Body (Fig. 1) yellowish brown to brown, mesosoma (Fig. 4) with blackish brown spots or reddish brown (Fig. 18), propodeum reddish brown (Fig. 19) or black-brown (Fig. 21), except for following: face, clypeus, mandible (teeth brown), gena, maxillary palpi, labial palpi, fore and mid coxae, trochanters, third to fifth hind tarsomeres, yellowish white. Median part of frons, occiput, temple and vertex, black-brown with some reddish. Median and upper parts of pronotum, mesoscutum, mesopleuron, except subtegular ridge and speculum, upper division of metapleuron, lower half of metapleuron, area basalis, area dentipara, dorsum of hind coxa except median spot, subapical part of tergite 1, and lateral part of tergite 2, dark brown to black-brown. Hind femur and tibia brown to reddish brown. Proximal and apical parts of flagellum, pterostigma and veins, brown to brownish black.

**Male.** Body (Fig. 2) length 5.8 to 6.7 mm. Fore wing length 5.4 to 6.0 mm. Antenna with 41 to 45 flagellomeres. Propodeum (Fig. 17) with fine oblique wrinkles at ante-
riorly, sub-laterally, or with transverse carina (Fig. 23), posterior half with fine granular texture; sub-median section of transverse carina interrupted; lateromedian longitudinal carinae absent; apical of lateral longitudinal carina vestigial. Body brown, mesosoma (Fig. 16) with blackish brown spots, except for following: posterior longitudinal spots dark reddish. Median and lower half of mesopleuron, metapleuron except lower-posterior corner, yellowish brown to brown; mesoscutum (Fig. 22) reddish brown except sub-median irregular spots with dark reddish. Other characteristics as in female.

**Distribution.** China (Guangxi, Guizhou, Sichuan).

**Etymology.** The specific name is derived from the short and evenly convex mesosternum.
Acknowledgements

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References

A new genus and species of Ctenopelmatinae from China


Batesian-Müllerian mimicry ring around the Oriental hornet (Vespa orientalis)

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Abstract
Mimicry is usually understood to be an adaptive resemblance between phylogenetically distant groups of species. In this study, we focus on Batesian and Müllerian mimicry, which are often viewed as a continuum rather than distinct phenomena, forming so-called Batesian-Müllerian mimicry rings. Despite potent defence and wide environmental niche of hornets, little attention has been paid to them as potential models in mimicry research. We propose a Batesian-Müllerian mimicry ring of the Oriental hornet (Vespa orientalis, Hymenoptera: Vespidae) consisting of eight species that coexist in the Mediterranean region. To reveal general ecological patterns, we reviewed their geographical distribution, phenology, and natural history. In accordance with the ‘model-first’ theory, Batesian mimics of this ring occurred later during a season than the Müllerian mimics. In the case of Batesian mimic Volucella zonaria (Diptera: Syrphidae), we presume that temperature-driven range expansion could lead to allopatry with its model, and, potentially, less accurate resemblance to an alternative model, the European hornet (Vespa crabro: Hymenoptera: Vespidae). Colour morphs of polymorphic species Cryptocheilus alternatus (Hymenoptera: Vespidae), Delta unguiculatum (Hymenoptera: Vespidae), Rhynchium oculatum (Hymenoptera: Vespidae), and Scoliia erythrocephala (Hymenoptera: Scoliidae) appear to display distinct geographical distribution patterns, and this is possibly driven by sympathy with alternative models from the European hornet (Vespa crabro) complex. General coevolution patterns of models and mimics in heterogeneous and temporally dynamic environments are discussed, based on observations of the proposed Oriental hornet mimicry ring.
Keywords
biogeography, Conopidae, Diptera, evolution of mimicry, Hymenoptera, phenology, polymorphism, Syrphidae

Introduction

Mimicry is an example of convergent evolution whereby similar appearances result in an evolutionary advantage, such as reduced risk of predation. Various defences in animals were described; however, most discussed are Batesian (Bates 1863) and Müllerian (Müller 1879) mimicry. Batesian mimicry is an asymmetrical interaction between a model, chemically or otherwise defended, and a palatable mimic (Bates 1863). Müllerian mimicry is a mutualistic interaction between two or more species, where their shared resemblance and defences protect them from predation with the learning costs, caused by naïve predators, spread among them (Müller 1879; Kapan 2001).

Although traditionally viewed as a parasitic interaction, Batesian mimicry could be beneficial to the defended model under certain circumstances, as it could decrease the error costs caused by a forgetful predator; this phenomenon is called quasi-Müllerian mimicry (Speed and Turner 1999). On the other hand, species involved in Müllerian mimicry could be unequally defended (Speed 1993), forming so called quasi-Batesian mimicry, where the least defended species gains more profit from the interaction (Speed 1993; Balogh et al. 2008). In addition, the level of defence could even vary within one species (Tuskes and Brower 1978; Ritland and Brower 1991) and the same defence could be unequally effective against various predators (Hotová Svádová et al. 2010). Therefore, Batesian and Müllerian mimicry are often viewed as a continuum, rather than distinct phenomena forming so called Batesian-Müllerian mimicry rings (Mallet and Gilbert Jr. 1995). However, species are usually assigned to a Batesian or Müllerian group for practical reasons (as in this study), hence the classification into subtle classes is problematic.

In various mimicry complexes we can find Batesian mimics, which resemble their models rather imperfectly (Sherratt 2002; McLean et al. 2019). The existence of imperfect mimicry has puzzled evolutionary ecologists for a long time (Bates 1862; McLean et al. 2019). Many hypotheses have been proposed so far to explain it, such as e.g. relaxed selection in small-bodied species (Penney et al. 2012), trade-off between mimicry and thermoregulation (Taylor et al. 2016b), effect of community diversity (Wilson et al. 2013), or resemblance to more than one model (Sherratt 2002). It might also be possible that the natural predators, such as insectivorous birds, perceive inaccurate mimics as rather perfect (Cuthill and Bennett 1993), as most studies have evaluated mimetic accuracy using human observers (Taylor et al. 2017; Hassall et al. 2019; Kelly et al. 2021) or image analysis (Penney et al. 2012; Taylor et al. 2016a), and only a few studies considered a perception of real predators (Mostler 1935; Dlusski 1984; Dittrich et al. 1993; Hotová Svádová et al. 2010).
The phenology of mimicry complexes can range from models and mimics occurring at the same time (temporal sympatry), models occurring first, or mimics occurring first in a season. Mathematical modelling (Bobisud 1978) and experiments with human observers (Hassall et al. 2019) supported the model-first scenario as the most beneficial for the models and predators, as the avoidance learning of predators is not biased by encountering a palatable prey of similar appearance. Moreover, it was observed in butterflies (Rothschild 1963), salamanders (Brodie 1981), and might be common among hoverflies (Howarth and Edmunds 2000; Hassall et al. 2019). Some hoverfly species occur earlier than their models (Waldbauer 1988; Howarth and Edmunds 2000; Hassall et al. 2019); however, such scenario is not necessarily harmful to a mimic's fitness, as during spring, the naïve fledglings are still fed by their parents, and the adult birds probably remember the aposematic colouration from the previous season (Waldbauer 1988). Some differences in phenological patterns probably stem from various ecology of the mimics (e.g. larval strategy, preferred habitat, community diversity, mimetic accuracy).

Mimics face increased predation when they occur outside the geographic range of their models (Pfennig et al. 2001), quite often limited by latitudinal gradient (Hines and Williams 2012) or biotope preferences (Wilston et al. 2012). Moreover, the distribution of models may limit the distribution of mimics (Ries and Mullen 2008). However, allopatry between mimics and models, especially at the edge of their distribution range, might be more common than previously thought (Pfennig and Mullen 2010). On the other hand, allopatry is sometimes rather illusory, as mimics could resemble different models in various parts of their distribution area (reviewed in Ruxton et al. 2019).

Here, we focus on the Batesian-Müllerian mimicry ring around the Oriental hornet (Vespa orientalis), a large and conspicuous social wasp occurring in Mediterranean, Southwest Asia, Central Asia and Northeast Africa. We identified seven species from various families of hymenopterans and dipterans that are likely Müllerian and Batesian mimics of Vespa orientalis. In the present paper, the information on ecology and biogeography of the Vespa orientalis mimicry ring are summarised and the following questions are addressed: 1) Which phenological pattern applies to the proposed mimicry ring (model first; mimic first; temporal sympatry)? 2) Are the mimics of the Oriental hornet (Vespa orientalis) sympatric with their model across their whole distribution area? 3) Is there spatial overlap between the mimicry rings of the Oriental hornet (Vespa orientalis) and the European hornet (Vespa crabro)?

Materials and methods

We observed the mimicry ring around the Vespa orientalis on the Aegean island of Lesvos (Greece), from 27. viii. to 17. ix. 2019. We explored various habitats (chestnut forest, steppes, salt marshes, macchia) on the island (Fig. 1) and collected specimens of seven (out of eight) species studied, see Table 1. All specimens were collected using
entomological net by Antonín Hlaváček and Jiří Hadrava and are deposited in their private collections. Letters in Fig. 1 refer to localities. Specimens were photographed with a Canon EOS 70 D camera equipped with a Canon EF-S 60 mm f/2.8 Macro USM lens. Zerene Stacker was used for photo stacking (P-max algorithm).

We searched for species with similar colouration pattern occurring in the Mediterranean area. Based on these criteria, we included *Scolia erythrocephala* F. 1775. However, we presume that the *Vespa orientalis* mimicry ring is probably much larger in the eastern (Asian) part of its distribution and might include species such as *Delta pyriforme* (F. 1775), *Laphria dizonias* Loew, 1864, *Monoceromyia eumenioides* (Saunders, 1842), *Rhodanthidium superbum* (Radoszkowski, 1876), *Scolia flaviceps* Eversmann, 1846 (present in Asia Minor, with some records from Greece and Turkey), or *Stiphrolamyra pleskei* (Becker, 1913). Nevertheless, those species were omitted due to the lack of data and will be explored in further studies.

We classified the species into Müllerian and Batesian mimicry groups. The Müllerian group was represented by five species of hymenopterans (*Cryptocheilus alternatus*, *Delta unguiculatum*, *Scolia erythrocephala*, *Vespa orientalis*, and *Rhynchium oculatum*). The Batesian group was represented by three species of dipterans (*Conops flavicaudus*, *Milesia crabroniformis*, and *Volucella zonaria*).

![Figure 1. Lesvos Island and collecting sites. From top: map of the Aegean Sea with Lesvos island highlighted; shrubland near the town of Petra, and shrubland in the western part of the island, typical habitat of species from *Vespa orientalis* complex. Letters refer to localities listed in the species list.](image-url)
Information on the distribution, phenology, and habitat preferences were adopted from Syrph the Net databases for hoverflies (Speight 2016), from single faunistic records and studies for hymenopterans (Maidl 1922; Betrem 1935; Giordani Soïka 1939; Carpenter and Kojima 1997; Archer 1998a, 1998b; Osten 2000; Tüzün et al. 2000; Ćetković 2002; Osten 2002; Tezcan 2005; Józan 2009; Schedl 2010; Özbek and Anlaş 2011; De Groot 2012; Yildirim 2012; Samin et al. 2014; Yildirim and Lelej 2016; Zachi et al. 2021), and Conopidae (Stuke et al. 2008; Zalat et al. 2009; Stuke et al. 2012). Furthermore, data from open diversity databases such as Fauna Europaea (de Jong et al. 2014), GBIF (2021), and iNaturalist (2021) were incorporated. Distribution ranges were assessed as presence or absence within each country. Records with uncertain taxonomical status were omitted.

We compared the *Vespa orientalis* and its Batesian mimic *Volucella zonaria* to the mimetic pair of two related species, the European hornet (*Vespa crabro*) and its mimic *Volucella inanis* (L. 1758).

Other potential mimics of the European hornet (e.g. *Asilus crabroniformis* L. 1758, *Cimbex connatus* (Schrank 1776), queens of *Dolichovespula media* (Retzius 1783), or *Volucella elegans* Loew, 1862) are neither displayed nor analysed, as it lies beyond the scope of this paper.

Similarity of geographic distribution (counted as presence/absence within the country) was calculated for every model-mimic pair using Lennon’s index of similarity (Lennon et al. 2001). Lennon’s index was chosen in order to avoid the bias caused by intraspecific variability in total area size. The UPGMA clustering method was used to

<table>
<thead>
<tr>
<th>Species</th>
<th>Collecting sites, date and recorded specimens</th>
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<tr>
<td><em>Conops flavicaudus</em> (Bigot, 1880)</td>
<td>A: Achladeri, 39°9.27038’N, 26°16.88825’E, 29.8.2019, 1♀, Collected on shrubs in an olive orchard near the coast. Several specimens were observed at this spot, but nowhere else on the island.</td>
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create a dendrogram based on the distribution of species. Phenological shifts between models and mimics were tested with Mann-Whitney U test (Mann and Whitney 1947), comparing the earliest recorded occurrence within a whole distribution area. Software R version 3.3.3 was used for all statistical analysis (R Core team 2021). Maps were created using QGIS software (2021).

Results

We reviewed the Batesian-Müllerian mimicry ring of eight species from various taxonomical and ecological groups: five species of hymenopterans in three families (Vespidae, Pompilidae, Scoliidae) forming the Müllerian part of the mimicry ring, and three Batesian mimics in two dipteran families (Conopidae, Syrphidae). Photographs, distribution maps, phenological charts and habitat preferences, compiled from previously published data, are presented in Fig. 3. Species accounts have been collated from the literature and can be found in Suppl. material 1: Appendix 1.

Figure 2. Dendrogram showing similarity between species areas. Lennon’s index was used to calculate similarities, the dendrogram was created using UPGMA clustering. Yellow branch: species of Eastern Mediterranean, extending in Levant. Red branch: species present in the entire Ponto-Mediterranean area. Brown branch: species that extended their range and are present even in central and northern Europe. Blue branch: *Vespa crabro* mimicry ring with *Volucella inanis*.

The phenology of all species overlaps to some degree. Batesian mimics occur later (median of first occurrence: 7, mean of first occurrence: 6.75; counted in months) than their models (median of first occurrence: 3.5, mean of first occurrence: 4.17) corresponding with the ‘model first scenario’ (p-value = 0.04, Mann-Whitney test).

The distribution of species was reviewed (Fig. 2). The *Vespa orientalis* ring occurs in the Ponto-Mediterranean area, where some species more or less extend the Mediterranean area and occur in central Europe or in the Middle East. The data presented in Fig. 2 suggests that species form 4 different branches: I) Species of Eastern Mediterranean, extending in Levant – *Conops flavicaudus*, *Scolia erythrocephala* and *Vespa orientalis* (yellow branch in Fig. 2); II) Species present in the entire Ponto-Mediterranean area
Figure 3. Members of *Vespa orientalis* and *Vespa crabro* mimicry rings: distribution maps, phenological charts, and preferred habitat. Phenology is simplified to a monthly scale, hab. - habitat. Photos were taken by the authors.
- *Milesia crabroniformis*, *Rhynchium oculatum* (red branch in Fig. 2), III) Species that extend their range and are present even in central and Northern Europe – *Cryptocheilus alternatus*, *Delta unguiculatum*, *Volucella zonaria* (brown branch in Fig. 2), which is therefore close to IV) *Vespa crabro* and its mimic *Volucella inanis* (blue branch in Fig. 2).

**Discussion**

In the Oriental hornet mimicry ring, the Batesian mimics were found to occur later in the season than the Müllerian mimics. All species overlapped in the late summer. These results are consistent with the ‘model-first’ scenario (Bobisud 1978), which seems to be the most advantageous scenario for the models (Hassall et al. 2019) and is common among hoverflies (Howarth and Edmunds 2000; Hassall et al. 2019). On the other hand, for the Batesian mimics, temporal sympatry with their models would be more beneficial than model-first scenario (Hassall et al. 2019). However, two of the Batesian mimics, *Volucella zonaria* and *Conops flavicaudus*, develop as commensals/parasites in the nests of social hymenopterans, which likely prevents them from activating earlier than the models; *Volucella zonaria* is commensal in ground nests of yellow-jacket wasps (*Vespula germanica*) (Morris and Ball 2004). *Conops flavicaudus* probably develops as a parasitoid of some hymenopterans, such as bumblebees, even though its larval ecology is unknown. This is in line with the previous results, that the constraints set by larval strategy might play a significant role in phenological patterns in some hoverflies (Howarth and Edmunds 2000).

Based on the analysis of geographic distribution, we assigned the species into three groups (‘branches’): Eastern Mediterranean branch (yellow in Fig. 2); Mediterranean branch (red in Fig. 2); and extending Mediterranean branch (brown in Fig. 2), which extends to the Central and/or Northern Europe. However, the distribution areas of the branches are partially overlapping; thus, some species are present in the area defined by the other branches. The Eastern Mediterranean branch is represented by *Vespa orientalis*, the rare Batesian mimic *Conops flavicaudus*, and Müllerian mimic *Scolia erythrocephala*, where all of them are also found in the Levant and in the Middle East. The Eastern Mediterranean could be considered as the centre of the mimicry ring as all species are present in Greece and Turkey (the geographic distribution might be incomplete due to missing observational data). The Mediterranean branch consists of species common in the whole Mediterranean area, i.e. Batesian mimic *Milesia crabroniformis* and Müllerian mimic *Rhynchium oculatum*. Three species (Batesian mimic *Volucella zonaria*, and Müllerian mimics *Cryptocheilus alternatus* and *Delta unguiculatum*) of the described mimicry ring are present in the whole Mediterranean area, and moreover, they extend their range into Central Europe or, in the case of *Volucella zonaria*, even into Northern Europe (Morris and Ball 2004), thus forming ‘extending Mediterranean’ branch, which partially overlaps with the distribution of the European hornet (*Vespa crabro*) and its mimicry ring.

We consider *Vespa orientalis* to be the ‘leading model’ of the studied mimicry ring.
**Vespa orientalis** is, in contrast with other Müllerian mimics in complex, habitat generalist, making it an ideal ‘leading model’. Unlike the other Müllerian mimics of the mimicry ring, **Vespa orientalis** is a social species, living in colonies which could number thousands of workers (Ishay 1976); therefore, it could occur in higher numbers than solitary hymenopterans. Moreover, the lethal capacity of venom is known to positively correlate with the degree of sociality in aculeate hymenopterans (Schmidt 2014), which might implicate that social hymenopterans possess generally more potent venom than their solitary relatives. However, **Vespa orientalis** is completely missing in the Western Mediterranean (yet some observations from past years were made by Hernández et al. 2013). That leads to the question, which species is the ‘leading model’ for Batesian mimics in this part of Europe. We propose the following: a) **Vespa crabro**, b) either **Cryptocheilus alternatus**, **Delta unguiculatum** or **Rhynchium oculatum**, c) combination of several of the listed species play the role together, and d) there is no ‘leading model’ outside the range of **Vespa orientalis**. Based on high noxiousness and sociality, we could hypothesize that **Vespa crabro** might be an important model in the Western Mediterranean. More observational data and experimental evidence would be needed to resolve the relationships between the Müllerian part of the mimicry ring.

Colour polymorphism was described in some members of the mimicry ring. Interestingly, black morphs occurred sympatrically with the European hornet (**Vespa crabro**). Specifically, Batesian mimic **Volucella zonaria** sometimes tends to be darker with a black, ‘**Vespa crabro**-like’ pattern on the thoracic dorsum in some locations, i.e. in Corsica (van der Goot 1961), or the Czech Republic (personal observation). Dark colouration of the thorax and petiole was also observed in German populations of Müllerian mimic **Delta unguiculatum** (Mader 2000). Dark morphs of **Cryptocheilus alternatus** occur on the Iberian Peninsula (personal observation). **Vespa crabro** occurs in the mentioned locations (Germany, Czech Republic, Corsica, Iberia), whereas **Vespa orientalis** does not. Even higher variability in colouration occurs in Müllerian mimic **Scolia erythrocephala**, where the colouration varies both between and within subspecies from yellow-and-black to ‘**Vespa orientalis**-like’ colouration. Moreover, it was argued that **Scolia** develops darker colouration when it is exposed to lower temperatures during development (Osten 2000). However, the taxonomical status of the **S. erythrocephala** subspecies and its whole species group (**erythrocephala-flaviceps**) is complicated and unresolved; thus, more work would be needed to reveal its geographical colouration patterns.

An interesting case of colour polymorphism occurs in the Müllerian mimic **Rhynchium oculatum**. Three subspecies (sometimes considered as colour forms) of **Rhynchium oculatum** with slightly different colour pattern have been described (Gusenleitner 2000). In the Eastern Mediterranean, we found **Rhynchium o. hebraeum** (Giordani Soika 1952), with a red thorax and yellow and red patterns on the abdomen, which occurs in sympatry with **Vespa orientalis**, which it closely resembles. In the Central Mediterranean, **Rhynchium o. oculatum** (F. 1781) is present; thus, it overlaps with **Vespa orientalis** as well as with **Vespa crabro**. Interestingly, co-occurrence with both hornet species may
have led to the evolution of a black pattern on the thoracic dorsum and black markings on the yellow abdomen in *Rhynchium o. oculatum*; therefore, it resembles *Vespa crabro* rather than *Vespa orientalis*. In contrast, *Rhynchium o. ibericum* Giordani Soika, 1966, which occurs on the Iberian Peninsula, where only *Vespa crabro* occurs, is mostly red, with a black pattern on the thorax and only small yellow markings on the 2nd tergite. The thorax is darker with less pronounced abdominal patterns, which means it resembles *Vespa crabro* rather imperfectly. Colour polymorphism is affected by abiotic factors such as temperature, documented in various mimics and models (e.g. Dušek and Láska 1974; Osten 2000; Knapp and Nedvěd 2013); thus, the shared black pattern might also be caused by convergent adaptation to the local climate conditions.

Batesian mimic *Volucella zonaria* displays variable mimetic accuracy based on geographic location. We compared the *Vespa orientalis* and its Batesian mimic, hoverfly *Volucella zonaria*, with the related mimetic pair of the *Vespa crabro* and its mimic *Volucella inanis*. Although distribution areas of both mimetic pairs overlap, the area of *Volucella inanis* and *Vespa crabro* is shifted more northwards. However, *Volucella zonaria* undergoes annual migration to Central and Northern Europe and it is expanding northward in recent years (Morris and Ball 2004), resulting in increasing geographical overlap with *Vespa crabro* and *Volucella inanis*, out of the range of *Vespa orientalis*. Thus, in the Mediterranean, *Volucella zonaria* might be a perfect mimic of *Vespa orientalis*, whereas in Northern Europe, it might be an imperfect mimic of *Vespa crabro*. However, as the colouration of this species seems to vary in some localities (van der Goot 1961), more evidence would be needed to confirm this assumption. Interestingly, perfect Batesian mimic *Volucella inanis* occurs in sympatry with its model *Vespa crabro* across its whole geographical range, although it also partly overlaps with *Vespa orientalis*.

In the last few decades a shift of geographic range has been observed in mimics (*Volucella zonaria* in Morris and Ball 2004) as well as models (*Vespa orientalis* in Zachi and Ruicănescu 2021). The rapidly changing climate of Anthropocene could give us a unique opportunity to observe interactions between mimics and their predators, where Batesian mimics are expanding their range beyond that of their models, with a possibility of then developing imperfect mimicry. In addition, climate could also affect the phenological patterns of mimics and their models, leading to more ‘model-first’ interactions (Hassall et al. 2019).

We characterized the Batesian-Müllerian mimicry ring of seven species around *Vespa orientalis* in the western Palearctic. Phenology, natural history, and the distribution of all species were reviewed. Previous studies on phenological patterns of mimics have provided ambivalent results; this study provides evidence that the *Vespa orientalis* mimicry ring fits the ‘model-first’ scenario. Review of distribution revealed differences in areas of species, forming Eastern Mediterranean, Mediterranean, and extending Mediterranean branches. We conclude that colour polymorphic species might resemble two different models (*Vespa orientalis*, *Vespa crabro*) across their distribution range. Moreover, we proposed that mimetic accuracy might vary across the distribution range of the migratory and expanding Batesian mimic *Volucella zonaria*, which seems to be a perfect mimic of *Vespa orientalis*, although an imperfect mimic of *Vespa crabro*. 
**Conclusion**

Our results highlight the complexity of the proposed Batesian-Müllerian mimicry ring around the Oriental hornet (*Vespa orientalis*). Bringing the information on phenology, ecological strategy, colouration patterns and geographical distribution together is an approach that could deepen our understanding of the ecology and evolution of mimicry. We encourage the application of the eco-evolutionary approach to mimicry research, as it could help in further investigations of mimicry rings and explanation of phenomena such as the existence of imperfect mimicry.

**Acknowledgements**

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**Supplementary material 1**

**Data of distribution**

Authors: Antonín Hlaváček, Klára Daňková, Daniel Benda, Petr Bogusch, Jiří Hadrava

Data type: excel file

Explanation note: Distribution data excerpted from literature.

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Link: https://doi.org/10.3897/jhr.92.81380.suppl1
Supplementary material 2

Appendix 1
Authors: Antonín Hlaváček, Klára Daňková, Daniel Benda, Petr Bogusch, Jiří Hadrava
Data type: Species account (docx. file)
Explanation note: Natural history of species within *Vespa orientalis* mimicry ring.
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.
Link: https://doi.org/10.3897/jhr.92.81380.suppl2
A new species of Methocha Latreille (Hymenoptera, Tippiidae, Methochinae) from China, with a key to the Chinese species

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Abstract

A new species, namely Methocha transcarinata sp. nov., is described and illustrated from Guangdong and Hainan, China. Additionally, M. cariniventris Narita & Mita, 2018 and M. kandyensis Krombein, 1982 are newly recorded from China. A key to all the known species of the genus from China is updated.

Keywords

China, Methochinae, Methocha, new record, new species
Introduction

The subfamily Methochinae is a relatively small taxon of parasitic aculeate wasps containing two genera *Methocha* Latreille 1804 and *Karlissa* Krombein 1979. The genus *Methocha* includes 89 species and three subspecies worldwide except for the Australian Region (Lin 1966; Krombein 1982; Terayama and Mita 2015; Narita and Mita 2018, 2021; Terayama 2019; Hanima et al. 2021; Agnoli 2022), among which 45 species are distributed in the Oriental Region, ten species and two subspecies in the Palearctic Region, 25 species and one subspecies in the Ethiopian Region, five species in the Nearctic Region, and four in the Neotropical Region. Members of the genus *Methocha* show distinct sexual dimorphism with wingless ant-like females and winged males. Although the biological habit of most species is still unknown, larvae of *Methocha* are considered to be specialized ectoparasitoids of tiger beetle (Carabidae: Cicindelinae) larvae (Narita and Mita 2018). In China, so far there is no systematic study on the genus except that a total of 13 species were sporadically recorded by Smith (1869), Strand (1913), Williams (1919), Lin (1966), Tsuneki (1986) and Narita and Mita (2021). In the present paper, a new species is described and illustrated in detail, and two species are newly recorded with main morphological characters and figures. Based on related references and our collections, an updated key to all Chinese species of *Methocha* is also presented.

Materials and methods

Specimens examined in this study are deposited in Chongqing Normal University, Chongqing, China (CNU), Yunnan Agricultural University, Kunming, China (YNAU), and Institute of Plant Protection, Guangdong Academy of Agricultural Sciences, Guangzhou, China (IPP-GAAS). They were collected mainly by active hand netting and Malaise traps which were set in various habitats and emptied once a month on average. The descriptions of specimens were made under an Olympus SZ2-ILST stereomicroscope. All photographs were taken and measured with a KEYENCE-VHX-5000 stereomicroscope, and plates were arranged with Photoshop CS 6. Body length was measured from the anterior margin of the head to the posterior margin of the terminal metasomal segment. For the density description of punctures, “sparse” means that interspaces are larger than one punctures diameter, “moderate” means equal to one diameter, and “dense” means less than one diameter. Morphological terminology follows Lin (1966) and Narita and Mita (2021). The following abbreviations are used in this paper: AOL = distance between anterior and posterior ocellus; DAO = diameter of anterior ocellus; POL = distance between posterior ocelli; S = metasomal sternum; T = metasomal tergum; A = Antennal segment.
A new species of the genus *Methocha*

Taxonomy

Genus *Methocha* Latreille, 1804


*Spinolia* A. Costa, 1858, Fauna Napoli Scol.: 21. Synonym of *Methocha* by Dalla Torre, 1897: 1. Type species: *Spinolia italica* Costa, 1858, by monotypy.


**Diagnosis.** Males winged and females wingless; antennal lobe developed (Fig. 3) in both sexes; eye setose (Figs 2, 10, 18) in both sexes; in female mid and hind tibia each with 1 spur, and hind tibial spur with a row of comb-like spines; in male mid and hind tibia each with 2 spurs, and one of the two spurs with a row of comb-like spines; forewing with 2 submarginal cells enclosed by tubular veins (Figs 1, 9, 17).

*Methocha transcarinata* Liao, Chen & Li, sp. nov.

https://zoobank.org/CF1211FB-ACE9-404E-BAF1-ADB363A4235E

Figs 1–8

**Material examined.** Holotype, ♂, China, Guangdong Province, Guangzhou City, Zengcheng Distinct, Xiaolou Town (Malaise trap), 23°55′20″N, 113°13′26″E, 114 m, 14.VI–1.VII.2019, Yi Guo (IPP-GAAS). Paratypes: 7♂, same as holotype; 1♂, China, Hainan Province, Changjiang County, Shilu Town, Baomeiling Nature Reserve (Malaise trap), 19°43′11.9″N, 109°37′48″E, 738 m, 3.VI–5.VII.2021, He-Shen Wang (CNU).

**Diagnosis.** This species can easily be separated from all other members of the genus by the following characters: dorsal surface of propodeum (Fig. 6) posteriorly with transverse carina between dorsal and posterior surfaces; meseipisternum anteriorly with strong carina followed by deep, smooth groove (Fig. 7).

**Description. Male.** (Figs 1–8). Body length 9.2–9.6 mm, fore-wing length 5.3–6.4 mm. Body (Fig. 1) almost black; antenna, mandible (Fig. 2), postero-lateral margin of pronotum, tegula, and leg dark brown to black. Wings untinted, veins and stigma brown.

**Head.** Head 0.71–0.75 times as high as wide in frontal view; clypeus distally circularly emarginated, and entire scleritized, without membranous area, surface with
Figures 1–8. *Methocha transcarinata* sp. nov., holotype, ♂. 1 habitus (dorsal view) 2 head (frontal view) 3 head (lateral view) 4 head (dorsal view) 5 pronotum (dorsal view) 6 propodeum (dorsal view) 7 mesosoma (lateral view, anterior to right) 8 T1 and T2 (dorsal view).
sparse and minute punctures, medially with obtuse prominence (Fig. 3); mandible distally not narrowed; ventral surface of A1 with longitudinal carina; frons with moderate to dense punctures; POL: AOL: DAO = 1: 1: 0.69 (Fig. 4), vertex (Fig. 4) and gena with sparse and minute punctures.

**Mesosoma.** Pronotal transverse carina absent (Fig. 5), dorsal surface of pronotum sparsely minutely punctate; anterior half of pronotum latero-ventrally with sparse minute punctures (Fig. 7), antero-ventrally carinate, with groove behind carina containing short striae, posterior half smooth and impunctate; mesonotum medially with sparse punctures and laterally with dense punctures; mesepisternum (Fig. 7) anteriorly with strong carina followed by deep, smooth groove, elsewhere with sparse and minute punctures; scutellum sparsely punctate; metanotum medially with U-shaped depression, elsewhere sparsely striate, and with smooth interspaces; dorsal surface of propodeum (Fig. 6) with broad median groove and granulate interspace, posteriorly with strong transverse carina between dorsal and posterior surfaces, antero-laterally with longitudinal striae, postero-laterally with irregular areolate sculpture; posterior surface of propodeum medially smooth, laterally with coarse and large punctures; lateral surface (Fig. 7) of propodeum antero-ventrally with oblique striae, postero-ventrally smooth, dorsally with coarse punctures. Claws of hind tarsus with subapical tooth shorter than half of apical tooth.

**Metasoma.** Metasomal terga sparsely punctate and with smooth interspaces. T1 (Fig. 8) antero-laterally with pair of strong longitudinal carinae, and with shallow median groove between longitudinal carinae. T1 transversely depressed posteriorly, T2–T6 and S2–S6 transversely depressed both anteriorly and posteriorly, anterior depressions of both T2 and S2–S6 costate, anterior ones of T3–T6 and posterior ones of both T1–T6 and S2–S6 smooth. S1 with sparse punctures; S2–S6 anteriorly with dense punctures, posteriorly with sparse ones, medially without longitudinal depression; S7 sparsely punctate and with smooth interspaces.

**Female.** Unknown.

**Distribution.** China (Guangdong, Hainan).

**Etymology.** The specific name *transcarinata* is derived from the two Latin words: *trans- (= transverse) + carinata (= carinate)*, referring to the propodeum with a transverse carina between dorsal and posterior surfaces.

*Methocha cariniventris* Narita & Mita, 2018, new record
Figs 9–16


**Material examined.** 4♂, China, Yunnan, Jinghong City, Menghai County, Bulang Mountain (Malaise trap), 21°37’43.87’’N, 100°24’18.97’’E, 1420 m, 25.IV–9.VIII.2018, Qiang Li (YNAU); 1♂, China, Yunnan, Hani-Yi Autonomous Prefecture of Honghe, Lvchun County, Water-shed, 22°59’18.5’’N, 102°27’14.7’’E, 1900–1980 m, 25.VII.2003, Jia Lu (YNAU).
Figures 9–16. *Methocha cariniventris*, ♂. 9 habitus (dorsal view) 10 head (frontal view) 11 head (lateral view) 12 head (dorsal view) 13 pronotum (dorsal view) 14 propodeum (dorsal view) 15 mesosoma (lateral view, anterior to the right) 16 T1 and T2 (dorsal view).
Diagnosis. Male (Fig. 9). Head 0.7 times as high as wide in frontal view (Fig. 10); clypeus (Fig. 10) distally with triangular membranous area, medially with carinate prominence (Figs 10, 11); mandible distally not narrowed (Fig. 10); ventral surface of A1 with longitudinal carina (Fig. 11); POL: AOL: DAO = 1.0: 1.0: 0.6 (Fig. 12); pronotum dorsally with sparse and minute punctures (Fig. 13), laterally strongly striate (Fig. 15); anterior margin of mesepisternum (Fig. 15) with strong carina followed by deep, costate groove, carina dorsally weak, surface reticulate; propodeum (Fig. 14) anteriorly with longitudinal striae, medially irregularly reticulate without groove, and posteriorly with transverse striae; lateral surface of propodeum antero-ventrally with oblique striae, dorsally with dense punctures; T1 (Fig. 16) anteriorly with pair of longitudinal carinae and median groove; anterior transverse depression of T2 (Fig. 16) costate; anterior transverse depression of T3 weakly costate; anterior transverse depression of T4–T6 smooth; S2–S6 medially without longitudinal depression.

Female. Unknown.

Distribution. China (new record: Yunnan); Laos.

*Methocha kandyensis* Krombein, 1982, new record
Figs 17–24


Material examined. 1♂, China, Fujian Province, Nanping City, Wuyi Mountain Nature Reserve (Malaise trap), 27°44′32.52″N, 117°40′56.23″E, 707 m, 08.VII.2021, Jin-Lan Li (CNU).

Diagnosis. Male (Fig. 17). Head 0.76 times as high as wide in frontal view (Fig. 18); clypeus (Fig. 18) distally with triangular membranous area, medially with carinate projection (Figs 18, 19); mandible distally not narrowed (Fig. 18); ventral surface of A1 with longitudinal carina (Fig. 19); POL: AOL: DAO = 1.0: 1.0: 0.83 (Fig. 20); pronotum anteriorly with short transverse striae, posteriorly with very sparse and minute punctures (Fig. 21), laterally medially strongly striate, latero-ventrally striate (Fig. 23); anterior margin of mesepisternum with strong carina followed by deep, costate groove, carina dorsally weak; propodeum anteriorly with longitudinal striae, posteriorly irregularly reticulate, laterally postero-ventrally with oblique striae, dorsally with dense punctures; T1 (Fig. 24) anteriorly with pair of longitudinal carinae, and with median groove and longitudinal striae between longitudinal carinae; anterior transverse depression of T2 (Fig. 24) costate; anterior transverse depression of T3–T6 smooth; S2–S6 medially without longitudinal depression.

Female. Unknown.

Distribution. China (new record: Fujian); Sri Lanka.
Figures 17–24. *Methocha kandyensis*, ♂. 17 habitus (dorsal view) 18 head (frontal view) 19 head (lateral view) 20 head (dorsal view) 21 pronotum (dorsal view) 22 propodeum (dorsal view) 23 mesosoma (lateral view, anterior to the right) 24 T1 and T2 (dorsal view).
A new species of the genus *Methocha* from China (modified from the key of Narita & Mita, 2021)

1. Winged (male) ................................................................. 2
   – Wingless (female) .......................................................... 13
2. Mesepisternum dorsally or ventrally with row of elongate foveae ............... 13
   – Mesepisternum wholly without elongate foveae (Fig. 7) ......................... 4
3. Clypeus distally deeply emarginate; mesepisternum dorsally foveolate ..........
   – Clypeus distally slightly emarginate; mesepisternum ventrally foveolate ....
   .................................................. *M. taiwanica* Tsuneki, 1986
4. Clypeus apically with triangular membranous area .................................. 5
   – Clypeus entirely sclerotized, apically without membranous area .............. 8
5. Claws of hind tarsus with subapical tooth shorter than half of apical tooth....
   – Claws of hind tarsus with subapical tooth almost as long as apical tooth....
   .................................................. *M. maai* Lin, 1966
6. Propodeum areolate; S2–S6 all distinctly depressed medially ...................... 9
   – Propodeum longitudinally striate; S2–S6 not depressed medially .............. 7
7. Pronotum anteriorly with transverse and short striae, posteriorly with sparse and minute punctures (Fig. 21), laterally strongly striate (Fig. 23) ....
   .................................................. *M. kandyensis* Krombein, 1982
   – Pronotum wholly with sparse minute punctures (Fig. 13), laterally weakly striate, latero-ventrally smooth (Fig. 15) .................. *M. cariniventris* Narita & Mita, 2018
8. Mandible distally not narrowed ....................................................... 11
   – Mandible narrowed in distal half or third ............................................
9. Dorsal surface of propodeum (Fig. 6) with transverse carina between dorsal and posterior surfaces .................. *M. transcarinata* Liao, Chen & Li, sp. nov.
   – Dorsal surface of propodeum evenly sculptured, without transverse carina between dorsal and posterior surfaces ........................................... 10
10. Propodeum dorsally distinct areolate, with smooth interspaces .............. *M. areolata* Lin, 1966
   – Propodeum dorsally longitudinally striate, with granulate interspaces ....
   .................................................. *M. cirrhocrus* Narita & Mita, 2021
11. Clypeus medially with obtuse prominence; pronotum anteriorly with transverse short striae .................. *M. mandibularis* (Smith, 1869)
   – Clypeus medially with acute prominence; pronotum anteriorly without striae, instead with dense large punctures ............... *M. cavipyga* Lin, 1966
13 All tarsal claws with subapical tooth equal to or longer than apical tooth..\textbf{14}
– All tarsal claws with subapical tooth shorter than apical tooth............\textbf{15}
14 Gena narrowed ventrally, posterior margin slightly incurved in lateral view; mesosoma entirely black .................................................................\textbf{M. maai Lin, 1966}
– Gena wider than that of the above species, posterior margin subangularly incurved in lateral view; mesosoma dark reddish...........\textbf{M. plana Lin, 1966}
15 Both frons and distal two-thirds of clypeus rugose\textbf{M. foveiventris Lin, 1966}
– Both frons and distal one-thirds of clypeus not rugose, instead impunctate or punctate........................................................................................................\textbf{16}
16 Frontal tubercles above antennal sockets absent ..................................\textbf{17}
– Pair of frontal tubercles above antennal sockets present............................\textbf{18}
17 Clypeal apex incurved........................................................................\textbf{M. emarginata Lin, 1966}
– Clypeal apex truncate..........................................................\textbf{M. formosana Williams, 1919}
18 Pronotum strongly convex, without median groove............................
.................................................................................................................................\textbf{M. articulata (Latreille, 1792)}
– Pronotum not strongly convex, and with weak median groove.............
.................................................................................................................................\textbf{M. priorrecta Lin, 1966}

\textbf{Acknowledgements}

We are very grateful to Prof. Qiang Li and Prof. Li Ma (Yunnan Agricultural University, Kunming, China) and Dr. Kai-Qin Li (Kunming Institute of Zoology, Kunming, China) for providing us with the specimens from collections under their care. We also thank Dr. P. Girish Kumar (Western Ghat Regional Centre, Zoological Survey of India, Kozhikode, Kerala, India) and Dr. Toshiharu Mita (Kyushu University, Fukuoka, Japan) for offering copies of some references. This study was funded by the National Natural Science Foundation of China (Nos: 31372247, 31000976) and China Agriculture Research System of MOF and MARA (No: CARS-32).

\textbf{References}


Latreille PA (1809) Genera Crustaceorum et Insectorum, etc. Tomus quartus et ultimus. Amand Koenig, Parisiiis et Argentorati (= Paris and Strasbourg), 399 pp.


New distributional records of *Celonites tauricus* (Hymenoptera, Vespidae, Masarinae) and new data on its behaviour at flowers

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Abstract

New records of *Celonites tauricus* Kostylev, 1935 are reported from Chios, Rhodes, Samos (Greece), Dagestan (Russia), Georgia, and the main portion of Azerbaijan (previous records were made from the Nakhchivan Autonomous Republic only). Flower visits of imagines were observed at six species of Lamiaceae, four of them being recorded for the first time as forage plants of *C. tauricus*. The newly recorded *Teucrium canum* Fisch. & C.A. Mey. and *Ziziphora taurica* M. Bieb. (both Lamiaceae) are principal forage plants in Dagestan and the Crimea, correspondingly. The behaviour of females at flowers of *Z. taurica* differs from that previously described at flowers of *Teucrium chamaedrys* L. and *Satureja thymbra* L. (also Lamiaceae) in that pollen removal from the anthers and nectar uptake take place separately from each other in temporal succession. This difference is obviously caused by the flower structure of the genus *Ziziphora*, specifically its much longer corolla tube. Females also try to collect pollen from flowers of *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó but usually without success, while nectar uptake from this species is successful. The specialized morphological structures of the females for pollen-uptake from the nototribic anthers and pollen-transfer from the exoskeleton to the mouthparts are described. They are similar to those of the closely related *Celonites abbreviatus* (Villers, 1789), and consist
of specialized stiff “knobbed” pollen-collecting setae covering the anterior surface of the head, particularly the frons and the clypeus, as well as comb-like rows of specialized, particularly strong pollen-brushing setae along the anterior margins of the inner surface of the first and the second segments of the fore tarsi. Males of *C. tauricus* patrol in flight along the forage plants of the females. Successful copulations occur either on flowers or on the ground.

**Keywords**
Caucasus, Crimea, mating behaviour, pollen wasps, *Salvia*, trophic relationships, *Teucrium*, *Ziziphora*

**Introduction**

With 374 described species (the latest calculation published by Rahmani et al. 2020), the pollen wasps or the subfamily Masarinae *s. l.* (including Gayellinae) are distributed through Mediterranean and temperate to hot semi-arid to arid areas of the world outside the tropics but not further north than 50°N or further south than 50°S (Gess 1996; Gess and Gess 2010). The females of pollen wasps live solitarily and provision their larvae with pollen instead of paralysed insect prey as a protein source (Gess 1996; Gess and Gess 2010; Mauss et al. 2019). This bee-like life form has probably evolved within the stem lineage of the Masarinae (Carpenter 1982, 1988; Mauss 2007), though a recent molecular phylogenetic analysis indicates that it might have evolved independently within the Gayellini and Masarini (Piekarski et al. 2018). Many pollen wasp species are oligolectic, i.e., adapted to collect pollen and nectar from a narrow range of forage plants (Gess 1996; Gess and Gess 2010). Most of them are poorly known and rarely collected insects. These wasps are particularly sensitive to habitat changes due to special requirements to the presence of their forage plants and a suitable nesting site (Gess and Gess 2010).

*Celonites tauricus* Kostylev, 1935 is a species of pollen wasps hitherto known from the Crimea, Kos, Armenia, Nakhchivan Autonomous Republic of Azerbaijan, Turkey, Cyprus, Syria, and Northern Iran (Mauss et al. 2016; Fateryga 2017; Fateryga et al. 2021). Bionomics of *C. tauricus* was studied in the Crimea and in Kos. The species is known to visit nototribic flowers of six species of Lamiaceae of the genera *Satureja* L., *Teucrium* L., *Thymus* L., and *Ziziphora* L. while the primary forage plants are *Teucrium chamaedrys* L. in the Crimea and *Satureja thymbra* L. in Kos. Pollen uptake from such flowers is performed with specialized stiff “knobbed” setae on the frons (Mauss et al. 2016). Nesting of *C. tauricus* is poorly known: only three nests of this species were found in the Crimea. They consisted of one, two, and three cylindrical mud cells attached to the underside of small stones (Mauss et al. 2016).

The purpose of the present contribution is to report new distributional records of *C. tauricus*, as well as new forage plant records, and to describe the behaviour of the imagines at flowers. Specialized pollen-collecting and pollen-brushing structures of the female of *C. tauricus* are also briefly described within the framework of this study.
New records of *Celonites tauricus* and its behaviour at flowers

**Materials and methods**

Field observations were carried out in Dagestan in the vicinity of Talgi (Makhachkala urban okrug, 42.876697°N, 47.445123°E, ca. 270 m a.s.l.) on 12.06.2019 and in the Crimea in Lisya Bay (Feodosiya urban okrug, 44.898251°N, 35.157508°E, ca. 25 m a.s.l.) on 07.06.2020 and 10.06.2020. The first locality (Fig. 1A) was an abandoned open mine covered with sparse herbaceous vegetation with solitary shrubs of *Cotinus coggygria* Scop. and *Rhus coriaria* L. (both Anacardiaceae). The most prominent plants in flower were *Cachrys microcarpos* M. Bieb. (Apiaceae), *Teucrium canum* Fisch. & C.A. Mey., *T. chamaedrys* (Lamiaceae), and *Capparis spinosa* var. *herbacea* (Willd.) Fici (Capparaceae). The second locality (Fig. 1B) was a dry stony streambed surrounded with semidesertic dry terraces with solitary trees of *Elaeagnus angustifolia* L. (Elaeagnaceae). Plants in flower were very scarce there; the most numerous one was the annual *Ziziphora taurica* M. Bieb. (Lamiaceae) that occurred within a small spot in the streambed while some other species were sparsely distributed across the terraces.

Wasp activity was observed visually and documented using a Canon EOS M6 camera with a Sigma AF 105 mm f/2.8 macro lens (scale up to 1:1). Flower preferences of the wasps were studied by counting the number of sightings (= first observations) of flower visiting individuals while walking randomly across the locality. Total investigation time was about two hours in the vicinity of Talgi and about 10 hours in Lisya Bay.

Additional material was examined in museum collections abbreviated as follows: **AMNH** – American Museum of Natural History (New York, USA), **FSCV** – Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences (Vladivostok, Russia), **MSNVE** – Natural History Museum of Venice (Venice, Italy), **OLML** – Upper Austrian State Museum (Linz, Austria), **ZISP** – Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), **ZMMU** – Zoological Museum of the M.V. Lomonosov Moscow State University (Moscow, Russia), **AF** – collection of A.V. Fateryga (Feodosiya, Russia), **JG** – collection of J. Gusenleitner (Linz, Austria), and **VM** – collection of Volker Mauss (Michelfeld, Germany). Every specimen examined by V. Mauss was labelled with an individual, serial database number (dbM = database Mauss) printed on the determination label.

The species affiliation of the specimens recorded in Dagestan that are lacking the characteristic dark antennal tips of typical *C. tauricus* (Mauss et al. 2016) was proofed by DNA barcoding in addition. Sequencing was accomplished by AIM Advanced Identification Methods GmbH Leipzig following standard methods of DNA extraction from a single female (dbM 5998) collected and stored in 96% pure ethanol, PCR for Cytochrome Oxidase subunit 1 (COI-5P), cycle sequencing of forward and reverse strand and sequence editing. The obtained COI-5P sequence is 286 bp long (BOLD process ID CECYP021-22) and clusters closely together with sequences available for typical specimens of *C. tauricus* from Kos.

SEM micrographs of the wasp structures were taken using a Hitachi SE3500 Scanning Electron Microscope. Two female specimens from Dagestan and one from the
Crimea were studied and compared with a female of *Celonites abbreviatus* (Villers, 1789) from Greece (dbM 2823). The wasp fragments were simply air-dried, mounted on stubs and coated with gold and palladium.

**Figure 1.** Habitats of *Celonites tauricus* Kostylev, 1935 **A** vicinity of Talgi in Dagestan **B** Lisya Bay in the Crimea.
Results and discussion

*Celonites tauricus* Kostylev, 1935

*Celonites abbreviatus tauricus* Kostylev, 1935: 108, [@♀]. Type locality: “Крым” [Crimea]; neotype (designated by Mauss et al. 2016), @♀ (dbM 4305): Crimea, vicinity of Feodosiya, Lisya Bay, 16.06.2010, A. Fateryga [OLML].

*Celonites spinosus* Gusenleitner, 1966: 359–362, @♀♂. Type locality: “Кусадаси” [Turkey]; holotype, @♀ (dbM 4665): Turkey, Kusadasi, 11.06.1964, J. Gusenleitner [JG]. Synonymized by Mauss et al. (2016).

*Celonites abbreviatus invitus* Gusenleitner, 1973: 58–59, @♀♂. Type locality: “Türkei, Gürün” [Turkey]; holotype, @♀ (dbM 4662): Turkey, Gürün, 05.06.1970, J. Gusenleitner [JG]. Synonymized by Mauss et al. (2016).


Russia: Dagestan: [Makhachkala urban okrug], vicinity of Talgi, 42.8767°N, 47.4451°E, 25.06.2018, 1 @♂, leg. Yu. Astafurova, K. Fadeev, V. Loktionov, M. Mokrousou & M. Proshchalykin [AF]; ibid., on *Teucrium canum*, 12.06.2019, 2 @♀, 1 @♂, leg. A. Fateryga [AF], 1 @♀ (dbM 5511), 1 @♂ (dbM 5510), leg. A. Fateryga [VM], 13.06.2021, 1 @♀, leg. A. Fateryga [AF], 18.06.2021, 1 @♀ (dbM 5998, BOLD process ID CECYP021-22), leg. A. Fateryga [VM]; Crimea: [Yalta urban okrug], Miskhor, [44.4289°N, 34.0855°E], 01.08.1887, 1 @♀ [ZISP]; Sudak urban okrug, Cape Meganom [44.7940°N, 35.0815°E], 27.05.2016, 1 @♂, leg. A. Fateryga [AF]; ibid., on *Ziziphora taurica*, 27.05.2016, 1 @♀, leg. A. Fateryga [AF]; Feodosiya urban okrug, Lisya Bay, [44.8983°N, 35.1575°E], 22.06.2016, 1 @♂, leg. A. Fateryga [AF].

Georgia: Kasbek, [42.6950°N, 44.5147°E], 1 @♀ [ZISP].

Azerbaijan: [Masally District], Zuvand, [39.0048°N, 48.4771°E], 08.06.1985, 1 @♂, leg. V. Tobias [FSCV].

Turkey: Ankara Dikmen, [39.8650°N, 32.8570°E], 05.07.1959, 1 @♀ (dbM 5652), leg. K. Guichard [MSNVE].

Cyprus: Ca. 5 km N Lemithou, Pinus-Zone, 34.9689°N, 32.8075°E, 15.06.2013, 1 @♀ (dbM 5348), leg. A. Ebmer [OLML]; Troodos, Mt. Olympos N, Pinus-Zone, 34.9289°N, 32.8703°E, 10.06.2013, 1 @♀ (dbM 5347), leg. A. Ebmer [OLML]; Troodos, Mt. Olympos N, Pinus-Zone, 34.9417°N, 32.8703°E, on *Nepeta troodi*, 11.06.2013, 1 @♀ (dbM 5346), leg. A. Ebmer [OLML]; Mt. Troodos, [34.9234°N, 32.8808°E], 28.06.1937, 1 @♀ (dbM 5622), leg. G. Mavromoustakis [MSNVE]; ibid., 12.08.1948, 1 @♀ (dbM 5620), leg. G. Mavromoustakis [MSNVE]; ibid., 02.08.1965, 1 @♀ (dbM 5621), leg.

**Distribution.** Greece (Chios, Kos, Rhodes, Samos), Russia (Dagestan, Crimea), Georgia, Armenia, Azerbaijan, Turkey, Cyprus, Syria, Iran. The species is new to Chios, Rhodes, Samos, Dagestan, Georgia, and the main portion of Azerbaijan (previous records were made from the Nakhchivan Autonomous Republic only). The examined specimen from Armenia was reported by Kostylev (1929) as *Celonites abbreviatus*.

**Flower-visiting records.** *Teucrium canum* was the only plant species observed to be visited by males and females of *Celonites tauricus* in Dagestan (Table 1), while they were not recorded on three other species of *Teucrium* flowering at the same locality, namely *Teucrium chamaedrys*, *Teucrium hyrcanum* L. and the species known in the flora of Dagestan (Murtazaliev 2009) as *Teucrium polium* L. “*Teucrium polium*” was previously recorded as a forage plant of *Celonites tauricus* in the Crimea (Mauss et al. 2016), but it has to be noted that there is a taxonomic problem with this plant taxon. True *T. polium* does not occur in Eastern Europe, while the species commonly known there as “*T. polium*” is currently treated as *Teucrium capitatum* L. (Tutin and Wood 1972; Govaerts et al. 2005–2022; Fateryga and Fateryga 2019). On the other hand, the lectotype designated for *T. capitatum* (Rosúa and Navarro 1987) does not correspond very well to “*T. polium*” from Eastern Europe (including Dagestan and the Crimea), and seems to belong to a different taxon.

Specimens of *Celonites tauricus* were observed in the Crimea in 2020 at flowers of five species of Lamiaceae (Table 1). Two of them, that is *Teucrium chamaedrys* and *Thymus tauricus* Klokov & Des.-Shost., were previously recorded as forage plants of this wasp (Mauss et al. 2016), while *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó and two annual species of *Ziziphora* are reported for the first time. The principal forage plant was *Ziziphora taurica* followed by *T. chamaedrys*, while visits to the remaining species were occasional.

The identity of the subspecies of *Salvia nemorosa* L. is also taxonomically complicated. It is generally accepted under the name “*Salvia nemorosa* subsp. *pseudosylvestris* (Stapf) Bornm.” (Govaerts et al. 2005–2022; Yena 2012) despite

<table>
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<tr>
<th>Plant taxon</th>
<th>Σ sightings of flower-visiting individuals</th>
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<td>Dagestan, 2019</td>
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<td>Lamiaceae</td>
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<td><em>Salvia nemorosa</em> subsp. <em>tesquicola</em> (Klokov &amp; Pobed.) Soó</td>
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<td><em>Teucrium canum</em> Fisch. &amp; C.A. Mey.</td>
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<td><em>Teucrium chamaedrys</em> L.</td>
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<td><em>Thymus tauricus</em> Klokov &amp; Des.-Shost.</td>
<td>13</td>
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<tr>
<td><em>Ziziphora capitata</em> L.</td>
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<td><em>Ziziphora taurica</em> M. Bieb.</td>
<td>25</td>
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<td>Other plant taxa</td>
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**Table 1.** Flower-visiting records of females and males of *Celonites tauricus* Kostylev, 1935.
the fact that such a nomenclatural combination was not validly published, because Bornmüller (1907) applied it to a variety *S. nemorosa* var. *pseudosylvestris* (Stapf) Bornm. (as “*pseudo-silvestris*”), not a subspecies.

**Behaviour of females at flowers.** The behaviour of females of *Celonites tauricus* at flowers of *Teucrium canum* in Dagestan was similar to the previously described behaviour of this species at flowers of *Teucrium chamaedrys* in the Crimea and at flowers of *Satureja thymbra* in Kos (Mauss et al. 2016). During these flower visits, the females stood on the lower lip of a flower and took up nectar and pollen simultaneously. The proboscis was protruded deeply into the corolla tube while the female performed rapid back and forth movements of the anterior part of her body, rubbing her head over the nototribic anthers. In this manner pollen grains were removed from the pollen sacs and accumulated on frons and clypeus. Periodically flower visiting was interrupted and the pollen grains were transferred from the frons to the mouthparts by alternating brushing movements of the fore legs and the pollen was being ingested. This pollen-brushing behaviour took place either on flowers or on the ground in the close vicinity of the plants. Similar behaviour was observed in the Crimea in 2020 at flowers of *T. chamaedrys* and *Thymus tauricus*.

The behaviour of females at flowers of *Ziziphora taurica* was different. The behavioural sequence of such a flower visit could be usually subdivided into three phases. During the first phase, a female stood on the lower lip of a flower and performed rapid movements of her head for a very short period (not longer than a second), rubbing its anterior parts over the anthers (Fig. 2A). In the following second phase, the female protruded her proboscis and moved her body headfirst deeply into the corolla tube so that only the posterior half of her body remained visible in outside view. During this phase, the anthers were in contact with the dorsal mesosoma and often also with the first and the second metasomal tergum (Fig. 2B). The duration of the second phase was much longer than the first one; usually it lasted for some seconds. The third phase started, when the female retracted her proboscis and appeared outside the corolla tube again. Then she was rubbing her head over the anthers once more so that pollen accumulated on her frons (Fig. 2C). Subsequently, the female usually performed pollen-brushing behaviour that took place on the same flower. Very often she brushed pollen from her frons while she was standing on the flower and continued to accumulate pollen on her clypeus that was still in contact with the anthers (Fig. 2D). After that, the pollen was brushed from the clypeus to the mouthparts as well (Fig. 2E). When the fore legs were brought between the mouthparts, the pollen was apparently ingested. After the pollen had been brushed from both the frons and the clypeus, the female sometimes repeated the rapid movements of her head, rubbing it over the anthers again, in the same way as in the first phase (Fig. 2F). The duration of the third phase was variable depending on how many times the wasp switched her behaviour from pollen removal from the anthers to brushing the pollen grains from the frons and the clypeus, and back; sometimes this phase was the longest. At regular intervals the females interrupted flower visits and stood on the ground. During this time, they performed alternating grooming movements of the fore legs over the body including the dorsal mesosoma and metasomal terga, covered with pollen grains.
Figure 2. Behaviour of females of *Celonites tauricus* Kostylev, 1935 at flowers of *Ziziphora taurica* M. Bieb. in Lisya Bay (details see text).
Thus, the pollen-collecting behaviour of the females of *Celonites tauricus* at flowers of *Ziziphora taurica* differs from that at flowers of *Teucrium*, *Satureja*, and *Thymus* in that pollen removal from the anthers and nectar uptake take place separately from each other in temporal succession. This difference is obviously caused by the flower structure of the genus *Ziziphora*, specifically its much longer corolla tube in comparison with that of the genera *Teucrium*, *Satureja*, and *Thymus*. Therefore, it is impossible for the wasps to reach the nectar with the proboscis and to make contact with the anthers with the frons simultaneously. A behavioural pattern similar to that of *C. tauricus* at flowers of *Z. taurica* is known for *Celonites sibiricus* Gusenleitner, 2007 at flowers of the genus *Dracocephalum* L. (also Lamiaceae) which also have a long corolla tube (Fateryga 2020). The main difference between them is that females of *C. sibiricus* do not return to pollen collection from the same flower after nectar uptake has been finished inside of the corolla tube.

The behaviour of females of *Celonites tauricus* at flowers of *Salvia nemorosa* subsp. *tesquicola* was similar to that at flowers of *Ziziphora taurica* in that the attempts to remove pollen from the anthers and nectar uptake also took place separately from each other in temporal succession. But in contrast, these pollen-collecting attempts by *C. tauricus* at *S. nemorosa* subsp. *tesquicola* usually failed. During the first phase, a female stood on the lower lip of a flower and attempted to rub over the anthers with her frons but usually she actually came into contact with the stigma instead of the anthers (Fig. 3A). During the second phase, the female protruded her proboscis deeply into the corolla tube while she performed rapid back and forth movements of the anterior part of her body, apparently trying to rub her head over the anthers, though the head was in fact not in contact with them (Fig. 3B). However, one female of *C. tauricus* was observed with yellow pollen of *Salvia* on the exoskeleton (well distinguishable from the white pollen of *Ziziphora*, the orange pollen of *Teucrium chamaedrys*, and the lilac pollen of *Thymus tauricus*). This means that at least sometimes the pollen-collecting attempts of *C. tauricus* females at *S. nemorosa* subsp. *tesquicola* are successful. There was no third phase observed at flowers of this species, i.e., the wasps did not return to separate pollen-collecting attempts after nectar uptake. Flower visits to *S. nemorosa* subsp. *tesquicola* occurred only occasionally (Table 1), i.e., this species was not a principal forage plant. Such visits to a suboptimal plant species might be caused by the scarcity of the pollen sources, since they were observed in a locality with very low abundance of flowering plants (see above).

The behaviour of *Celonites tauricus* at flowers of *Salvia nemorosa* subsp. *tesquicola* was somewhat similar to that observed for the closely related *Celonites abbreviatus* at flowers of *Salvia officinalis* L. (Schremmer 1959). In the latter case, the pollen removal from the anthers and nectar uptake also took place separately from each other in temporal succession. But in contrast to the situation in *C. tauricus*, the pollen-collecting attempts by *C. abbreviatus* at *S. officinalis* were always successful.

**Pollen-collecting and pollen-brushing structures.** Examination of a female of *Celonites tauricus* under a SEM revealed that it possesses the same morphological structures for pollen-uptake and pollen-transfer that were previously described in detail for the closely related *Celonites abbreviatus* (Schremmer 1959; Müller 1996). The pollen-
Figure 3. Behaviour at flowers and mating of *Celonites tauricus* Kostylev, 1935 in Lisya Bay. **A, B** females on flowers of *Salvia nemorosa* subsp. *tesquicola* (Klokov & Pobed.) Soó. **C** a male on a flower of *Ziziphora taurica* M. Bieb. **D, E** copulation on flowers of *Z. taurica*. **F** copulation on the ground.
New records of *Celonites tauricus* and its behaviour at flowers

Figure 4. SEM micrographs of the pollen-collecting and pollen-brushing structures of a female of *Celonites tauricus* Kostylev, 1935 A head in lateral view B close up of the frons (marked rectangular area in A) showing specialized stiff “knobbed” pollen-collecting setae C close up of “knobbed” setae (marked rectangular area in B) D inner surface of the left fore tarsal segments 1–3 E close up of the tarsomere 1 (left marked rectangular area in D) showing a comb-like row of specialized, particularly strong pollen-brushing setae along its anterior margin F the same for the tarsomere 2 (right marked rectangular area in D).
collecting apparatus consists of specialized stiff “knobbed” setae covering the anterior surface of the head, particularly the frons and the clypeus (Fig. 4A–C). Such a setation of the head is an apomorphic character of the members of the so-called C. abbreviatus-complex (Mauss 2013). Pollen grains are removed from the anthers with the aid of these “knobbed” setae and accumulate between them on the front of the head. Then the pollen grains are transported towards the mouthparts with the fore legs, which bear comb-like rows of specialized, particularly strong pollen-brushing setae along the anterior margins of the inner surface of the first and the second segment of the fore tarsi (Fig. 4D–F). Pollen grains that occasionally accumulate on other parts of the body, particularly on the dorsal mesosoma and metasomal terga, are also transferred towards the mouthparts with the help of these “combs” on the fore tarsi.

It is of note that the spherically swollen ends of the “knobbed” setae look somewhat flattened and often concave from one side in the SEM images (Fig. 4C). Such depressions on the spherical distal ends of the setae were not reported for C. abbreviatus (Schremmer 1959; Müller 1996) but were present in all four specimens of both species in our study and are also visible in some original SEM images provided by A. Müller from his investigation of C. abbreviatus published in 1996. These depressions may be artifacts resulting from air-drying, in which the original spherical shape of the swollen ends of the setae seems to collapse partially.

Male behaviour. Males of Celonites tauricus were mainly observed at the site with flowering Ziziphora taurica, where they patrolled in flight along the plants or visited flowers. During flower visits they always inserted their proboscis into the corolla tube indicating the uptake of nectar. After that, they often performed pollen-brushing behaviour in the course of which the pollen grains were transferred from the frons towards the mouthparts, indicating pollen consumption as well (Fig. 3C). Patrolling males pounced on females that were visiting flowers or standing on the ground. Successful copulation was observed five times: four times on flowers (Fig. 3D, E) and one time on the ground (Fig. 3F). Each time, the whole copulation lasted less than 10 s, which is similar to the documented copulation length in two other previously studied species of Celonites, namely C. abbreviatus (Mauss 2006) and C. fischeri Spinola, 1838 (Mauss and Müller 2014).

Conclusions

New records of Celonites tauricus from Dagestan, Georgia, and the main portion of Azerbaijan fill the gaps in its known distribution. The occurrence of the species in these areas was to be expected, since it was already known from neighbouring regions such as Armenia, Nakhchivan Autonomous Republic of Azerbaijan, and Northern Iran. The same is true for the records from Chios, Rhodes, and Samos. New data on forage plants and the flower-visiting behaviour of the wasps enlarge our bionomical knowledge of this species. The reported data confirm that C. tauricus is broadly oligolectic (sensu Müller and Kuhlmann 2008) exclusively visiting Lamiaceae. Moreover,
New records of *Celonites tauricus* and its behaviour at flowers

the observations point to a certain plasticity of the foraging behaviour of the females, which enables them to exploit the floral resources of a relatively broad range of various nototribic flowers of Lamiaceae as long as they fit in with their body proportions and pollen-collecting structures.

Oligolecy of variable degree seems to be typical of the genus *Celonites* Latreille, 1802. It was particularly confirmed to exist in other Palaeartic species visiting nototribic flowers of Lamiaceae that also use specialized pollen-collecting setae for pollen uptake from the anthers. From these species *Celonites abbreviatus*, which is closely related to *C. tauricus*, is evidently broadly oligolectic (Mauss 2006), while the just distantly related *Celonites sibiricus* has been recorded only on flowers of a single plant genus and thus can be treated as presumably narrowly oligolectic (Fateryga 2020). Species adapted to the pollen uptake from flowers of Boraginaceae with narrow corolla tubes, e.g., *Celonites heliotropii* Gess, 2007 from Namibia (Gess 2007; Gess and Gess 2010), *Celonites ivanovi* Mauss & Fateryga, 2022 from the Caucasus and *Celonites cagrii* Mauss & Yildirim, 2022 from east Anatolia (Mauss et al. 2022) are presumably also narrowly oligolectic, visiting exclusively flowers of plants belonging to the genus *Heliotropium* Tourn. ex L.

Most Afrotropical species of *Celonites* are broadly oligolectic visiting only a few closely related genera of either Scrophulariaceae or Campanulaceae (rarely Asteraceae in the case of *Celonites wheeleri* Brauns, 1905) but they are lacking specialized pollen-collecting structures and consume pollen directly from the anthers (Gess and Gess 1989, 2010). *Celonites capensis* Brauns, 1905 is, however, a clearly polylectic species visiting flowers of Asteraceae, Geraniaceae, Aizoaceae, Boraginaceae, Campanulaceae, Scrophulariaceae, and Iridaceae. These records indicate a certain plasticity of its behaviour. Another Afrotropical species, *Celonites promontorii* Brauns, 1905, collects pollen principally from Asteraceae but has been also recorded on flowers of two other plant families (Gess and Gess 1989, 2010). A few Palaeartic species that consume pollen directly from the anthers are known as narrowly oligolectic. These are *Celonites fischeri*, which is restricted to flowers of *Echium* Tourn. ex L. (Boraginaceae with broad corolla tubes) (Mauss and Müller 2014), and *Celonites kozlovi* Kostylev, 1935 that has been exclusively observed to collect pollen from nototribic flowers of *Dracocephalum* (Lamiaceae) but visits also several genera of Asteraceae for nectar uptake (Fateryga 2020). However, the narrow oligolecy of *C. kozlovi*, should be proofed in more detail, because it is not correlated with any specialized pollen-collecting structures present in other species of the genus that are adopted to pollen uptake from nototribic anthers. Finally, the presented data suggest that the trophic relationships of the genus *Celonites* with the angiosperm plants are still insufficiently studied (especially in the Palaeartic region) and that more field data are necessary to improve our knowledge on the ethology of these wasps.

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New records of *Celonites tauricus* and its behaviour at flowers


Mauss V (2013) Description of *Celonites andreasmuelleri* sp. n. (Hymenoptera, Vespidae, Masarinae) from the Middle East with a key to the Palaearctic species of the *C. abbreviatus*-complex of the subgenus *Celonites s. str*. Journal of Hymenoptera Research 31: 79–95. https://doi.org/10.3897/JHR.31.4235


A new species of Bocchus from upper Eocene Rovno amber (Hymenoptera, Dryinidae)

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Abstract

A new fossil species of Dryinidae (Hymenoptera, Chrysidoidea) from upper Eocene Rovno amber (Ukraine) is described: Bocchus rex sp. nov. It is compared with two other species of Bocchus known from European amber: B. primaevus Martins & Melo from Baltic amber and B. schmalhauseni Perkovsky, Olmi, Vasilenko, Capradossi & Guglielmino from Rovno amber. A new key to the Cretaceous and Paleogene species of Bocchus is presented. The Dryininae are the most common representatives in all the amber drynid faunas since the mid-Cretaceous. The Rovno amber fauna is an exception; possible explanations for the abundance of Bocchus species within this amber are presented.

Keywords

Bocchinae, Bocchus rex, Chrysidoidea, key, systematics
Introduction

Dryinidae (Hymenoptera, Chrysidoidea) are parasitoids of Auchenorrhyncha (Hemiptera) (Olmi 1984; Guglielmino et al. 2013). This family is present in all continents, except for Antarctica, and comprises about 1900 species (Olmi et al. 2021a).

Eighty fossil species of Dryinidae have been described, among which the following six have been recorded from upper Eocene Rovno amber (Ukraine; 35–38 Ma) (Martynova et al. 2019; Perkovsky et al. 2020; Olmi et al. 2022): Bocchinae: *Bocchus schmalhauseni* Perkovsky, Olmi, Vasilenko, Capradossi & Guglielmino, 2020; Dryininae: *Dryinus janzeni* Olmi, 2000, *D. reifi* Olmi & Bechly, 2001, *D. wunderlichi* Olmi & Bechly, 2001; Apodryininae: *Rovnodryinus khomychi* Olmi, Guglielmino, Vasilenko & Perkovsky, 2022; Palaeoanteoninae: *Palaeoanteon janzeni* Olmi, 2000. In contrast, Baltic and Scandinavian amber (coeval of Rovno amber) are known to include 21 and two species of Dryinidae (Martynova et al. 2019; Olmi et al. 2021b), respectively. All known specimens from Ukraine have been collected in the Varash district of the Rovno region (which includes the former Vladimirets and Zarechnoye districts) and most of the important new taxa described from Rovno amber during the last few years (Matalin et al. 2021; Perkovsky and Nel 2021; Tshernyshev and Perkovsky 2021; and references therein).

Recently, we received two pieces of Rovno amber: one from a site in the Volyn region adjacent to the Varash district and the second most probably from the Varash district. They included specimens of Dryinidae that proved to belong to a new species, which we describe below.

Materials and methods

Terms

The description follows the morphological terminology of Olmi et al. (2019). All measurements reported are relative, except for the total length (head to metasomal tip, without antennae and sting). Antennal proportions refer to the lengths of the relevant segments as proportions of each other, with the values rounded to the nearest whole number. The following abbreviations are used: POL, distance between the inner edges of the two lateral ocelli; OL, shortest distance between the edge of a lateral ocellus and the median ocellus; OOL, distance from the outer edge of a lateral ocellus to the compound eye; OPL, distance from the posterior edge of a lateral ocellus to the occipital carina; TL, distance from the posterior edge of the eye to the occipital carina.

The term “disc of metapetal-propodeal complex” is used here in the sense of Kawada et al. (2015) and Lanes et al. (2020). It corresponds to the term “dorsal surface of propodeum” *sensu* Olmi (1984) and Olmi et al. (2019). The term “propodeal declivity” *sensu* Kawada et al. (2015), used here, corresponds to the term “posterior surface of propodeum” *sensu* Olmi (1984) and Olmi et al. (2019). The names of veins of the fore wing are here used in the sense of Azevedo et al. (2018) and Lanes et al. (2020). The “stigmal vein” (*sensu* Olmi 1984 and Olmi et al. 2019) is named here the “second radial cross & radial sector (2r-rs&Rs)”. 
The term “ADOs” (= Antennal Dorsal Organs) is used here in the sense of Riolo et al. (2016). It corresponds to the term “rhinaria” sensu Olmi (1984). According to Riolo et al. (2016), ADOs are sensory structures that might mediate the antennal responses to vibratory stimuli. As far as we know, they are usually present in the antennae of dryinid females attacking Fulgoromorpha (Perkovsky et al. 2019).

Specimens

The specimens studied in this paper have been deposited in the following collections:

Specimen 1: Schmalhausen Institute of Zoology (SIZK), National Academy of Sciences of Ukraine, Kiev, Ukraine.
Specimen 2: State Museum of Natural History Stuttgart (SMNS), Stuttgart, Germany.

Stereomicroscopy

The multifocal photos were taken using a mirrorless Sony Alpha 6100 camera (Sony Group Corporation, Tokyo, Japan), with Canon bellows and three-way revolver for optical microscopy (Canon Inc., Tokyo, Japan). The following objectives were used: LOMO 3.7 × 0.11 (LOMO, St. Petersburg, Russia) for magnifications from 20 to 50×; Zeiss Semiplan 6.3 × 0.11 (Carl Zeiss GmbH, Jena, Germany) for magnifications from 50 to 100×. The motorized focus was managed by a Cognisys stackshot controller (Cognisys Inc., Traverse City, MI, USA). Captured images were merged into a single in-focus image by using ZereneStacker™ version 1.04 (Zerene Systems LLC, Richland, WA, USA). Images were processed with GIMP version 2.10.30 (https://www.gimp.org).

Synchrotron X-ray phase-contrast microtomography (SR-μCT) and image processing

Synchrotron X-ray microtomography (SR-μCT) (Betz et al. 2007) was performed at the UFO-I station of the Imaging Cluster at the KIT light source of Karlsruhe Institute of Technology (KIT, Karlsruhe, Germany) by using a parallel polychromatic X-ray beam produced by a 1.5 T bending magnet. Specimen 2 was glued onto a plastic pin and mounted onto the goniometer head of the sample stage for tomography. The beam was spectrally filtered with 0.5 mm aluminium with a spectrum peak around 15 keV and a full-width at half maximum bandwidth of about 10 keV. A fast indirect detector system was employed, consisting of a 13 μm LSO:Tb scintillator (Cecilia et al. 2011), diffraction limited optical microscope (Optique Peter) (Douissard et al. 2012) and a 12bit pco.dimax high-speed camera with a resolution of 2016 × 2016 pixels; 3000 projections were recorded at 70 frames per seconds and an optical magnification of 10×, resulting in an effective detector pixel size of 1.22 μm. Two separate overlapping image stacks were acquired because the specimen was larger than the field of view. Therefore, the sample was repositioned in between the imaging procedure, resulting in
a certain overlap of two consecutive images. The control system concert (Vogelgesang et al. 2016) was used for automated data acquisition and online reconstruction of tomographic slices for data quality assurance. Execution of the pipelines, including online tomographic reconstruction, was performed by the UFO framework (Vogelgesang et al. 2012). Final tomographic reconstruction was carried out with *tofu* (Faragó et al. 2022).

The two resulting tomograms were registered and calibrated with Fiji (Schindelin et al. 2012) (https://imagej.net/Fiji) and further imported to the plugin TrakEM2 (Cardona et al. 2012) for stitching and cropping. Subsequently, the resulting image stack was imported to Amira version 6.0 (FEI Company, Hillsboro, OR, USA) to pre-segment the various cuticular and internal structures in the software’s segmentation editor by manually labelling every 50th virtual slice. These labels served as an input for automated segmentation by using the Biomedical Image Segmentation App ‘Biomedisa’ (Lösel et al. 2020) (https://biomedisa.org). After some minor manual corrections to the segmentation results of the ‘Biomedisa’ output by using Amira, we converted them into polygon meshes. We thereby applied some minor smoothing and polygon reduction to create the final 3D model (surface mesh).

**Results**

*Bocchus rex* sp. nov.

https://zoobank.org/C24153EA-53FD-40CD-96FB-08BEA582D2BE

**Type material.** *Holotype* (= specimen 1; Fig. 1): f#, in SIZK: Ukraine: Les-1, specimen in upper Eocene Rovno amber, collected in Lisove amber mine in Volyn Region of W Ukraine, 9 km east of Manevichi (the former Manevichi district, now Kamen-Kashirsky district). Horizon: Priabonian (35–38 Ma). *Paratype* (= specimen 2; Figs 2, 3): 1f#, in SMNS: UKR-1, specimen in Rovno amber (unknown locality).

**Diagnosis.** Macropterous female of *Bocchus* (Figs 1a–d, 2a–c) with OOL more than three times as long as OPL (Fig. 1b); epicnemium concealed (Fig. 1d); notauli incomplete, reaching about 0.75× length of mesoscutum (Figs 1b, 2c); fore wing with one dark transverse band (Figs 1a, 2c); petiole distinctly visible (Fig. 1a); enlarged claw (Figs 1e, f, 2d, 4a) with one long row of small teeth, in addition to one lamella; protarsomere 5 (Figs 1e, f, 2d, 4a) with distal apex broad and dark pigmented, with one preapical lamella and inner band, without bristles on inner margin.

**Description of the female** (Figs 1–4a). Fully winged (Figs 1a–d, 2a–c); length 2.8–3.2 mm (holotype 3.2 mm). Holotype ferruginous-black; paratype black. Antenna clavate (Fig. 1a, b), without ADOs; antennomeres in following proportions: 9:6:6:5:5:4.5:4.5:4.5:4.5:6; antennomere 9 slightly longer than broad (4.5:3). Head dull, completely granulate, not reticulate rugose; frontal line complete; occipital carina complete; POL = 3; OL = 2; OOL = 5; OPL = 6.5; TL = 6; greatest breadth of lateral ocellus shorter than POL (2:3). Mandible quadridentate, with one
New species of *Bocchus* from Rovno amber

smaller intermediate tooth (Fig. 1d). Mesosoma longer than head (18:7), shorter than metasoma (18:23). Pronotum crossed by strong transverse impression, with sculpture not distinct, laterally with some longitudinal keels; pronotal tubercle reaching tegula. Mesoscutum dull, granulate. Notauli incomplete, reaching about 0.80× length of mesoscutum (Figs 1b, 2c). Sculpture of mesoscutellum and metanotum not distinctly visible. Epicnemium concealed (Fig. 1d). Metapetal-propodeal complex not distinctly visible. Fore wing with one dark broad transverse band (Figs 1a, 2c); distal part of 2r-rs&Rs vein much longer than proximal part (17:5). Petiole very long, much shorter than rest of metasoma (4:19). Proleg ratio: 12 (procoxa): 10 (protrochanter): 24 (profemur): 17 (protibia): 13 (protarsomere

**Figure 1.** Stereomicroscopical images of *Bocchus rex* sp. nov., female, holotype (= specimen 1) a, b habitus, dorsal view c habitus, lateral view d habitus, ventrolateral view e fore leg f chela.

**Male.** Unknown.

**Hosts.** Unknown.

**Etymology.** Bocchus was the name of two kings of Mauretania (the first being father-in-law to the Numidian King Jugurtha) and *rex* is an appropriate epithet of this nice species with its regal look.

**State of preservation of paratype (= specimen 2).** The head and thorax are well preserved but each have a fissure dorsally (Fig. 3c, e). The metasoma has been completely crushed (Figs 2c, 3a, c, e, g, Suppl. material 1: Video S1). Its size and form can be roughly estimated from the cavity formed in the amber. However,

![Figure 2](image-url)

**Figure 2.** Stereomicroscopical images of *Bocchus rex* sp. nov., female, paratype (= specimen 2) a, b habitus, ventral view c habitus, dorsal view d chela.
cavities are also present laterally between the head and the thorax (Figs 2a–c, 3a, c, e, g, i, Suppl. material 1: Video S1). Unfortunately, the resolution of the SR-μCT scan was too low to 3D-reconstruct the chelae in great detail. In the head, the partially preserved optical ganglion complex, presumably the optic lobes (= medullae), is clearly visible (Fig. 3b, d, f, h, j, Suppl. material 1: Video S1). It is the second report of optic lobe preservation for Rovno amber arthropods (cf. fig. 1 of Sukhomlyn et al. 2022). Other internal structures are partially preserved; however, it is unclear whether they belong to the optical system or different brain regions, or are partially preserved muscles of the mouthparts (Fig. 3b, d, f, h, j, Suppl. material 1: Video S1). In addition, many muscles in the thorax, the legs and, occasionally, in the metasoma are still preserved (Fig. 3b, d, f, h, j, Suppl. material 1: Video S1). However, as the depicted set of muscles is by no means complete and plays no role in species identification, it will not be discussed further here.

**Remarks.** After the description of *Bocchus rex* sp. nov., the key published by Perkovsky et al. (2020) can be modified as follows.

**Key to the Cretaceous and Paleogene species of the genus *Bocchus* Ashmead, 1893**

**Female:**

1. Petiole very short, almost absent (cf. fig. 4 of Perkovsky et al. 2020) ..................

   ................................. **B. cenomanianus Olmi, Rasnitsyn & Guglielmino**

  – Petiole distinctly visible, one sixth to one ninth of rest of metasoma (cf. fig. 1 of Perkovsky et al. 2020; Fig. 1a) .............................................................. 2

2. Enlarged claw with teeth present only in the distal half of the inner margin (Fig. 4c) ........................................................................................................

   ................................. **B. schmalhauseni** Perkovsky, Olmi, Vasilenko, Capradossi & Guglielmino

  – Enlarged claw with teeth distributed along the entire inner margin (Figs 2d, 4a, b) ............................................................................................. 3

3. Head with OOL about 62% of OPL; notauli complete, posteriorly separated (cf. fig. 9 of Perkovsky et al. 2020); protarsomere 5 with distal apex slender and not pigmented, with two bristles on inner margin (Fig. 4b) ......................... ................................. **B. primaevus** Martins & Melo

  – Head with OOL about 77% of OPL (Fig. 1b); notauli incomplete, reaching about 0.80× length of mesoscutum (Figs 1b, 2c); protarsomere 5 with distal apex broad and dark pigmented, without bristles on inner margin (Fig. 4a) ................ ................................. **B. rex** sp. nov.

**Male:**

Unknown.
Figure 3. Segmented 3D model of *Bocchus rex* sp. nov., female, paratype (= specimen 2) based on SR-μCT data (perspective view; cf. Suppl. material 1: Video S1; parts of the left antenna and the tarsus of the right hind leg are outside of the dataset) *a, b* ventral view *c, d* dorsal view *e, f* dorsolateral view *g, h* lateral view *i, j* frontal view. The cuticular elements in *a, c, e, g, i* are depicted in various shades of brown, whereas the cavity of the wasp in the amber is shown as being semi-transparent. The partially preserved optical ganglion complex is shown in blue, the potential brain regions or head muscles in purple, and the muscles (in the thorax, the legs and the metasoma) in red, whereas the cuticular elements in *b, d, f, h, j* are semi-transparent and the cavity in the amber is omitted.
Discussion

The above-described new species is attributed to the genus *Bocchus* (Hymenoptera, Dryinidae, Bocchinae) because of the following characters: ocelli present; epicnemium concealed; protarsus chelate; chela with rudimentary claw.

The genus *Bocchus* includes 103 species present in all zoogeographical regions, except for Antarctica (Perkovsky et al. 2020). The hosts of *Bocchus* are Tropiduchidae and Caliscelidae (Hemiptera, Auchenorrhyncha) (Guglielmino et al. 2013). These two families of planthoppers are only known from the Cenozoic (Perkovsky et al. 2020).

Fossil species of *Bocchus* are known from the Cenozoic (i.e. from Baltic and Rovno amber) as follows: *B. primaevus* Martins & Melo, 2019 (2021) from upper Eocene Baltic amber, Priabonian, 35–38 Ma; *B. schmalhauseni* Perkovsky, Olmi, Vasilyenko, Capradossi & Guglielmino, 2020 and *B. rex* sp. nov. from Rovno amber, coeval of Baltic amber. Probably the hosts of the above three species were Tropiduchidae, as they are known from both Baltic and Rovno amber (Perkovsky and Bogdasarov 2009; Perkovsky et al. 2020; Olmi et al. 2022). The oldest tropiduchid is known from the lower Eocene of the Green River Formation (CO, USA) (Shcherbakov 2006). Fossil Caliscelidae are also known from the Cenozoic, but only from Dominican amber (Burdigalian, lower Miocene; 16–20 Ma) (Bourgoin et al. 2015).

A fourth species has been attributed to the genus *Bocchus*: *B. cenomanianus* Olmi, Rasnitsyn & Guglielmino, 2010. It is a compression fossil in extremely bad condition from Obeschchayushchiy, Magadan region, Russian Federation (Santonian-Campanian, Upper Cretaceous, 72–85 Ma). However, its attribution to *Bocchus* is doubtful, because Caliscelidae and Tropiduchidae are not known from the Cretaceous (Perkovsky et al. 2020).

Figure 4. Schematic drawings of chelae of species of *Bocchus* known from amber. **a** *Bocchus rex* sp. nov. **b** *B. primaevus* Martins & Melo (from Perkovsky et al. 2020) **c** *B. schmalhauseni* Perkovsky, Olmi, Vasilyenko, Capradossi & Guglielmino (from Perkovsky et al. 2020). Abbreviations: e, enlarged claw; t, protarsomere 5.
2020). Of course, the host at the Obeschchayushchiy site might well have belonged to other families of planthoppers. However, according to Perkovsky et al. (2020), angiosperms (hosts of extant Caliscelidae and Tropiduchidae) were extremely rare at that site. On the other hand, no evidence exists for possible Bocchus hosts feeding on gymnosperms or ancient ferns predominant at the Obeschchayushchiy site (Nadein and Perkovsky 2018; Perkovsky et al. 2020). Hence, B. cenomanianus might have been misidentified.

The new Bocchus described here is the first hymenopteran and seventh named fossil arthropod from the Volyn Region, Ukraine (Martynov et al. 2021; Telnov et al. 2021; Legalov et al. 2022). The discovery of B. rex is indicative of the richness of Bocchus species in Rovno amber in comparison with Baltic amber: two species (29% of all dryinid species) in Rovno amber versus one (4.8% of all dryinid species) in Baltic amber. In addition, one specimen from Varash district could not be determined to the species level. This difference might be related to the climate of the Rovno amber forest being warmer than that of the Baltic amber forest (Kupryjanowicz et al. 2022; Yamamoto et al. 2022; and references therein), especially since their potential hosts (i.e. Tropiduchidae) are mainly tropical and subtropical (Bourgoin 2020).

To date, Bocchus is the most common genus of Dryinidae in Rovno amber fauna and Bocchinae is the dominant subfamily (44.4% of specimens versus 33.3% for Dryinus and Dryininae) at the specimen level. This is unusual, as Dryininae strongly dominate not only in Baltic amber, but also in Kachin (33 Dryininae species according to Olmi et al. 2022) and Dominican (ten Dryininae species versus one belonging to Bocchinae; Martynova et al. 2019; Martins and Melo 2020) ambers, both at the specimen and species levels.

The biology of Bocchus species is poorly known so far. The species with known biology live in open environments. An even more important reason for the abundance of Bocchus is that open environments were more common in the Priabonian Ukraine than in the Baltic amber forest (Lyubarsky and Perkovsky 2012; Perkovsky 2013; Lyubarsky and Perkovsky 2019; Dietrich and Perkovsky 2020).

A comparison with the extant Bocchus species shows that their body shape is similar to the species known from European Eocene amber. The chela of B. rex and B. schmalhauseni follows the same general scheme as in the extant species. The only difference can be observed in the chela of B. primaevus and is attributable to the anomalous long and slender protarsomere 5 (Fig. 4b). A similar type of protarsomere 5 has not been found in any extant or fossil species of Bocchus. However, the significance of this anomalous chela remains unknown.

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New species of *Bocchus* from Rovno amber


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Supplementary material I

Video S1
Authors: Massimo Olmi, Benjamin Eggs, Leonardo Capradossi, Thomas van de Kamp, Evgeny E. Perkovsky, Adalgisa Guglielmino, Dmitry V. Vasilenko
Data type: video file (mp4)
Explanation note: Animation of the rotating segmented 3D model of *Bocchus rex* sp. nov., female, paratype (= specimen 2) based on SR-µCT data (perspective view; cf. Fig. 3; parts of the left antenna and the tarsus of the right hind leg are outside of the dataset). The cuticular elements are depicted in various shades of brown, whereas the cavity of the wasp in the amber is shown as being semi-transparent. The partially preserved optical ganglion complex is shown in blue, the potential brain regions or head muscles in purple, and the muscles in red.
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Link: https://doi.org/10.3897/jhr.92.87084.suppl1
The first Pacific insular orchid bee (Hymenoptera, Apidae): A new species of Eufriesea from the Islas Marías

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Abstract
A new species of the orchid bee genus Eufriesea Cockerell (Apidae: Apinae: Euglossini) is described and figured from the Islas Marías of Nayarit State, México in the Pacific. Eufriesea insularis sp. nov., is a member of the coerulescens species group and is restricted to Islas Marías. The species is readily recognized by its dark blue integument with purple iridescence, black pubescence, dark wings, and clypeus green with purple hues and a prominent elevated ridge along the midline. The new species is known only from the female.

Resumen
Se describe e ilustra una especie nueva de abeja de las orquídeas del género Eufriesea Cockerell (Apidae: Apinae: Euglossini) de las Islas Marías en el estado de Nayarit, en el pacífico de México. Eufriesea insularis sp. nov. es parte del grupo de especies coerulescens y está restringida a las Islas Marías. La especie se reconoce fácilmente por su integumento azul oscuro con brillos púrpuras, pubescencia negra, alas oscuras y el clípeo verde con brillos púrpura y con un borde elevado a lo largo de la línea media. La nueva especie se conoce únicamente de la hembra.
**Keywords**
Anthophila, Apoidea, Euglossini, México, new species, orchid bees

**Introduction**

The purpose of this paper is to describe a new species of the orchid bee genus *Eufriesea* Cockerell (Apidae: Euglossini) from the Pacific islands of Islas Marías, an archipelago consisting of four islands located 100 km from the coast of the state of Nayarit in México. This archipelago was designated as the Islas Marías Biosphere Reserve in 2010 by UNESCO and the Mexican Government, and it is currently under the protection of the Ministry of the Environment and Natural Resources of México (SEMARNAT-CONANP). We have been aware of the novelty of this species for more than a decade (Ayala and Engel 2008; Gonzalez et al. 2017), but it was awaiting description because of the limited number of available specimens. The new species was initially known to us from two females captured during an expedition led by the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM) in the mid-1980s on the island of María Madre (Fig. 1), the largest of the four islands and which housed a federal prison, established in 1905 and closed in 2019. Two additional females captured in the mid-1990s on the same island were located at the insect collection of the Universidad de Guadalajara. Unfortunately, appraisal of museum specimens in other Mexican collections as well as in U.S. institutions has not yielded additional material and further sampling on the island has not been possible.

*Eufriesea* consists of about 60 species confined to the Neotropical region, most of which occur in South America (Ramírez et al. 2002). These bees are readily recognized by their large, robust body with frequently metallic coloration that ranges from black to blue or green with yellow, reddish, or purple iridescence. The genus, like its relatives in the tribe Euglossini, is also noteworthy for its role in pollination of orchids and many other plants, such as those in the families Bignoniaceae (*Allamanda* L., *Astianthus* D.Don, *Melloa* Bureau, *Tecoma* Juss., *Tabebuia* Gomez), Convolvulaceae (*Ipomoea* L.), Fabaceae (*Senna* Mill.), and Apocynaceae (*Thevetia* L., *Cascabela* Raf., *Stemadenia* Benth., *Prestonia* R.Br.) (records from specimens in the Chamela bee collection and personal observations). Males visit orchid flowers, among others, to collect essentials oils that are then carried and modified in their metatibiae, and which are presumably used to attract females (e.g., Moure 1965, Dressler 1967, 1968a, 1968b; Kimsey 1980, 1982; Roubik and Hanson 2004; Michener 2007).

The new species documented here belongs to the *coerulescens* species group, which was recently revised by Gonzalez et al. (2017). This species group consists of six species presumably restricted to México along tropical dry forests, as well as in pine and oak forests, from sea level to about 1500 m in elevation. *Eufriesea coerulescens* (Lepeletier de Saint Fargeau), the most widespread species of the group, has also been recorded from the Guadalupe Mountains of western Texas and southeastern New Mexico, USA (Griswold et al. 2015). Records of this species from Honduras, Costa Rica, and Panama
remain to be confirmed (Gonzalez et al. 2017). We hope that this contribution brings this species to the attention of melittologists and encourages further work on the biology of this isolated orchid bee.

**Materials and methods**

Morphological terminology for the description follows that of Michener (2007), Engel (2001), and Engel et al. (2021), with the abbreviations T and S for metasomal tergum and sternum, respectively. Illustrations were made using a Canon 7D digital camera and a 60 mm Canon macro lens. The images were stacked using the HeliconFocus program and edited with Affinity Photo. The species description is based on the holotype and paratypes available to us and emphasizes structural characters that are reliable for species recognition in the female, such as length of the glossa, punctation and pubescence of the mesoscutellum, metasomal terga, and tegula; shape of the posterior subapical projection and width of the distal intersp depression of the metatibial proventral surface; and width of the metabasitarsus. Measurements were taken with an ocular micrometer on a Leica MZ6 stereomicroscope and are in millimeters with the variation in size across the type series in parentheticals (n = 4). Intertegular distance was measured as the shortest distance between the mesal margins of the tegulae, while the forewing length was measured from the posterior margin of the tegula to the wing tip. Type material is deposited in the Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, México (IBUNAM) and the Colección Entomológica, Centro Universitario de la Costa Sur, Universidad de Guadalajara, Atlán Jalisco, México (CUCSUR).

**Systematics**

Genus *Eufriesea* Cockerell, 1908

*Eufriesea insularis* sp. nov.

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Figs 2–7

**Diagnosis.** The new species is similar in appearance to other species in the *coerulescens* group, but with a noticeably darker integument with blue and purple iridescence and generally with black pubescence (Figs 2, 3), but yellowish to black on TIV–VI (Figs 2, 5), all of which contrasts with *E. oliveri* Gonzalez and Griswold and *E. micheneri* Ayala and Engel in which such setae are whitish. In addition, the new species has the glossa long, extending beyond SII (Fig. 2); the head, labrum, and clypeus metallic greenish but purple on the discal area of the latter (Fig. 7), and contrasting with the dark metallic blue of the rest of the head; the clypeus has strong elongate punctures that converge towards the midline, and which are stronger than those present on the bordering par-
aocular area; the clypeus has a prominent mediolongitudinal ridge, strongest in apical half of the clypeus (Fig. 7); frons doubly punctate, the largest punctures separated by about their diameter, between the small and large punctures the integument is smooth and shiny; exceptionally narrow impunctate and shiny area between torulus and inner ocular margin, width about one-fifth torular diameter; scape dark reddish brown, flagellum dark brown to nearly black, but flagellomeres I, II, and apical flagellomeres darker (Fig. 7); pronotum partially dark brown, and lateral margins of mesoscutum, axilla, and mesoscutellum dark brown to nearly black (Fig. 6); forewing hyaline and infumate throughout although darker in costal cell, along anterior margin of marginal cell (particularly apically), and slightly so in first submarginal cell (Fig. 3); lighter patch in second medial cell (Fig. 3); femora, metatibia (corbicula), and metabasitarsus dark brown to nearly black in some areas (Figs 2, 4).

**Description.** ♀: Total body length 19.5 mm (19.5–19.9 mm). Head wider than long, length 5.4 mm (vertex-margin of clypeus) (5.4–5.7 mm), width 6.6 mm (6.5–6.6 mm); compound eye length 4.6 mm (4.6–4.8 mm), width 2.2 mm (2.1–2.2 mm); upper interorbital distance 2.7 mm (2.6–2.9 mm), lower interorbital distance 3.3 mm (3.3–3.5 mm), interorbital distance at tangent of upper third of compound eye length 3.6 mm (3.5–3.6 mm); glossa long, extending beyond SII, length 12.2 mm (12.2–12.6 mm); mandible black and robust, width at base 1.5 mm (1.5–1.6 mm), length 2.4 mm (2.4–2.5 mm); apical tooth largest, projecting beyond medial tooth, forming

![Figure 1. Geographical location of the Marías Islands in the Pacific Ocean, off the coast of Nayarit, México. María Madre Island is the type locality of *Eufriesea insularis* sp. nov.](image-url)
an orthogonal notch between teeth; labrum with coarse irregular punctures, with short elevated medial carinae, larger than sublateral carinae, sublateral carinae converging apically; distal extreme of labrum with subapical depression and distally and distal margin prominently covered with short pubescence; clypeus with elongate punctures (Fig. 7) that converge towards midline, such punctures stronger than those on remainder of face, integument between punctures shining, finely and microscopically imbricate, with prominent elevated medial ridge (Fig. 7); impunctate and shiny area between toruli and inner margin of compound eye, area between torulus and eye exceptionally narrow, about one-fifth torular diameter; frons doubly punctate, largest punctures separated by about their diameter, integument between punctures smooth and shiny; frontal line well defined between torulus and anterior margin of median ocellus (1.55 mm, 1.53–1.67 mm long); supraclypeal area with impunctate line extending to clypeal margin. Scape length 2.1 mm (2.1–2.2 mm), midlength width 0.33 mm (0.32–0.33 mm), apical width 0.41 mm (0.41–0.42 mm); pedicel length 0.30 mm (0.28–0.30 mm), flagellum length 3.8 mm (3.8–4.0 mm), width 0.40 mm (0.38–0.42 mm), flagellomere I length 0.45 mm (0.45–0.46 mm), flagellomere II length 0.32 mm (0.32–0.33 mm); distance between antennal torulus and compound eye 0.75 mm (0.75–0.81 mm), with punctures small and dense in respect to those of frons; torulus width 0.50 mm (0.49–
0.51 mm), distance between antennal toruli 1.18 mm (1.18–1.21 mm). Ocellocular distance 0.60 mm (0.60–0.62 mm), ocellocular area impunctate; posterior distance between lateral ocelli 0.85 mm (0.85–0.93 mm), distance between medial and lateral ocelli 0.37 mm (0.37–0.44 mm), width of medial ocellus 0.40 mm (0.40–0.41 mm); interocellar furrow (*sensu* Engel 1999) and postocellar furrow present; integument between posterior ocellus and vertex with punctures denser in respect to frons. Gena with small punctures distinctly separated by shiny integument; gena width 1.10 mm (1.07–1.10 mm) at midlength of compound eye; vertex slightly elevated in facial view.
in respect to upper tangent of compound eyes. Mesoscutum width 5.5 mm (anterior inter-tergal distance) (5.5–5.7 mm), length 4.9 mm (4.9–5.1 mm); mesoscutum and mesoscutellum with dense punctation, punctures separated by less than a puncture width (Fig. 6), integument between punctures smooth and shiny; tegula with small and uniform punctation, although with some larger punctures along mesal margins, mesal margin demarcated by narrow furrow; mesoscutellum width 4.6 mm (4.3–4.7 mm), length 2.8 mm (2.8–3.0 mm); mesoscutellum slightly rounded in profile, with exceptionally weak medial depression, posterolateral angles rounded; propodeum posterior surface generally smooth, with only fine setigerous punctures; forewing length 15.2 mm (15.1–15.2 mm), width 4.8 mm (4.8–5.1 mm); jugal comb present at base of hind wing, setae of jugal comb longer than width of jugal lobe; distal area of hind wing homogeneously papillate. Metatibia medial length 5.9 mm (5.4–5.9 mm), width 2.8 mm (2.8–3.0 mm); metabasitarsus length on posterior margin 2.7 mm (2.7–3.0 mm), width at base 1.4 mm (1.3–1.6 mm). TI with punctures larger than those of remaining terga, with posterior marginal zone impunctate and longer than those of remaining terga; TII–IV with small, homogeneous punctation, distance between punctures similar to their diameter; TV–VI with punctation denser than on preceding terga; TII–IV with marginal zones short, narrow, impunctate (Fig. 5).

Integument generally dark metallic blue, with purplish hues (Fig. 2); mandible largely black; labrum and clypeus with metallic green, darker on former, and medially with purple iridescence, discal area mostly purple; supraclypeal area as on clypeus (Fig. 7); paraocular area and frons dark metallic blue; antenna dark reddish brown; flagellum

Figure 6. *Eufriesea insularis* sp. nov., female, dorsal view of mesoscutum and mesoscutellum.
dark brown to nearly black; gena and vertex with purple and yellowish iridescence; pronotum dark brown except dark metallic blue anteriorly; mes- and metepisterna dark metallic blue, with some purplish highlights; mesoscutum and mesoscutellum dark metallic blue with purple iridescence, but lateral margins of mesoscutum, axilla, and mesoscutellum dark brown to nearly black, without prominent highlights; propodeum dark metallic blue but more brown on posterior surface. Wings with veins dark brown, nearly black in some places, membranes hyaline and darkly infumate (Fig. 3), darker in costal cell, along anterior margin of marginal cell, and somewhat in first submarginal cell; second medial cell with distinct lighter patch (Fig. 3). Femora and tibiae dark reddish brown, with dark blue to purplish iridescence; probasitarsus and tarsi black; metafemur, metatibia, and metabasitarsus dark reddish brown to nearly black, darker on retrodorsal margin of metatibia (Fig. 4). Metasomal terga and sternae dark brown with dark blue, purplish, and greenish iridescence, posterior marginal zones brown to dark brown.
In general, pubescence dark, nearly black; setae particularly dense anteriorly on mesoscutum; abundant and uniform setae on mes- and metepisterna (Fig. 2). Metasomal terga IV–VI with yellowish pubescence in paratype (Fig. 5), black in holotype (Fig. 2); sterna with black pubescence.

♂: Unknown.


**Paratypes.** 1 ♀, same data as holotype but collected by L. Cervantes (IBUNAM, RA 1014). 2 ♀♀, same locality as holotype but collected X-1995 [October 1995] by I. Cuedriello (CUCSUR).

**Etymology.** The specific epithet is the Latin adjective *insulae*, meaning, “of or pertaining to an island”, and refers to the restricted distribution of this species on the Islas Marias.

**Distribution.** This species is known only from Isla Maria Madre, Nayarit State, México. This is the only species of the genus known from an island in the Pacific Ocean. The vegetation on the Islas Marias islands is primarily tropical dry forest, but a good part of the island has scrub, while the denser and higher arboreal vegetation is concentrated in canyons (CONANP 2021).

**Discussion**

In the key to the Mexican species of *Eufriesea* of Gonzalez et al. (2017), the female of *E. insularis* runs to couplet 3(2) because of its concolorous body coloration and glossa reaching the second metasomal sternum. In that couplet, it would run to *E. oliveri* because of the mesoscutellum with a weak medial longitudinal groove and without the row of dense setae. However, it can be easily separated from that species, as well as any other of the group, by the dark color of the body integument and pilosity, including setae on the sterna. The clypeus has distinct green and purple hues and a strong elevated ridge along the midline (Fig. 7) not present in any other species of the group. In the female of *E. oliveri* the integument is blue throughout with purple hues, and the setae on the metasoma are off-white intermixed with black. In addition, the posterior subapical projection of the metatibial proventral surface is more acutely pronounced than in *E. oliveri* (cf. figs. 7 and 33 of Gonzalez et al. 2017).

Proposing a new species based on a limited number of specimens is not ideal as one has a limited (or no) perspective on potential variation, but it is at times still necessary and justified, particularly for exceptionally distinctive taxa. In the current instance, the new species is morphologically distinct and reliably recognized from all other species of the *coerulescens* group. It is likely that *E. oliveri* is the closest relative to *E. insularis* given the morphological similarity between them and the type of habitats they inhabit (dry forests). Other species of the *coerulescens* group exhibit a different combination of features and inhabit different vegetation types, such as *E. micheneri*, which is found in pine forests and other mountainous environments (Gonzalez et al. 2017). Molecular analyses are necessary to explore the relationship of *E. insularis* with the other species of the group, as well as to infer the time of separation between these lineages. The lithologies of Isla María
Madre strongly resemble that of the Jurassic-Cretaceous plutonic and metamorphic rocks found in the Los Cabos Block of Baja California Sur and rocks from the Mexican continental margin between Sinaloa and Jalisco. Thus, the Islas Marias are fragments of the Baja California Peninsula that separated from the mainland of México (Pompa-Mera et al. 2013), all of which suggests a relatively recent arrival of this orchid bee to the islands.

The captured specimens of *E. insularis* are not associated with floral records. However, considering the host plants recorded for other species of the *coerulescens* group that occur along the coast of the states of Jalisco and Nayarit, it is likely that *E. insularis* visits the following plants that are present on Islas Marias as indicated by iNaturalist records: *Cascabela ovata* (Cav.) Lippold, *Tabernaemontana amygdalifolia* Jacq. (Apocynaceae), *Astianthus viminalis* (Kunth) Baill., *Handroanthus impetiginosus* (Mart. ex DC.) Mattos, *Tecoma stans* (L.) Juss. ex Kunth (Bignoniaceae), *Ipomoea hederacea* Jacq. (Convolvulaceae), *Senna pallida* (Vahl) H.S.Irwin & Barneby, *Canavalia rosea* (Sw.) DC., *Indigofera australis* Willd. (Fabaceae), *Salvia apiana* Jeps. (Lamiaceae), *Encyclia parviflora* (Regel) Withner, *Laelia aurea* A.V. Navarro (Orchidaceae), *Antigonon leptopus* Hook. & Am. (Polygonaceae). However, aside from *S. pallida*, which species of this group frequently buzz pollinate, it would be difficult to determine other sources of pollen and from which plants the males would obtain fragrances, as there are few species of orchids present on the islands. Based on the time of collection, *E. insularis* appears to be active during the rainy season (July to November), and until the beginning of winter. Admittedly, we have only two dates of collection but considering that two of the type specimens have heavily damaged wings we may presume that they began activity months prior, during the rainy season. We hope this contribution encourages further studies to explore the biology and phylogeography of this unique insular pollinator.

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**References**


An insular species of *Eufriesea*


Nest structure, associated parasites and morphology of mature larvae of two European species of *Pseudoanthidium* Friese, 1898 (Hymenoptera, Megachilidae)

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Abstract

The bee genus *Pseudoanthidium* is represented by nine species in Europe. Of these nine species, *Pseudoanthidium nanum* is the most widespread, occurs mainly in xerothermic open habitats and creates nests in various cavity types. In this study, we provide information on the nest structure of this species in reed stalks and oak galls and about its parasitic species. We provide the first report of *P. nanum* as a host of *Xylophrurus augustus* (Ichneumonidae).

The biology of the much rarer related species *Pseudoanthidium tenellum* is described here for the first time. This species occurs in terrestrial reed beds and wet meadows with the presence of reed galls and flowering plants in the family Asteraceae and is rare throughout its entire distribution area. This species nests inside reed galls induced by *Lipara* frit flies, and the nest structure is very similar to that of *P. nanum*. We report new parasitic species of this bee, namely, the cuckoo bee *Stelis punctulatissima*, the predator-inquiline *Gasteruption nigrescens* and two parasitoids, *Leucospis biguetina* and *Miltogramma punctata*. This bee collects pollen mainly from wetland plants in *Bidens* and *Pulicaria*. We also describe mature larvae of both species. The larvae do not differ greatly from one another; only the shape of mandibles and sclerotisation of mouthparts are slightly different. Further research should address the ecological requirements of *P. tenellum*, a poorly understood reed gall inquiline.

Keywords

*Andricus*, Megachilidae, oak gall, plant stem, *Pseudoanthidium*, reed bed, reed gall, wetland
Introduction

The bee genus *Pseudoanthidium* Friese is a genus of small bees in the tribe Anthidiini, family Megachilidae, comprising 64 species worldwide (Michener 2007). This genus is divided into 12 subgenera, of which the subgenus *Pseudoanthidium* has the most species (Litman et al. 2016, 2021). In total, around 20 species are known from the western part of the Palaeartic biogeographic region, including nine species that occur in Europe (Kuhlmann et al. 2021; Litman et al. 2021). Of these nine species, *Pseudoanthidium nanum* Mocsary (syn. *P. lituratum* (Panzer)) is the most widespread, occurring in southern and central Europe, Russia and the Middle East (Banaszak and Romasenko 1998; Westrich 2018; Lhomme et al. 2020; Kuhlmann et al. 2021; Litman et al. 2021), and was recently introduced into several parts of the USA (Portman et al. 2019). This species prefers steppic formations and similar open habitats (Macek et al. 2010; Westrich 2018). The other species are much rarer: *Pseudoanthidium alpinum* Morawitz and *Pseudoanthidium tenellum* Mocsáry are rare species distributed in several countries of southern Europe and reach their northern distribution borders in central Europe – Austria, Germany, Hungary and Slovakia (Westrich 2018; Kuhlmann et al. 2021), and *Pseudoanthidium scapulare* Latreille is present in southwestern Europe and North Africa (Scheuchl and Willner 2016; Kuhlmann et al. 2021). *Pseudoanthidium stigmaticorne* (Dours) occurs in south Europe, North Africa, and the Middle East and *Pseudoanthidium canariense* (Mavromoustakis) on Canary Islands (Kuhlmann et al. 2021; Litman et al. 2021). Recently, Litman et al. (2021) described two new species that occur in the Middle East and worked on the taxonomy of the subgenus.

Multiple authors have studied the biology of *P. nanum* (Ferton 1908; Enslin 1925; Bischoff 1927; Micheli 1934; Grandi 1961; Schremmer 1985), and their results have been summarized in major European bee monographs (Banaszak and Romasenko 1998; Macek et al. 2010; Scheuchl and Willner 2016; Westrich 2018). This species creates its nests in various types of cavities in dead wood, plant stems (see Westrich (2018) for a list of plant species, in the stems of which the nests were recorded) and oak galls (Banaszak and Romasenko 1998). Bogusch et al. (2015) reported a specimen obtained from reed galls, but the specimen was probably hiding only inside, not nesting. Multiple parasitic species were associated with nests of this species – three species of cuckoo bee genus *Stelis* Panzer (*Stelis ornatula* (Klug), *S. punctulatissima* (Kirby) and *S. signata* (Latreille)), one sapygid wasp (*Sapyga quinquepunctata* (Fabricius)), six species of cuckoo wasps (Banaszak and Romasenko 1998; Wiesbauer et al. 2020), and six genera of chalcid wasps (Banaszak and Romasenko 1998; Scheuchl and Willner 2016). Grandi (1961) and Banaszak and Romasenko (1998) described the nest structure, Martynova (2020) described the structure of the cocoon of parasitic *Chrysis interjecta* Buysson in the nest of *P. nanum*, and Romasenko (1995) and Banaszak and Romasenko (1998) described the morphology of mature larvae. The species is oligolectic on Asteraceae (Banaszak and Romasenko 1998; Scheuchl and Willner 2016; Westrich 2018; Litman et al. 2021). Regarding *P. tenellum*, previous reports have mentioned only that it is oligolectic on Asteraceae and have provided distribution notes, but the
Nests, parasites and larvae of *Pseudoanthidium*

biology of this species has never been studied in detail (Banaszak and Romasenko 1998; Scheuchl and Willner 2016; Westrich 2018; Litman et al. 2021). Only Astapenková et al. (2017) recorded this species in cigar galls caused by *Lipara* Meigen frit flies (Diptera: Chloropidae) on common reeds, and Bogusch et al. (2020) reported the habitat requirements of this species.

We recorded specimens of *P. tenellum* in wetland habitats in Hungary and Slovakia and reared several of them from cigar galls induced by frit flies in the genus *Lipara* Meigen. We found the nests of this species inside the galls, and thus, we can provide information on habitat preferences, nest structure, parasites associated with *P. tenellum*, and the first description of its mature larvae. These records were compared with our records of nests of *P. nanum*, which we report from trap nests made of reed stalks and goldenrod stems and from oak galls of cynipid wasps.

**Materials and methods**

The studies of wetland fauna of Hungary and Slovakia were conducted mainly in Kiskunság National Park in central and southern Hungary in 2011–2018 and in the Danube Valley in southern Slovakia and northern Hungary in 2015–2021. The bees were captured using an entomological net, while in selected locations, reed galls were collected in winter (January – March) in numbers of 200–500 per locality and in smaller numbers in summer (June – July). The insects and other invertebrates were reared in special rearing bags, as described by Heneberg et al. (2014) and Bogusch et al. (2015). Only galls older than one year (greyish or darker in appearance, usually without leaves and with the apex broken) were collected because of our focus on cavity-nesting Hymenoptera (bees and wasps) instead of the *Lipara* spp. (inducing the galls) or their parasitoids. In the first years of the study (2015), we collected at least 500 reed galls at each sampling site, of which 200 were longitudinally cut, their contents were analysed, and the rest were allowed to rear (Bogusch et al. 2015; Astapenková et al. 2017). In 2017–2021, all collected galls were longitudinally cut to find nests of *P. tenellum*.

The trap nests were located in wetland and steppic parts of selected localities in the Czech Republic, Slovakia and Hungary, in numbers of 10 + 10 in 2017–2018. Each trap nest consisted of ten reed stalks and ten goldenrod stems fixed together by tape. The nests were placed on a bamboo stick 50–70 cm above the ground. They were installed in winter and early spring (February – April) and collected in autumn and winter (October – January). All reed stalks and goldenrod stems from all trap nests were longitudinally cut, and their inner contents were studied in the same way as in reed galls.

The oak galls of various species of the genus *Andricus* Hartig (Hymenoptera: Cynipidae) were collected in selected locations in the Czech Republic, Slovakia, Hungary, Austria, Croatia and Italy in 2017–2019 in winter months (December – March). All galls from one locality were placed into a plastic container, and reared insects were collected and studied. In 2018 and 2019, oak galls of *Andricus kollari* (Hartig) from four localities in the Czech Republic and two in Hungary were collected and cut to study their inner contents.
In the longitudinally cut reed galls, trap nests, and cut oak galls, we studied the material of the walls separating the brood cells (henceforth termed partitions) and the closing plugs at the top of each nest (henceforth termed closures), the structure and number of brood cells, and the morphology and colouration of larvae and pupae. In the descriptions, “first cell” denotes the bottom, i.e., first-built cell of the nest. The “last cell” denotes the uppermost cell, i.e., the one nearest to the nest entrance. When the larvae were in cocoons, we removed them from the cocoons but left the others inside. For each species, we first attempted to rear the adults. For nests containing more than three larvae, we conserved part of the brood for morphological studies. To rear the larvae, the living larvae were removed from the nests, placed in Eppendorf 1.5 ml microtubes, plugged with cotton wool, left at room temperature with ambient moisture, and reared similarly as described by Astapenková et al. (2017). The adults usually hatched within three to four weeks after pupation, after which they were fixed, similar to larvae, i.e., in 96% ethanol. The obtained material was identified by the first author. Representative specimens (including the nests of each species) are available in the collections of Petr Bogusch (University of Hradec Králové, Czech Republic).

We documented the representative part of the nests using a digital camera (photographs of entire nests) and a macrophotographing apparatus consisting of a macro-camera Canon attached to a stereomicroscope (brood cells and entire larvae). For the detailed photographs and photographs of morphological characters for the drawings, we used Keyence VHX digital microscope with camera and stacking software. We took photos of living larvae as well as the larvae fixed in Pampel solution (30 volumes of distilled water, 15 volumes of 96% ethanol, 6 volumes of formaldehyde and 4 volumes of glacial acetic acid) as described by Švácha and Danilevsky (1987). To describe the morphology of larval specimens, we transferred representative larvae into Pampel solution, while other larvae from the same nests were allowed to develop to adults, in order to identify them to species. After we took photographs of the intact larvae, we focused on their sclerotized parts. For this purpose, we placed the larvae into a 10% solution of hot (60 °C) potassium hydroxide for 12 hours to clear all parts of the body except the integument. Then, we coloured the integument in 5% chlorazol black E (Sigma Aldrich) for two seconds and moved the specimens into 96% ethanol for conservation. To observe the identifiable features, we placed the integument into glycerol and separately observed the head, mouthparts, spiracles and other important parts of the integument under a light microscope. We used the same specimens for the study of small structures such as setae, sensillae or mouthparts. We drew figures of (1) the head with a focus on the clypeus, labrum, maxillae, and labium; (2) the mandibles from the anterior view; and (3) the spiracles of larvae of each species.

Pollen samples were obtained from brood cells of selected nests from three localities. We collected all pollen from a selected brood cell in all cases. The pollen was stored in 75% ethanol. Then it was acetolyzed according to Faegri and Iversen (1989) and coloured with Safranin. Pollen grains were identified to taxa or pollen types (groups of taxa with morphologically unidentifiable pollen grains). Taxonomic identifications followed Punt and Hoen (2009) and Beug (2004).
Results

Records of *Pseudoanthidium tenellum* in Hungary and Slovakia

We recorded *P. tenellum* in seven localities in Hungary and two in southern Slovakia. All localities were terrestrial reed beds rich in bee and wasp fauna. The distribution of the localities is shown in Fig. 1. Detailed locality information includes the following.


![Figure 1](image-url) Map with localities of *Pseudoanthidium tenellum* in Slovakia and Hungary.
We collected 24 nests of *P. tenellum* from nine localities – seven localities in Hungary and two localities in Slovakia. The nests comprised 2–5 brood cells (median 3; mean $2.7 \pm 0.5$ cells per nest; $n = 24$ nests). The inner space of the gall was completely filled with whitish or yellow plant fibres, and brood cells were placed inside this matter (Figs. 2A-C). The filling was the same inside the entire nest, and no other material was used for the construction of the closing plug, partitions between brood cells, etc. The cocoons of oval shape with a typical projection on the bottom were light brown (Fig. 2D), and their length was between 7.32 and 8.02 mm (median 7.77, mean
Nests, parasites and larvae of *Pseudoanthidium*

7.70 ± 0.06 SD, n = 13) and maximal width was between 4.02 and 4.51 mm (median 4.35, mean 4.32 ± 0.04 SD, n = 13). Between the brood cells, there were faeces of yellow-orange colour (Fig. 2C).

**Parasites associated with *Pseudoanthidium tenellum***

We recorded one larva of *Stelis punctulatissima* (Megachilidae), of which the adult hatched, in a nest from the Virt-Marcelová locality and one adult *S. punctulatissima* inside a cocoon in the nest from Mocsa. Two larvae of *Gasteruption nigrescens* Schletterer (Gasteruptiidae) were recorded in two nests from Szeged. Additionally, two nests from Szeged were completely parasitised by *Leucospis biguetina* Jurine (Leucospidae), three and four adults hatched. *Miltogramma punctata* Meigen (Diptera: Sarcophagidae) was recorded in three nests from Buzsák, two nests from Szeged and one from Sándorfalva in total number of 34 pupariums, from which 25 adults hatched. These records are the first published parasite associations with *P. tenellum*.

**Pollen preferences of *Pseudoanthidium tenellum***

Because no information on pollen specialisation of *P. tenellum* occurs in the literature, we decided to do the analysis of pollen grains in brood cells of this species. Three nests, each from a different sampling site (Naszály, Virt and Zemianska Olča), contained pollen of plants in the family Asteraceae. The other plant families were represented only by single pollen grains, which were probably only accidentally introduced into the nest. The *Bidens tripartita* pollen type was the most abundant in all three nests, representing 73% of all pollen (53% in Virt, 68% in Zemianska Olča and 97% in Naszály). *Carduus* and *Arctium* were represented similarly in nests from Virt and Zemianska Olča (13% and 12%) and *Cirsium* with 2% in Naszály. Therefore, females of *P. tenellum* are oligolectic on Asteraceae and probably exploit wetland and ruderal species, which grow in places with the presence of reed galls (see Table 1). The pollen grains of *B. tripartita* from Virt are shown in Fig. 3.

**Description of mature larva of *Pseudoanthidium tenellum***

**Material examined**

Two larvae from Szeged and one larva from Virt.

**Diagnosis**

The mature larva of *P. tenellum* is similar to the larva of *P. nanum*. In general, the body is thickened with small head and multiple setae on the surface. The main difference is in the shape of mandibles, which have blunter apical teeth, smaller antennal orbits and slightly different chaetotaxy. It corresponds in size with larva of *P. nanum*. The
mandibles are light-brown coloured and less sclerotized than those of *P. nanum*. All studied larvae are very similar in general appearance and do not differ in the chaetotaxy and morphology.

**Description**

**Body:** Body length 5.8 – 7.1 mm (N = 3). Body vestiture without spicules, and with many thick, pale setae, tapering to fine points, arising from small but distinct alveoli. The distribution of setae is on the whole body, while the dorsal parts of body are more setose. Only mandibular apices, area around mandibular condyli, part of maxillae and labium and maxillar and labial palpi brownish coloured. Body form of postdefecating

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**Table 1.** Proportions (in %) of pollen types in three samples from nests of *Pseudoanthidium tenellum*.

<table>
<thead>
<tr>
<th>Pollen type</th>
<th>HU: Naszály</th>
<th>SK: Virt</th>
<th>SK: Zem. Olča</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bidens tripartita</td>
<td>97</td>
<td>53</td>
<td>68</td>
<td>73</td>
</tr>
<tr>
<td>Cirsium palustre</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
</tr>
<tr>
<td>Arctium lappa</td>
<td>0</td>
<td>24</td>
<td>16</td>
<td>12</td>
</tr>
<tr>
<td>Carduus crispus</td>
<td>0</td>
<td>21</td>
<td>16</td>
<td>13</td>
</tr>
</tbody>
</table>

**Figure 3.** Pollen from brood cells of *Pseudoanthidium tenellum* with the dominance of the *Bidens* pollen type.
larva fusiform, slightly dorsoventrally flattened, robust; all body segments of similar width (Fig. 4A). Dorsal tubercles present but ill-developed, only on metathorax and T1-T3, other body segments without body tubercles. Paired lateral tubercles on metathorax and T1-T8 but ill-visible, without any border. Body shape of predefecating larva in lateral outline with first abdominal segments having greatest diameter and outline tapering forward and very slightly backward from there. Abdominal segment 10 wide; anus positioned medially and transverse. Spiracles (Fig. 4D) light-brown, subequal in diameter; atrium globular, slightly wider than deep, projecting little above body wall, with rim; atrial opening diameter vs. peritreme width ratio 0.75; atrial inner surface with rows of wrinkles concentric with primary tracheal opening; primary tracheal opening with collar; subatrium short, with only four chambers of approximately equal size. Sex characters unknown.

**Head:** Head heart-shaped, small in relation to body size and ill-separated from prothorax; oriented in normal, hypognathous position relative to thorax. Setae long and sparse on upper part of head capsule; those of maxillary and labial apices large,

![Figure 4. Mature larva of *Pseudoanthidium tenellum*](image)
straight, and conspicuous. Head capsule unpigmented except at points of articulations with mandibles; mandibles moderately pigmented except mandibular apices and areas of articulation with head capsule strongly pigmented; maxillary sclerites faintly pigmented; salivary lips projecting and pigmented; maxillary and labial palpi all uniformly moderately pigmented (Fig. 4B). Coronal ridge present, postoccipital ridges absent. Tentorium mostly absent because of impending ecdysis. Parietal bands absent. In lateral view, clypeus slightly convex but more than of *P. nanum*, projecting beyond frons, antenna arising from large but ill-developed prominence, and labrum extending beyond clypeus. Diameter of basal ring of antenna about ½ of the distance from closest point on ring to centre of anterior tentorial pit; antennal papilla only slightly pigment- ed, elongate, bearing two sensillae apically. Frontal area between antennae with only two setae on each side. Parietal region with many setae - three setae from pleurostomal ridge to front tentorial pit and several sensillae on the sides. Three setae on the top of parietal area. Clypeus wide with ill-developed basal and well-developed apical margin, four setae subapically on each side. Labrum C-shaped, distinctly emarginated apically in the middle, with two rows of more than ten setae and sensillae and a row of sensillae apically; labral sclerite not defined and only very poorly pigmented. Epipharynx simple without any visible spinulae. Mandible moderately robust; apex brownish pig- mented, with two blunt apical teeth longest and two blunt lateral tubercles (Fig. 4C). Maxillary apex slightly bent mesad in frontal view, so that maxillary palpus subapical in position; cardo distinct, posterior end directed toward posterior tentorial pit; stipes weakly sclerotized; maxillary palpi elongate, probably more than four times basal di- ameters, both pigment- ed. Stipes with ten conspicuous setae, which are slightly larger than those on other parts of head. Maxillar palpus elongate, with three sensillae on the top. Labium not divided into prementum and postmentum; apex moderately narrow in frontal view. Four setae on both sides and three smaller on ventral surface. Salivary lips transverse, very wide and well visible, with inner surface bearing parallel longitudinal grooves; width of lips more than half of width of labium. Labial palpus elongated with three sensillae in middle.

**Nest structure of Pseudoanthidium nanum** in plant stems and oak galls

The nests of *P. nanum* in reed stalks and goldenrod stems from trap nests differed in several cases. More nests were recorded in trap nests made from reed stalks (132 of 156 nests in total) than in trap nests made from goldenrod stems (24 nests), although both were made available in similar quantities. The number of brood cells per nest was 2–17 (median 6; mean 6.6 ± 3.2 cells per nest; n = 156 nests). The number of brood cells in goldenrod stems was lower (range 2–12, median 5; mean 5.2 ± 2.3 cells per nest; n = 24 nests) than that in reed stalks (range 2–17, median 6; mean 6.7 ± 3.3 cells per nest; n = 132 nests). However, the number of brood cells was limited by the cavity length. The inner space of the cavities was filled by plant fibres usually of white or whit- ish colour; several times, the colour was light-brown, yellow, orange or reddish, and in several nests, the colour varied in the length of the nest, certainly according to the
matter used by the nesting female. The nest did not have any matter at the base or closing plug. The entire inner space was filled with plant fibres (Figs. 5A). Cocoons were located inside the filling; they were brown coloured and of the same shape as cocoons of *P. tenellum*. The only difference was the darker colour of the cocoons than those of *P. tenellum* (Fig. 5E). The size of the cocoons was similar to that of *P. tenellum*, length 7.02–8.41 mm (median 7.84; mean $7.8 \pm 0.4$ mm; $n = 42$ cocoons measured) and width 4.02–4.61 mm (median 4.32; mean $4.35 \pm 0.3$ mm; $n = 42$ cocoons measured).

The nests in oak galls were much smaller, and they contained 2–6 brood cells (median 3; mean $3.1 \pm 1.2$ cells per nest; $n = 19$ nests). The brood cells were located in the soft parenchymatic tissue between the central brood cell of *A. kollari* and the gall outer layer (Figs. 5B-D). They were usually oriented ideally. The basal parts of the cocoons were usually located near the centre of the cell. The cells were covered by plant fibres of usually whitish or light grey colour. The sizes of cocoons were similar to those in reed stalks and goldenrod stems: length 7.10–7.99 mm (median 7.65; mean $7.68 \pm 0.40$ mm; $n = 12$ cocoons) and width 4.09–4.53 mm (median 4.30; mean $4.33 \pm 0.20$ mm; $n = 12$ cocoons).

**Figure 5.** Nests of *Pseudoanthidium nanum* **A** nest in a twig of *Rosa* sp. **B, C** nests in oak galls of *Andricus kollari*, **D** – two cocoons in an oak gall, and **E** – cocoon.
Parasites associated with *Pseudoanthidium nanum*

We recorded one cuckoo bee, one cuckoo wasp, two species of chalcids and one ichneumonid in nests of *P. nanum*. *Stelis punctulatissima* (Megachilidae) was the most abundant species, recorded from 38 nests in reed stalks, while eight of these nests contained only the brood of *S. punctulatissima* (but the nest structure was certainly from *P. nanum*). This parasitic species was also reared from nine nests with *P. nanum* in oak galls (from the Czech Republic, Slovakia, Hungary and Italy) of *A. kollari* and from two nests in oak galls of *Andricus quercustozae* (Bosc) from Italy. *Chrysis interjecta* (Chrysididae) was found in seven nests in reed stalks from Hungary, in two oak galls of *A. kollari* (from Slovakia and Hungary) and in three oak galls of *A. quercustozae* (from Italy). *Melittobia acasta* (Walker) (Chalcidoidea: Eulophidae) was recorded in six nests in reed stalks, one in goldenrod stems and two in oak galls of *A. kollari*. *Eurytoma* sp. (Chalcidoidea, Eurytomidae) was recorded in two nests in reed stalks, and *Xylophrurus augustus* (Dalman) (Ichneumonidae) was recorded in two nests in reed stalks.

**Description of mature larva of *Pseudoanthidium nanum***

**Material examined**

Ten larvae from Lanžhot, Břeclav-Pohansko, Kurdějov and Hodonín.

**Diagnosis**

The mature larva of *Pseudoanthidium nanum* is similar to larva of *P. tenellum*. In general, the body is thickened with small head and multiple setae on the surface. The main difference is in the shape of mandibles, which have blunt apical teeth, larger antennal orbits and slightly different chaetotaxy. It corresponds in size with larva of *P. tenellum*. The mandibles are brownish coloured and more sclerotized than that of *P. tenellum*. Both studied larvae are very similar in general appearance and do not differ in the chaetotaxy and morphology.

**Description**

**Body:** Body length 6.1 – 7.9 mm (*N* = 10). Body vestiture without spicules, and with many thick, pale setae, tapering to fine points, arising from small but distinct alveoli. The distribution of setae is on the whole body, while the dorsal parts of body are more setose. Only mandibular apices, area around mandibular condyli, part of maxillae and labium and maxillar and labial palpi brownish coloured. Body form of postdefecating larva fusiform, slightly dorsoventrally flattened, robust; body segments similarly wide on whole length (Fig. 6A). Dorsal body tubercles present but ill-developed only on metathorax and T1-T3, other body segments without body tubercles. Paired lateral tubercles present on metathorax and T1-T8 but ill-visible, not separated. Body shape
Nests, parasites and larvae of *Pseudoanthidium*

of predefecating larva in lateral outline with first abdominal segments having greatest diameter and outline tapering forward and very slightly backward from there. Abdominal segment 10 wide; anus positioned medially and transverse. Spiracles (Fig. 6D) light-brown, subequal in diameter; atrium globular, slightly wider than deep, projecting little above body wall, with rim; atrial opening diameter vs. peritreme width ratio 0.75; atrial inner surface with rows of wrinkles concentric with primary tracheal opening; primary tracheal opening with collar; subatrium short, with only four chambers of approximately equal size. Sex characters unknown.

**Head:** Head heart-shaped, small in relation to body size and ill-separated from prothorax; oriented in normal, hypognathous position relative to thorax. Setae long and sparse on upper part of head capsule; those of maxillary and labial apices large, straight and conspicuous. Head capsule unpigmented except at points of articulations with mandibles; mandibles moderately pigmented except mandibular apices and ar-

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**Figure 6.** Mature larva of *Pseudoanthidium nanum* **A** lateral view **B** head, frontal view **C** mandible, lateral view, and **D** spiracle.
eads of articulation with head capsule strongly pigmented; maxillary sclerites faintly pigmented; salivary lips projecting and pigmented; maxillary and labial palpi all uniformly moderately pigmented (Fig. 6B). Coronal ridge present, postoccipital ridges absent. Tentorium mostly absent because of impending ecdysis. Parietal bands absent. In lateral view, clypeus only slightly convex, projecting beyond frons, antenna arising from large but ill-developed prominence, and labrum extending beyond clypeus. Diameter of basal ring of antenna similar to the distance from closest point on ring to center of anterior tentorial pit; antennal papilla only slightly pigmented, elongate, bearing two sensilla apically. Frontal area between antennae only with two setae on each side. Parietal region with four setae and four sensillae laterally near mandibular condyli and three setae and one sensilla on each side near the coronal ridge. Clypeus wide with ill-developed basal and well-developed apical margin, four setae subapically on sides. Labrum C-shaped, distinctly emarginated apically in the middle, with two rows of more than ten setae and similarly large sensillae on the surface and one row apically. Labral sclerite not defined and only very poorly pigmented. Epipharynx simple without visible spinules. Mandible moderately robust; darkly pigmented, with two apical teeth longest and sharp and with one subapical and one lateral tubercle (Fig. 6C). Maxillary apex slightly bent mesad in frontal view, so that maxillary palpus subapical in position; cardo distinct, posterior end directed toward posterior tentorial pit; stipes weakly sclerotized; maxillary palpi elongate, probably more than four times basal diameters, both pigmented, with three sensillae apically. Cardo with six, stipes with thirteen conspicuous setae, which are larger than setae on other parts of head. Labium not divided into prementum and postmentum; apex moderately narrow in frontal view. Three large setae on both sides and five smaller on ventral surface. Salivary lips transverse, very wide and well visible, with inner surface bearing parallel longitudinal grooves; width of lips more than half of width of labium. Labial palpus elongated with three sensillae in middle.

Discussion

Summarizing the previously published data on the nesting biology of *P. nanum*, we can obtain a good overview of most aspects of the nesting biology of this species. This bee uses various types of cavities for nesting, while those in wood and plant stems are the most preferred. In trap nests composed of reed stalks and goldenrod stems, this species was the second most numerous in all habitats, while it highly preferred nesting in reed stalks with an existing cavity. Comparing the wetland and steppic habitats, it was much more abundant in steppic habitats, where it was the most abundantly nesting bee species in a survey by Heneberg et al. (unpublished). However, we did not observe this species as nesting in reed galls, although many thousands of reed galls were analysed for this purpose (summarized by Astapenková et al. 2017 and Bogusch et al. 2020). *Pseudoanthidium nanum* certainly uses pre-existing cavities for its nesting, and it is likely unable to enter the gall, where the entrance is hidden (see Bogusch et al. 2020).
Reed galls have the entrance hidden among old leaves and nesting species must evolve specific strategies to get into, which is more complicated than in the case of open entrances of reed stalks. *Pseudoanthidium nanum* was also recorded as a very numerous species nesting in oak galls (P. Bogusch & P. Heneberg, pers. obs.). In oak galls of various species of cynipid wasps in the genus *Andricus*, *P. nanum* preferred galls of *A. kollari*, probably because of their high abundance, positions low above the ground, and large openings formed by reared cynipid wasps. Several nests were also in galls of *A. quercustozae* but none in those of *Andricus hungaricus*, probably because these galls do not stay on twigs but fall on the ground at the end of the season.

The structure of the nest reflects the cavity type. In linear cavities, all or most of the inner space is filled by plant fibres (see Fig. 5A), as reported by Grandi (1961), Basnaszak and Romasenko (1998) and Westrich (2018). The brood cells are not separated, and there are only pollen balls of oval shape with eggs or larvae inside the plant fibre matter. In oak galls, brood cells are usually formed separately in cavities, from which the nesting female removed the parenchymatic tissue before (see Figs. 5B-D). This corresponds with the hypothesis that *P. nanum* is ecologically plastic and can utilize many types of cavities (Banaszak and Romasenko 1998; Westrich 2018).

Regarding *P. tenellum*, we recorded nests only in reed galls. This species occurs in near-natural terrestrial reed beds with meadows or semiruderal sites, where a high number of flowering plants (both in abundance and diversity) exists. However, this species is rare, and only unexpected findings at two localities during our survey of reed galls in Hungary (Astapenková et al. 2017) led us to study the biology of this species in detail. Certainly, it is a question, whether this species has the same natural history in its whole very large distribution area, or is restricted to wetland habitats with reed galls only in the westernmost part of its area of occupancy. Contrary to *P. nanum*, *P. tenellum* found a way to enter the reed gall and created nests in galls with hidden entrances. The nest can be identified at first sight, as plant fibres, with brood cells inside, which filled all or most of the hollow. This nest structure is very similar to that of *P. nanum* in linear cavities. The brood cells are not separated; there are only pollen partitions of oval shape with eggs or larvae inside the plant fibre matter. Contrary to *P. nanum*, whose nests in linear cavities frequently contain ten or more brood cells, the number of brood cells in nests of *P. tenellum* inside the limited space of reed gall is much lower.

*Pseudoanthidium tenellum* is certainly a species occurring predominantly in wetlands and reed beds. During our long-lasting surveys on bees in Hungary (since 1999), we recorded only the specimens listed in this study, and all originated from wetland localities. Many of the localities contain high proportions of salt in the ground and can thus be classified as inland salines. Westrich (2018) also reported the occurrence of this species in saline habitats, but the species also occurs in habitats with low concentrations of salt in the ground. The pollen obtained from nests also confirms this habitat requirement (described by Astapenková et al. 2017 and Bogusch et al. 2020) because most pollen in nests of this species was identified as the *Bidens* pollen type – pollen of the wetland plants of the genus *Bidens* according to Beug (2004). Litman et al. (2021) recorded *Limonium* as a host plant, but they explained that this plant was visited by a
single male only. More authors have reported steppic plants visited by this species, but they may serve as a source of nectar. We did not study the diet of *P. nanum*, Westrich (2018) cited mostly steppic (*Centaurea* and *Inula*) and ruderal plant species (*Solidago*) of the family Asteraceae.

Although no parasitic species associated with *P. tenellum* were recorded (perhaps because the biology of this species was previously unknown), we surprisingly identified one *Stelis punctulatissima* in a nest from Virt. This species is an unspecialized nest cleptoparasite of multiple genera of bees in the family Megachilidae (see Banaszak and Romasenko (1998) and Westrich (2018)). It was also occasionally reared from nests of *Hoplistis leucomelana* (Kirby) in reed galls (Bogusch et al. 2015). It was found in high numbers in nests of *P. nanum* both in reed stalks and cynipid galls (this study). Interestingly, *G. nigrescens* larvae inside two nests from Szeged (Hungary) were also found. This rare species of open habitats in central Europe (both xerothermic and wetland) is associated with *H. leucomelana* as the main and best-known host (Schmid-Egger and Saure 2010). However, the host spectrum could be broader because Bogusch et al. (2018) reported this species frequently parasitizing nests of *Heriades rubicola* Pérez, which is recently enlarging its area in central Europe towards the north. Finding this species in the nests of another megachilid bee, *P. tenellum*, is thus not surprising. Interestingly, larvae of *Gasteruption* usually eat out the entire inner space of the nest, and only a single larva survives in the nest of the host (see Parslow et al. 2020). However, in the case of *G. nigrescens* parasitising nests of *H. rubicola* and *P. tenellum*, the larvae usually remained in the brood cells and did not move between cells inside the cavity like larvae of this genus usually do (Bogusch et al. 2018; Bogusch 2021). *Leucospis biguetina* is a parasitoid associated with many species of bees s. l. (Baur and Amiet 2000) nesting in cavities. Similar is the situation with the sarcophagid fly *M. punctata*, which also attacks nests of many species of bees and wasps, both nesting in soil and cavity (Westrich 2018). This species is widespread in Europe and has probably the broadest spectrum of hosts within the genus, of which all members are nest cleptoparasites of solitary bees (Whitmore et al. 2020). Thus, the findings of both species in nests of *P. tenellum* are not surprising, although *L. biguetina* is not very common species (Baur and Amiet 2000).

Regarding the parasites of *P. nanum*, we recorded those whose association with *P. nanum* is well known. The very rare species *Chrysis interjecta* was frequently recorded, usually in warmer regions south of Slovakia and in Hungary and Italy and only in oak galls. The only new host record was the finding of *Xylophrurus augustus* in nests of *P. nanum*. However, this fact is not surprising because this species is not specialized, and many species of bees, sawflies, and saproxylic beetles have been reported as hosts (for a review, see Yu et al. 2012).

The larva of *P. nanum* was described by Romasenko (1995), and our findings generally agree with the original description. It is a typical megachilid larva with a heart-shaped head, bidentate mandible, elongated antennal projection and integument with many short spinules. Larvae obtained from oak gall did not differ from those from reed stalks. Although the larvae of *P. tenellum* look very similar, we can find several differ-
ences between mature larvae of both species. The main difference is the blunt apical tooth on the mandible, in contrast to the sharp tooth of *P. nanum*, and less sclerotized and thus lighter coloured parts of the head. In general, it corresponds with the fact that both species are closely related, although they developed very different ecologies.

*Pseudoanthidium nanum* is a relatively common species of open habitats in central Europe. It usually occurs on forest-steppe grassland slopes, where it forms strong populations. Adults can be found easily on flowers of various plants in the family Asteraceae. They need shrubs and/or large and thick plant stems for their nesting or the presence of abandoned oak galls. They are common and numerous at suitable sites and many parasitic species have adapted to exploit nests of this bee species. *Pseudoanthidium tenellum* is a much rarer species in terrestrial reed beds and wet meadows with the presence of flowering plants (especially in the family Asteraceae) and reed galls. It is very rare and occurs in habitats that are near-natural and well preserved. In this study, we recorded the first four parasitic species associated with *P. tenellum* and described its nest structure, nesting biology and mature larva. Because the distribution and probably several aspects of the biology of this rare bee remain unknown, our study can serve as a starting point for future studies on this bee species, reed beds and reed galls.

**Acknowledgements**

We would like to thank Martin Schwarz (Linz, Austria) for identification of ichneumonids, Petr Janšta (Praha, Czech Republic) for identification of chalcids and Domenico Bonelli (Torino, Italy) for identification of flesh flies. This study was supported by the Excellence Project of the University of Hradec Králové Nr. 2210/2021.

**References**


Nests, parasites and larvae of *Pseudoanthidium* 303


Review of the *Epeolus cruciger* species group (Hymenoptera, Apidae, *Epeolus* Latreille, 1802) of Asia, with the description of two new species

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Abstract

The six species of the *Epeolus cruciger* species group from Asia are reviewed. Two new species, *Epeolus asiaticus* Astafurova & Proshchalykin, *sp. nov.* (Mongolia, Russia) and *E. gorodkovi* Astafurova, *sp. nov.* (Tajikistan, Afghanistan) are described and illustrated. *Epeolus alpinus* Friese, 1893 is newly recorded from Kazakhstan; *E. cruciger* (Panzer, 1799) is newly recorded from Turkmenistan, Uzbekistan, and Kyrgyzstan; and *E. mongolicus* Astafurova & Proshchalykin, 2021 is newly recorded from Kyrgyzstan and Russia. An identification key for both sexes of all Asian members of this species group is presented.

Keywords

Anthophila, Apiformes, cleptoparasites, Palaearctic region, taxonomy

Introduction

The present paper is part of a series of works dealing with the bees of the genus *Epeolus* Latreille, 1802 of the Asian Palaearctic (Astafurova and Proshchalykin 2021a, b, c). The genus *Epeolus* includes more 118 species spread across much of the globe; they occur throughout the Holarctic zone, from the west coast of the United States and eastwards to Europe and as far as Japan (Michener 2007). About 40 species are known.
from the Palaearctic region, of which 25 species are found within Asia (Astafurova and Proshchalykin 2021a, b, c; Bogusch 2021; Ascher and Pickering 2022; current data).

There, the cruciger species group includes *Epeolus alpinus* Friese, 1893, *E. cruciger* (Panzer, 1799), *E. laevifrons* Bischoff, 1930, *E. schummeli* Schilling, 1849, *E. sigillatus* Alfken, 1930, and *E. mongolicus* Astafurova & Proshchalykin, 2021 (Bogusch and Hadrava 2018; Astafurova and Proshchalykin 2021b; Le Divelec 2021). Species of the *E. cruciger* group show considerable intraspecific variation, making it difficult to discern their identities and the status of the species. For these reasons, we paid special attention to their considerable variability.

Here, we add two new species to this group: *E. asiaticus* Astafurova & Proshchalykin, sp. nov. and *E. gorodkovi* Astafurova, sp. nov. from various territories of Central Asia.

**Materials and methods**

The results presented in this paper are based on 640 *Epeolus cruciger* species group specimens currently housed in the Zoological Institute, Russian Academy of Sciences (St. Petersburg, Russia, ZISP); Zoological Museum of the Moscow State University (Moscow, Russia, ZMMU); Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of Russian Academy of Sciences (Vladivostok, Russia, FSCV); and Oberösterreichisches Landesmuseum, Biologiezentrum (Linz, Austria, OLBL).

The taxonomy and synonymy of species follow those of Bogusch and Hadrava (2018). Morphological terminology follows that of Engel (2001) and Michener (2007). The density of integumental punctures is described using the following formula: puncture diameter (in μm) / ratio of distance between punctures to average puncture diameter, e.g., 15–20 μm / 0.5–1.5.

Abbreviations T and S are used for metasomal tergum and metasomal sternum, respectively.

The species are listed alphabetically. We have used the following abbreviations for collectors: AL – A. Lelej; DS – D. Sidorov, JH – J. Halada, MK – M. Kozlov, MP – M. Proshchalykin; PK – P. Kozlov, SB – S. Belokobylskij, SL – S. Luzyanin; VL – V. Loktionov.

Specimens were studied with an Olympus SZ51 stereomicroscope and photographs were taken with a combination of stereomicroscope (Olympus SZX10) and digital camera (Olympus OM-D). Final images are stacked composites generated using Helicon Focus 7.7.4 Pro. All images were post-processed for contrast and brightness using Adobe Photoshop. New distributional records are noted with an asterisk (*).

**Taxonomy**

**Genus Epeolus Latreille, 1802**

### Epeolus cruciger species group

**Diagnosis.** Labrum with apical margin straight or medially slightly curved, with small distinct medial tooth; sub-apically (as opposed to medially, as in species in the *Epeolus variegatus* species group, or apically, as in species in the *E. julliani* species group) with two obvious teeth (tubercles). Axilla flat, with small apical tooth or without distinct tooth. Species of the group are quite variable in the body size, coloration and pubescence.


### Key to Asian species (not including Crete-endemic *E. sigillatus*)

1. Vertex not elevated, hardly visible as seen as frontal view .......................................................... 2
   - Vertex elevated, obvious, distance from top of head to upper margin of lateral ocellus about two lateral ocellar diameters as seen in frontal view .......................................................... *E. schummeli* Schilling

2. Upper half of frons with short simple setae and confluent punctures. Terga with apical bands of tomentum interrupted. Male gonostylus mostly parallel-sided as seen in lateral view (Fig. 9H), with narrow apical area (membranous area with setae) as seen in ventral view (Fig. 9D) .................. *E. cruciger* (Panzer)
   - Upper half of frons with relatively long, erect simple setae (can be mixed with adpressed, plumose pubescence) and usually with polished interspaces between punctures (confluent punctures without distinct polished interspaces as in *E. gorodkovi* sp. nov.). Terga with apical bands of tomentum uninterrupted or interrupted. Male gonostylus apically distinctly curved and triangular as seen as lateral view (Fig. 9E–G); with apical area (membranous area with setae) wider as seen as ventral view (Fig. 9A–C) .......................................................... 3

3. Pubescence coloration monochromatic (golden or copper); terga entirely covered with dense tomentum.......................................................... *E. mongolicus* Astafurova & Proshchalykin (male unknown)
   - Pubescence coloration mixed (whitish/yellowish and brownish) or yellowish monochromatic; tergal pubescence heterogeneous, dense tomentum foming light, well-visible spots or bands .................................................................... 4

4. Tergal discs entirely black. Labrum, pronotal lobes, axillae and mesoscutellum black, reddish or amber .......................................................... *E. asiaticus* sp. nov.
   - Tergal coloration variable, but yellow-reddish pattern usually well-developed or at least on posterior half of T5 (Fig. 7A–I). Labrum, pronotal lobes, axillae and mesoscutellum yellow-reddish (amber) .................... *E. asiaticus* sp. nov.

5. Terga each with uninterrupted apical band of tomentum; marginal zones pale-yellow to golden .......................................................... *E. gorodkovi* sp. nov.
   - Terga each with interrupted apical band of tomentum; marginal zones black or brownish .......................................................................................................................... 6
Mesoscutum and mesoscutellum sparsely punctate with punctures separated by more than one puncture diameter ...................... *E. laevifrons* Bischoff

– Mesoscutum and mesoscutellum densely punctate with confluent punctures to separated by about one puncture diameter ...................... *E. alpinus* Friese

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**Epeolus alpinus** Friese, 1893
Figs 5A, B, 9C, G

*Epeolus alpinus* Friese, 1893: 34, ♂, ♀ (type locality: Goeschenen, Switzerland), Natural History Museum, Berlin.


*Epeolus glacialis* Alfken, 1913: 36, nomen novum for *E. variegatus* Thomson, 1872.

*Epeolus montanus* Bischoff, 1930: 9, ♀, ♂ (type locality: Warnemünde, Germany), Natural History Museum, Berlin.

*Epeolus pilosus* Bischoff, 1930: 9–10, ♀, ♂ (type locality: Rositten [=Rybachi], Kaliningrad Prov., Russia), Natural History Museum, Berlin.


Epeolus cruciger species group in Asia

309

Epeolus cruciger species group in Asia

**Variability.** Asian specimens examined are on average bigger than European ones (6.0–8.0 mm vs 5.0–6.0 mm). Female. Unlike *E. cruciger* and *E. asiaticus* sp. nov., this species does not have individuals with a red pattern on integument of the metasomal terga. The pronotal lobe, mesoscutellum and axillae are red in most of studied Asian specimens; these structures are mostly black in specimens from the European range; only 6% of all examined females have a red labrum. Pubescence of the head and mesosoma, tergal bands or spots of tomentum are white or pale yellow. The mesoscutum is without tomentum in most specimens, rarely with weak tomentum anteriorly. Most examined specimens have widely interrupted apical bands of pale tomentum on T1 and T2 and two pairs of spots of pale tomentum on T3 and T4 (Fig. 5A), but sometimes the lateral spots on T3 and T4 are reduced and only a medial pair is present. Specimens examined from isolated populations of Sakhalin Isl. (Russia) differ from typical forms in having well-developed tomentum on the marginal zones of the terga, which are present as narrowly interrupted bands or even uninterrupted bands on T3 and T4 (Fig. 5B); the mesoscutum is denser punctate than in continental specimens. Male. The males do not show significant variability in coloration. Yellow-red coloration is absent, except on the mouth parts, legs (partly), tegulae and rarely the pygidial plate. Tergal bands of white tomentum are widely or narrow interrupted medially by regular brownish tomentum, sometimes reduced to two pairs of spots on T3 and T4; T1 apical bands can be rarely uninterrupted. Specimens from Sakhalin Isl. as well as females differ in having well-development apical bands of tomentum, which are present as uninterrupted bands on all terga or at least on T3 and T4. Further molecular studies might help to determine whether the forms from Sakhalin merit separate subspecies or species status.

**Distribution.** Europe, Turkey, Iran, Russia, *Kazakhstan (Kokchetau Province), Mongolia (Bogusch and Hadrava 2018; Astafurova and Proshchalykin 2021b). Bogusch (2018) mentioned records from North Africa.

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**Epeolus asiaticus** Astafurova & Proshchalykin, sp. nov.

https://zoobank.org/AAF37DDD-7282-43B9-9F0C-70EC3E1E7C21

Figs 1, 2, 7, 8, 9B, F

**Material examined. Holotype:** ♀, Mongolia, Terkhin-Gol, Chulut and Khoit Rivers, 30.VI.1975, E. Narchuk [ZISP]. **Paratypes:** 1 ♀, 2 ♂, the same label as in the holotype [ZISP]; 1 ♀, Russia, Altay Republic, 8 km SW of Kurai, 11.VII.2007,
Diagnosis. Structurally and in sharing long setae on the upper half of frons the new species is closest to *Epeolus alpinus*, *E. laevifrons*, *E. gorodkovi* sp. nov. and *E. mongolicus*. The new species differs from *Epeolus alpinus*, *E. laevifrons* and *E. gorodkovi* in having yellow-reddish (amber) pattern on metasomal terga (vs entirely black) and from *E. mongolicus* in having sparser pubescence on tergal discs (vs dense, as well as tomentum on marginal zones in *E. mongolicus*). Differences between the new species and other species of the *cruciger* group are outlined in Table 1 and the key.

*Figure 1.* *Epeolus asiaticus* Astafurova & Proshchalykin, sp. nov., holotype, female (A, B), paratype, male (C). A–C habitus, lateral view (A), dorsal view (B, C). Scale bars: 1.0 mm.
Table 1. Differences between females and males of *Epeolus cruciger*, *E. mongolicus*, *E. asiaticus*, *E. alpinus*, and *E. gorodkovi*.

<table>
<thead>
<tr>
<th>Female</th>
<th>cruciger</th>
<th>mongolicus</th>
<th>asiaticus</th>
<th>alpinus</th>
<th>gorodkovi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upper half of frons</td>
<td>with short setae and mostly confluent punctures</td>
<td>with relatively long erect simple setae (can be mixed with appressed plumose pubescence usually extending ocelli); with polished interspaces between punctures</td>
<td>with relatively long erect setae; with polished interspaces between punctures</td>
<td>with relatively long erect setae and mostly confluent punctures</td>
<td></td>
</tr>
<tr>
<td>Labrum on apical margin</td>
<td>curved medially</td>
<td>slightly curved medially or more distinctly curved in large specimens</td>
<td>straight or slightly curved medially</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Punctuation of mesoscutum</td>
<td>with punctures from mostly confluent to separated by a half puncture diameter, without distinct interspaces</td>
<td>with punctures from confluent to separated by at least a puncture diameter, usually with distinct polished interspaces</td>
<td>with punctures from mostly confluent to separated by a half puncture diameter, without distinct interspaces</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pubescence of mesoscutum</td>
<td>without tomentum or with a pair short paramedial strips</td>
<td>entirely covered with tomentum (but tomentum can be strongly shabby)</td>
<td>usually well developed on an anterior half, but without distinct paramedial strips</td>
<td>slightly developed, usually without paramedial strips</td>
<td>developed only on anterior margin</td>
</tr>
<tr>
<td>T2 apical band or spots of tomentum</td>
<td>widely interrupted band forming a pair of lateral spots, sometimes reduced to two pair small lateral spots</td>
<td>uninterrupted band, visually merged with dense discal pubescence</td>
<td>uninterrupted or narrowly interrupted medially</td>
<td>widely interrupted medially band (narrowly interrupted in Sakhalin specimens)</td>
<td>uninterrupted band</td>
</tr>
<tr>
<td>T3-T4 apical band or spots of tomentum</td>
<td>two pair (or extremely rare only a pair) whitish spots</td>
<td>uninterrupted bands, visually merged with dense discal pubescence</td>
<td>variable, usually uninterrupted or narrowly interrupted medially bands, or rarely with additional lateral interruption forming 2 or 4 spots</td>
<td>with a pair of large spots (sometimes with an additional pair of small lateral spots); in Sakhalin specimens with narrowly interrupted medially band or T4 uninterrupted band</td>
<td>uninterrupted bands</td>
</tr>
<tr>
<td>Coloration of labrum, pronotal lobes, axilla and mesoscutellum</td>
<td>variable from black to red or yellowish (amber)</td>
<td>always yellow-reddish (amber)</td>
<td>always yellow-reddish (amber)</td>
<td>variable from black to red or yellowish (amber)</td>
<td>black</td>
</tr>
<tr>
<td>Coloration of terga</td>
<td>extremely variable from black to reddish</td>
<td>yellow-reddish (amber); marginal zones yellowish</td>
<td>variable, from mostly black with small yellow-reddish (amber) pattern to mostly yellow-reddish; marginal zones light</td>
<td>black; marginal zones always dark (black or brownish)</td>
<td>black; marginal zones yellowish</td>
</tr>
<tr>
<td>Coloration of tergal band/spot of tomentum</td>
<td>white or yellow</td>
<td>copper or gold</td>
<td>yellowish (from pale to golden)</td>
<td>whitish or yellowish</td>
<td>whitish and yellowish</td>
</tr>
<tr>
<td>Pubescence on tergal disc</td>
<td>sparser than tomentum on marginal zones, from black or dark brownish to light brownish and rarely yellowish</td>
<td>dense (as well as tomentum on marginal zones), copper or golden</td>
<td>sparser than tomentum on marginal zones; yellowish, golden, brown (the same coloration or darker than tomentum on marginal zones)</td>
<td>sparser than tomentum on marginal zones; dark brown</td>
<td>sparser than tomentum on marginal zones, dark brown</td>
</tr>
<tr>
<td>Male</td>
<td>cruciger</td>
<td>mongolicus</td>
<td>asiaticus</td>
<td>alpinus</td>
<td>gorodkovi</td>
</tr>
<tr>
<td>------</td>
<td>----------</td>
<td>------------</td>
<td>-----------</td>
<td>---------</td>
<td>-----------</td>
</tr>
<tr>
<td>Upper half of frons</td>
<td>with short setae and confluent punctures</td>
<td>unknown</td>
<td>with relatively long erect simple setae (can be mixed with appressed plumose pubescence extending ocelli); with polished interspaces between punctures</td>
<td>with relatively long erect simple setae (maybe shabby); with polished interspaces between punctures</td>
<td>relatively with long setae and confluent punctures</td>
</tr>
<tr>
<td>Apical band or spots of tomentum</td>
<td>whitish; on T1 and T2 widely interrupted bands; on T3 and T4 two pairs of spots</td>
<td>uninterrupted yellowish band</td>
<td>T1-T3 with interrupted medially whitish band, on T4 narrowly interrupted or uninterrupted band, or on T3 and T4 often reduced to 4 spots</td>
<td></td>
<td>uninterrupted whitish band</td>
</tr>
<tr>
<td>Coloration of terga</td>
<td>black</td>
<td>variable, with different proportion black and yellow-red, marginal zones transparent and pale-yellow or yellow.</td>
<td>black, marginal zones black or brownish</td>
<td>black, marginal zones pale-yellow to golden</td>
<td></td>
</tr>
<tr>
<td>Gonostylus apical area [membranous area with long setae and curved towards central axis]</td>
<td>narrow as seen as ventral view</td>
<td>relatively wide as seen as ventral view</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gonostylus in lateral view</td>
<td>almost parallel-sided</td>
<td>apically triangular, distinctly curved</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Description. Female (holotype). Total body length 8.0 mm (Fig. 1A, B); forewing length (without tegula) 6.0 mm.

Structure and sculpture: Head (Fig. 2A) transverse, 1.26 times as wide as long. Labrum (Fig. 2E) 1.6 times as wide as long, rounded basally and laterally, apical margin slightly curved with small distinct medial tooth; sub-apically with two well-visible teeth; integument shiny, coarsely and densely punctate (15–30 μm / confluent–0.5). Clypeus densely and finely punctate (10–15 μm / confluent–0.5), narrowly impunctate along apical margin. Frons with developed frontal keel. Upper half of frons and ocellocular area with shiny interspaces between punctures (15–30 μm / confluent–1.5). Flagellomeres ca 1.1 times as long as wide. Mesoscutum coarsely punctate (25–40 μm / confluent–1.5), interspaces between punctures shiny and smooth; mesoscutellum areolate-punctate. Axilla short and flat, pointed apically, but without distinct tooth. Mesoscutellum with shallow medial longitudinal impression; posterior margin scarcely extending over propodeum. Mespisternum mostly areolate-punctate, with few interspaces ca one puncture diameter. Propodeal triangle shagreened; posterior vertical surface of propodeum shiny and smooth. Metasomal terga densely and finely punctate (10–15 μm / 0.5–1), interspaces shiny and smooth. Pseudopygidial area short, triangular. Pygidial plate trapezoidal, apically truncate. Processes on sides of S6 normal, with short projections. Sterna densely punctured like terga (Fig. 2D). S5 wide, straight as seen in lateral view.

Integument coloration: Head mostly black, but mandibles (excluding dark apex), labrum, clypeus along apical margin, and F1 (partly) yellow-red (amber). Mesosoma mostly black; pronotal lobe, tegulae, axillae, mesoscutellum, metanotum medially and legs (including spurs) yellow-red (amber); wings with brownish darkening, stigma and veins brown. Metasomal terga mostly black, but yellow-red on posterior half of T1, along marginal zones of T2–T4 (narrow strip), and posterior half of T5; marginal zones amber, transparent. Pygidial plate yellow-red with brownish edging. Sterna brownish, yellow-red laterally and along marginal zones; marginal zones pale yellow.

Pubescence: Pale tomentum yellow to white. Labrum with sparse thin golden setae. Paraocular and supraclypeal areas with dense tomentum obscuring integument, clypeus with sparse pubescence. Upper half of frons with long simple setae (Fig. 2C). Vertex with sparse thick (plumose) setae. Genal integument almost obscured by tomentum. Pronotum dorsally with tomentum obscuring integument. Mesoscutum with thick plumose setae, dense on anterior third and peripherally; with a few erect simple setae. Metanotal integument almost entirely obscured by tomentum. Mespisternum with tomentum denser on upper half and laterally. Ventral parts of mesosoma with dense white tomentum. Legs with white setae. T1 with wide basal band of pale tomentum connected with apical band laterally; marginal zones on T1–T4 with uninterrupted bands of pale tomentum, but medially tomentum sparser and not obscuring integument. Setae on tergal discs brownish; sparser and shorter than on apical bands. Pseudopygidial area with silvery pubescence. Sterna with golden short and sparser setae; marginal zones of T2–T4 with white tomentum.

Male. Structure, sculpture, coloration and pubescence are similar to those of the female (Fig. 1C). Head (Fig. 2B) transverse, ca 1.2 times as wide as long. F1 1.2–1.4
times as wide as long, remaining flagellomeres about as long as wide or little longer. Pygidial plate (T7) shiny, coarsely and densely punctate, 1.1–1.2 times as long as basal width narrowed toward apex, with shallow punctures; apical margin slightly curved. Clypeus with dense tomentum obscuring integument. Marginal zones of S2 and S3 with dense uninterrupted white tomentum bands; S4 and S5 normal, with golden long setae. Gonostylus as on Fig. 9B, F.
Variability. Female. Total body length is 4.5–9.0 mm. The mesoscutellum is usually flattened with a weak medial longitudinal impression, but in large specimens this impression can sometimes be deep. The labrum, mandible, pronotal lobe, tegulae, legs,
axillae and mesoscutellum are always yellow-reddish (amber); the clypeus is usually yellow-reddish apically as well as scape and partly F1. The females of this new species exhibit considerable intraspecific variation in the metasomal coloration and degree of development of the tergal tomentum bands. This variability is expressed in a huge variety of combinations of these features (Fig. 7A–G). Among all the specimens examined, there is not one where such a combination was more or less the same. The coloration of terga on discs ranges from mostly black (but never wholly) to a well-developed yellowish pattern; the proportion of yellow differs, but yellowish coloration is common on pos-

Figure 4. *Epeolus gorodkovi* Astafurova, sp. nov., holotype, male (A, C–F), paratype, female (B, G) A, B head, frontal view C labrum, frontal view D T7, dorsal view E, G mesosoma, dorsal view F metasoma, dorsal view. Scale bars: 0.5 mm (A, B, E–G); 0.3 mm (C, D).
terior half T1 and T5 and as a narrow strip along marginal zones of T2–T4. The sterna are yellow-reddish on marginal zones and can be reddish, brownish or black on discs.

Apical bands on T1–T4 typically uninterrupted (Fig. 7E), but tomentum medially can be sparser and darker (Fig. 7C, D, F, G); or bands are distinctly interrupted (Fig. 7B). The tomentum coloration is yellowish, but varies from pale yellow to bright golden. The coloration of pubescence on tergal discs ranges from yellowish to brownish (i.e. can be contrasting or not with coloration of tomentum bands).

In nine (5%) female specimens, the second submarginal crossvein is incomplete or lacking completely (Fig. 8A). A single teratological specimen has an additional submarginal cell (Fig. 8B).

**Male.** Total body length 5.0–7.0 mm. The apical margin of the pygidial plate is sometimes straight or rarely slightly bilobed. The coloration of pedicel, scape and F1 varies from partly yellow-red to brownish. Variation in metasomal integument coloration is similar to that of the female with different proportions of black and yellow-red (Fig. 7H, I). Apical tomentum bands are typically uninterrupted (Fig. 7I), but sometimes tomentum setae medially are sparser and darker (Fig. 7H). Tergal discs setae are white, yellowish, golden or rarely brownish. The sterna can be brownish or black on discs, but typically it is with yellow-reddish pattern laterally and along marginal zones; marginal zones pale-yellow or yellow.

**Etymology.** The specific name “asiaticus” is an adjective in the nominative singular that means “Asian” in Latin and refers to the occurrence of this species in Asia.
**Epeolus cruciger species group in Asia**

**Distribution.** Russia (Tyva Rep., Zabaikalskiy Terr.), Mongolia (Arkhangai, Bayankhongor, Bayan-Ölgii, Dornod, Dornogovi, Govi-Altaï, Khuvsgul, Omnogovi, Selenge, Sukhbaatar, Tuv, Ulaanbaatar, Uvs, Uvurkhangai, Zavkhan).

**Epeolus cruciger** (Panzer, 1799)

Fig. 6

**Nomada crucigera** Panzer, 1799: 20, ♂ (type locality: Austria), Natural History Museum, Berlin.


**Epeolus marginatus** Bischoff, 1930: 11, ♀, ♂ (type locality: Warnemünde, Germany), Natural History Museum, Berlin.


**Remarks.** We also have examined 80 specimens of this species (36 ♀, 44 ♂) from the European part of Russia and from the Caucasus. We have not listed materials from Yakutia published by Davydova and Pesenko (2002). A few specimens were misidentified by these authors and belong to *E. alpinus* (*vide supra*). A record from Sakhalin (Proshchalykin et al. 2004) also corresponds to *E. alpinus*.

**Distribution.** Europe, Turkey, Syria, Iran, Russia, Kazakhstan, *Turkmenistan, Uzbekistan, Kyrgyzstan, Mongolia* (Dornod, Khentii, Khovd, Khuvsgul) (Bogusch and Hadrava 2018; Astafurova and Proshchalykin 2021b).

**Variability. Female. Integument coloration.** There are two main forms: dark with black/brownish metasoma (Fig. 6A, B) and light with reddish metasoma (Fig. 6C, D). Extremely dark specimens have yellow only on the mouth parts, tegulae and legs; this form is rare. A reddish labrum and mesoscutellum were found in most of the dark specimens examined. Extremely light individuals have a reddish or amber labrum, antennae, clypeus, lateral and lower part of mesosoma, mesoscutellum, axillae, metanotum, and mesosoma. In this case, the mesoscutum is partly reddish (laterally and with reddish spots posteriorly). Darker forms predominate in the forest zone and are rarer in the steppe zone. However, both forms can occur in the same location. **Pubescence coloration.** Pubescence of the head and mesosoma and tergal bands or spots of tomentum are white or pale yellow. Bright individuals (with yellow pubescence) are extremely
rare and occur in the southern part of the range of this species. Coloration of tergal disc pubescence is quite variable and correlates with integument coloration: black or dark brownish in dark forms and light brownish (rarely yellowish) in light forms. Development of tomentum. The mesoscutum lacks tomentum or has only a pair of short paramedial strips. The development of white tomentum apical band or spots on terga is variable, but this tomentum is always interrupted medially. T1 and T2 have widely interrupted apical tomentum bands forming a pair of lateral spots, on T2 sometimes reduced to two pairs of small lateral spots (Fig. 6C). T3 and T4 are with two pairs of lateral spots or rarely with a single pair. Male. Males do not show significant variability. Yellow-red coloration is usually absent, except mouth parts, legs, tegulae and pygidial plate; labrum, pronotal lobe, mesoscutellum, axillae are only rarely reddish. To mentum is white or pale-yellow.

**Epeolus gorodkovi** Astafurova, sp. nov.
https://zoobank.org/28FE7A01-AF79-4ABA-BB66-E2A29D9A308B
Figs 3, 4, 9A, E

**Material examined.** Holotype: ♂, Tajikistan, Pamir Mts, Murgab River Valley, Zapadny Pshart River, 3325 m, on Myricana squamosa, 29.VI.1958, K. Gorogkov [ZISP]. Paratypes: 1 ♀, 16 ♂, the same label as in the holotype [ZISP]; 1 ♂, Afghanistan, Ghazni, Moqr, 2000 m, 24.VI.1970, Kabakov [ZISP].

**Diagnosis.** Structurally and in coloration, the new species is very similar to *Epeolus alpinus* but differs in having uninterrupted apical tergal bands, denser and lighter pubescence on tergal discs (light brown to yellowish) and yellowish marginal zones.
on terga (black or brownish in *alpinus*). The upper half of frons, ocellocular area and mesoscutum are mostly confluent punctate (with a few shiny interspaces) and similar to those in *E. cruciger*. Differences between the new species and other species of the *cruciger* group are outlined in Table 1.

**Description.** Male (holotype). Total body length 6.5 mm (Fig. 3C); forewing length (without tegula) 5.0 mm.

Structure and sculpture: Head (Fig. 4A) transverse, ca 1.3 times as wide as long. Labrum (Fig. 4C) 1.6 times as wide as long, rounded basally and laterally, apical margin slightly curved medially with small distinct medial tooth; sub-apically with two well-visible teeth; integument shiny, coarsely punctate (15–25 μm / confluent–1). Clypeus densely and finely punctate (ca 10 μm / confluent). Frons with well-developed frontal keel. Upper half of frons mostly with confluent punctures (15–20 μm), sparser on ocellocular area. Antennae short, flagellomeres ca as long as wide. Mesoscutum and mesoscutellum (Fig. 4E) coarsely (25–40 μm) and mostly areolate-punctate with a few interspaces at most a half puncture diameter. Axillae short and flat, apically with small tooth (Fig. 4E). Mesoscutellum with medial longitudinal impression; posterior margin scarcely extending over propodeum. Mesepisternum areolate-punctate, with shiny interspaces on hypopimpleral area. Propodeal triangle shagreened; posterior vertical surface shiny and smooth. Metasomal terga densely and finely punctate (10–15 μm / 0.5–1), interspaces shiny and smooth. Pygidial plate (T7) coarsely and densely punctate, shiny between punctures, 1.0–1.1 times as long as basal width, narrowed toward apex, with shallow punctures; apical margin slightly curved (Fig. 4D). Sterna punctured like terga, but sparser.

Integument coloration. Head black, except partly red-yellowish mandibles, brownish antennae and apically yellowish F1. Mesosoma black, except red-yellowish tegulae, tibiae and tarsi. Metasomal terga black, but marginal zones pale-yellow to golden. Sterna brownish with marginal zones the same color as on terga.

Pubescence: Tomentum whitish to yellow (except sometimes brownish on tergal discs). Labrum apically with sparse thin setae. Paraocular and supraclypeal areas with dense tomentum obscuring integument, pubescence on clypeus sparser, shorter and shabby. Upper half of frons with long simple setae. Vertex with sparse thick (plumose) setae. Gena with dense tomentum, but not obscuring integument. Pronotum dorsally with tomentum obscuring integument. Mesoscutum with tomentum of adpressed plumose setae (dense on anterior third and peripherally) and long erect simple setae. Metanotum integumentalmost obscured by short tomentum. Mesepisternum and ventral parts of mesosoma with long tomentum obscuring integument. Legs with white setae. Terga (Fig. 4F) with uninterrupted apical (on marginal zone) light bands of tomentum; T1 entirely covered light tomentum, but with setae medially sparser and shorter; pubescence on other tergal discs short, relatively dense, the same color as on marginal zones or darker to brownish. Marginal zones of S2 and S3 with dense uninterrupted white bands of tomentum; S4 and S5 normal, with golden long setae. Gonostylus as in Fig. 9A, E.

**Female.** Structure, sculpture, coloration and pubescence are similar to those of the male (Fig. 3A, B). Head (Fig. 4B) 1.25 times as wide as long. Flagellomeres ca 1.1 as long as wide. Pseudopygidial area short, triangular. Pygidial plate trapezoidal, apically truncate. Processes on sides of S6 normal, with short projections. S5 wide, straight as seen
in lateral view. Head with adpressed tomentum around antennal sockets (in the single female specimen). T1 with wide basal whitish band of tomentum medially separated by brownish sparser pubescence and connected with apical band laterally; brownish pubescence on tergal discs contrasting with light tomentum bands on marginal zones.

**Figure 7.** *Epeolus asiaticus* Astafurova & Proshchalykin, sp. nov., females (A–G), males (H, I) A–I metasoma, dorsal view. Scale bars: 0.5 mm.
Variability. The male specimen from Afghanistan has a red labrum, F1, pronotal lobes and pygidial plate.

Etymology. The new species is named in honor of famous Russian entomologist and zoogeographer Kirill B. Gorodkov (1932–2001), the collector of the type series.

Distribution. Tajikistan, Afghanistan.

_Epeolus mongolicus_ Astafurova & Proshchalykin, 2021

_Epeolus mongolicus_ Astafurova & Proshchalykin, 2021b: 19, ♀ (holotype: ♀, W Mongolia, Zavkhan, 40 km SW of Uliastay [OLBL]).


Remarks. Male unknown.

_Epeolus schummeli_ Schilling, 1849

_Epeolus schummeli_ Schilling, 1849: 104, ♀ (type locality: Schlesien), type lost.
_Epeolus ruthenicus_ Radoszkowski, 1891: 245, ♂ (type locality: Minsk, Belarus), Natural History Museum, Berlin.


Figure 8. *Epeolus asiaticus* Astafurova & Proshchalykin, sp. nov., females (A, B) A, B part of the forewing, lateral view. Scale bars: 0.5 mm.
**Distribution.** Central and southern Europe, Caucasus, Turkey, Middle East, Ukraine, Belarus, Russia (south of the European part) (Bogusch 2018, 2021; Bogusch and Hadrava 2018; Le Divelec 2021).

**Discussion**

The *Epeolus cruciger* species group is distributed only in the Palaearctic region, and its range extends from northern Africa to the Russian Far East and China. *Epeolus cruciger* is most widespread and occurs from Europe over Central Asia to the Russian Far East. *Epeolus alpinus* is also widespread from Europe to the Far East, but it is mostly a boreal species and in the southern part of its range occurs in mountainous areas. *Epeolus schummeli* is a Western Palaearctic species, but is not known north of Poland. The rest of the species have narrow ranges or are endemic: *Epeolus laevifrons* (North Africa, Turkey), *E. sigillatus* (Greece: Crete), *E. mongolicus* and *E. asiaticus* (Mongolia and adjacent territory) and *E. gorodkovi* (mountains of Tajikistan and Afghanistan). No specimens of the group are recorded in Japan.
The females of several species demonstrate considerable intraspecific variation, but the males are less variable. Two species—*E. cruciger* and *E. asiaticus*—exhibit extreme variation in metasomal integumental coloration, having dark and light forms. In *E. cruciger*, the black forms predominate in the forest zone and are rarer in the steppe zone. However, both forms can be found in the same location. The same rule works for pubescence coloration, as brighter pubescence is generally exhibited by individuals from the southern area of its range. The large variation in body size is characteristic of most of species of this group (difference up to 1.5–2 times between the smallest and largest specimens). It should be noted that *E. alpinus* specimens from Asia are on average bigger than European ones. The Sakhalin population of *E. alpinus* represents a great example of differences between isolated island populations and typical continental forms, expressed in the development of the apical tomentum on terga. However, this case needs further investigation to determine whether subspecies or species status is warranted. Remarkable vitiation is seen in the reduction of the second submarginal crossvein (incomplete or lacking completely) found in 5% of female specimens of *E. asiaticus*. A similar phenomenon was also found in species from North America (Scarpulla 2018), including *E. americanus* (Cresson, 1878) and *E. asperatus* Cockerell, 1909 (Onuferko 2018).

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