

# A new species of *Baeomorpha* (Hymenoptera, Rotoitidae) from mid-Cretaceous Burmese amber

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## Abstract

A fossil species from mid-Cretaceous Burmese amber, *Baeomorpha liorum* Huber, Shih & Ren, **sp. nov.** (Rotoitidae: Hymenoptera), is described and illustrated. Its relationship to other extinct and extant taxa of Rotoitidae is discussed. The location of the amber deposits in which this species was found is well south of the “*Baeomorpha* Realm” proposed by previous authors who suggested that the origin and diversification of Rotoitidae occurred in North Laurasia. Based on the Burmese specimens, we suggest instead that the most parsimonious explanation for the past and present distribution of the family is to assume that Rotoitidae is an ancient lineage of Chalcidoidea that was originally widespread in suitable habitats across both Laurasia and Gondwana and later became extinct everywhere except Chile and New Zealand where the two extant genera occur.

## Keywords

Chalcidoidea, Rotoitidae, Burmese amber, Laurasia, Gondwana

## Introduction

Two extant genera of Rotoitidae (Hymenoptera), each containing one described species, are known: *Rotoita* Bouček & Noyes, 1987 and *Chiloe* Gibson & Huber, 2000. Gibson and Huber (2000) reviewed the family, at the time thought to be known only

from extant taxa, and discussed its relationships to other families of Chalcidoidea. Gumovsky et al. (2018) transferred to Rotoitidae the genus *Baeomorpha* Yoshimoto, with four species from Canadian Cretaceous amber classified by Yoshimoto (1975) in Baeomorphinae (Tetracampidae). They described from Cretaceous Taimyr amber 11 new species of *Baeomorpha* and 1 species of a new genus, *Taimyromorpha* Gumovsky. They also placed Baeomorphinae as a junior synonym of Rotoitidae and synonymized two of the four Cretaceous Canadian species of *Baeomorpha*. The world fauna of Rotoitidae thus contains two described extinct genera with 13 described extinct species from northern Laurasia and two described extant genera with one described species each, one in Chile and one in New Zealand. Here, a new fossil species is described from mid-Cretaceous Burmese amber and its relationships to extinct and extant taxa are discussed.

## Methods

The new species is described from two specimens in a polished piece of Burmese amber from a deposit dated at about 99 ma (Shi et al. 2012). The amber piece also contains a few fragments of debris and an incomplete specimen of a nematoceran fly (Diptera). Morphological terms used in the descriptions mostly follow Gumovsky et al. (2018). Measurements of the two specimens, taken with an ocular micrometer attached to a Leitz binocular microscope at 100× magnification, are given in micrometers (µm) except for antennal segments, which are given as ratios. For the most part body sculpture and setation, especially of the mesosoma, is not clearly visible so is not described. Photographs of slide mounts were taken with a ProgRes C14<sup>plus</sup> digital camera attached to a Nikon Eclipse E800 compound microscope, and a selection of the resulting layers combined electronically in Zerene Stacker. Abbreviations used in the descriptions are: fl for funicle segment. The amber piece containing the type specimens is deposited in the collection of Key Lab of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China (CNUB).

## Taxonomy

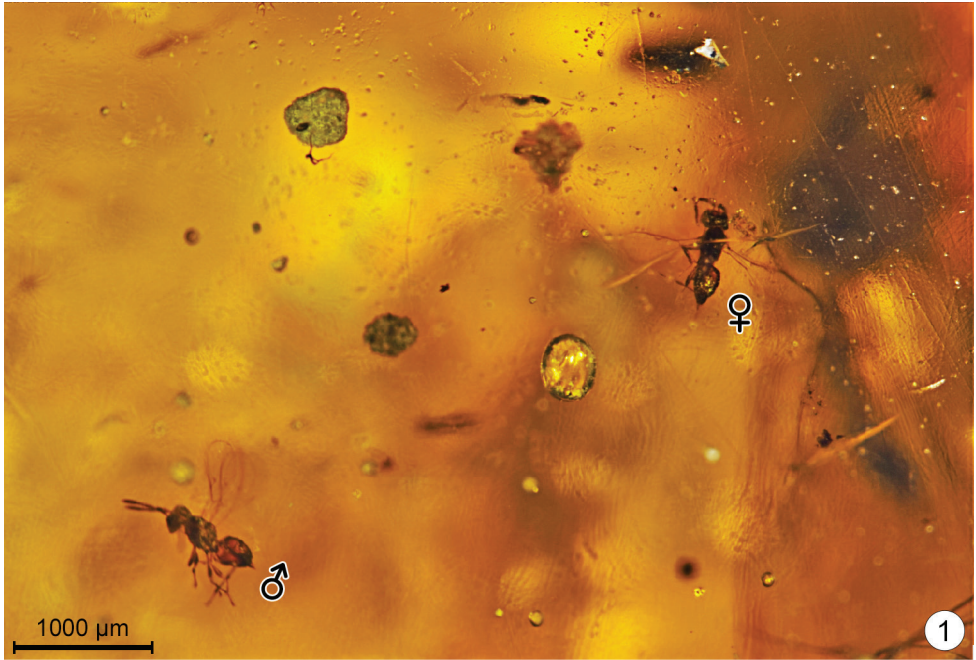
### *Baeomorpha liorum* Huber, Shih & Ren, sp. nov.

<http://zoobank.org/1B11F935-B7E7-4B2B-9DC1-8B8C45E529C5>

Figs 1–7

**Type material.** Holotype female (Fig. 2, CNU-HYM-MA-2015007) and allotype male (Fig. 5, CNU-HYM-MA-2015008) (CNUB), in a single piece of polished amber (Fig. 1). Two labels are added to the container: “Holotype ♀ *Baeomorpha liorum* Huber, Shih & Ren” [red label] and “Allotype ♂ *Baeomorpha liorum* Huber, Shih & Ren” [yellow label].





**Figures 1, 2.** **1** Amber piece containing the holotype and allotype of *Baeomorpha liorum* **2** *Baeomorpha liorum*, holotype female, habitus.

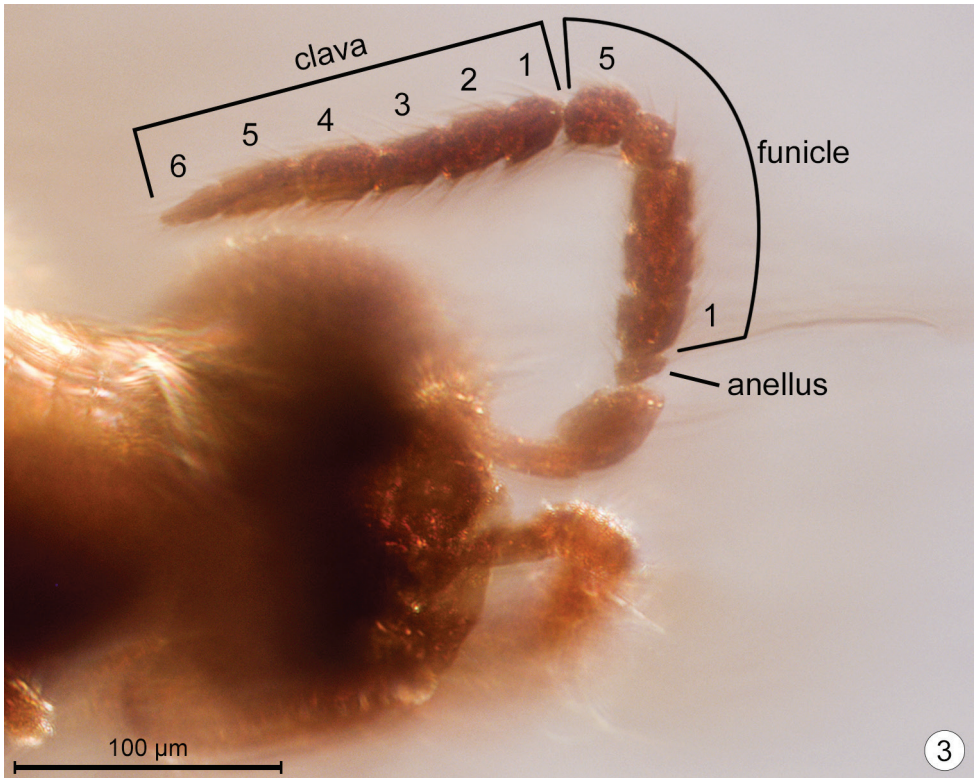
**Diagnosis. Female.** Antenna (Fig. 3) with 1 anellus, 5-segmented funicle and 6-segmented clava;  $fl_1$ – $fl_3$  with wider junctions than those between  $fl_3$ – $fl_5$ , and  $fl_5$  and clava;  $fl_4$  the smallest funicle segment. **Male.** Antenna (Fig. 6) with 1 anellus, 5-segmented funicle and 5-segmented clava.

**Description. Female.** Body length 645. Colour fairly uniformly brown, with slight green metallic tinge (may be an artefact) under certain angles of reflected light; legs slightly lighter. Sculpture and setation not visible. Wings hyaline, with venation, including basal vein, brown. **Head** width 210, length  $\approx 125$ . **Antenna.** Scape (not clearly visible) in dorsal view narrow (Fig. 3); pedicel slightly wider than long (40: 30) and slightly wider than any flagellar segment; clava slightly longer than funicle + anellus (160: 140). Anellus  $0.5\times$  as long as wide and somewhat triangular;  $fl_1$ – $fl_3$  and  $fl_5$  distinctly longer and wider than either anellus or  $fl_4$ ;  $fl_1$  about  $0.95\times$  as long as wide,  $fl_2$  about  $0.88\times$  as long as wide,  $fl_3$  about as long as wide,  $fl_4$  about  $0.85\times$  as long as wide and the smallest funicle segment, and  $fl_5$   $1.2\times$  as long as wide. Multiporous plate sensilla (mps) visible on  $fl_1$ – $fl_3$ ,  $fl_4$ ,  $fl_5$  and at least the apical three claval segments (not clear on remaining claval segments, but probably present); mps absent on anellus and  $fl_4$ . The number of mps cannot be ascertained but there are at least two on each segment that has mps. **Mesosoma** length  $\approx 250$ , metasoma length  $\approx 335$ . Pronotum length  $\approx 50$ , mesonotum length  $\approx 140$ , metanotum length  $\approx 20$ , propodeum length  $\approx 40$ . **Wings.** Fore wing length 600, width 220, longest marginal setae 70; hind wing length 355, width 30, longest marginal setae 30. Submarginal vein 190, parastigma + marginal vein 100, stigmal vein 50, with uncus distinct; postmarginal vein  $\approx 150$ ; postmarginal vein about  $3.4\times$  stigmal vein length. **Metasoma** length 340. Ovipositor not clearly visible, slightly exerted beyond apex of gaster (Fig. 4) (a slight deformity/crack? in the amber makes it difficult to determine the true extent of the exerted part).

**Male.** Body length 600. Colour as in female. **Head** width not measurable, length  $\approx 90$ . Mandibles crossing when closed, apparently with 3 equal teeth. Vertex with sculpture consisting of isodiametric reticulations. **Antenna.** Scape width  $\approx 30$ , length  $\approx 90$ , in lateral view (Fig. 6) as wide as pedicel and about  $2\times$  as long; pedicel about  $1.0\times$  as long as wide; anellus  $1.5\times$  as long as wide;  $fl_1$ – $fl_3$  and  $fl_5$  distinctly longer and wider (on one antenna) than or subequal (on other antenna) to  $fl_4$  and distinctly longer and wider than anellus (probably on both antennae, the anellus not clearly visible on one antenna). **Mesosoma.** Slightly shorter than metasoma (250:270); sculpture of dorsum apparently consisting of small isodiametric reticulations. Pronotum not clearly visible, presumably short; mesonotum  $\approx 50$ ; scutellum  $\approx 90$ ; metanotum  $\approx 20$ ; propodeum  $\approx 50$ . **Wings.** Fore wing length  $\approx 590$ , width  $\approx 240$ , longest marginal setae  $\approx 50$ ; postmarginal vein  $\approx 3.2\times$  stigmal vein length; hind wing length 375, width 40, longest marginal setae about width of hind wing. **Metasoma.** Gaster 270, with gastral terga subequal in length (Fig. 7), each  $\approx 40$ – $50$  (measured along dorsal margin). Genitalia  $\approx 60$  (almost entirely exerted).

**Etymology.** The specific epithet is a patronym honoring Mr. Li Jun and his wife from Jinan, Shandong Province, who obtained the fossil and kindly donated it to CNU.





**Figures 3, 4.** **3** *Baeomorpha liorum*, holotype antenna **4** *Baeomorpha liorum*, holotype metasoma.

**Discussion.** The new species belongs clearly in *Baeomorpha* as defined by Gumovsky et al. (2018). They distinguished it from the other extinct genus, *Taimyromorpha*, by the stigmal vein long and narrower than stigma, and uncus present (stigmal vein short, as wide as stigma and uncus absent in *Taimyromorpha*). *Baeomorpha* differs from the two extant genera as follows: both sexes fully winged (micropterous in *Chiloe*), with notauli (only visible in male) complete and linear (notauli absent in *Rotoita*).

On the basis of the pedicel being about as wide as  $fl_1$ , the female of *B. liorum* keys fairly well to *B. yantardakh* Gumovsky but their images of the female antenna (Gumovsky et al. 2018, fig. 17) are very different so we conclude the Burmese female cannot be that species. If one continues past couple 9, their key becomes difficult to use because not all features mentioned, e.g., scape length and width and head width, can be seen properly or accurately measured on the female of *B. liorum*. Similarly, at their couplet 10, not all features can be assessed properly but the most likely species in those couplets are either *B. zherikhini* Gumovsky or *B. gracilis* Gumovsky. The male of *B. liorum* keys best to *B. gracilis* because it has the distance between the junction of the stigmal vein with the marginal vein and the junction of the basal vein with the submarginal vein (PSM of Gumovsky et al. 2018) about 3.2× as long as stigmal vein, exactly as in *B. gracilis*. Assuming the two sexes of *B. liorum* are conspecific, we doubt that *B. liorum* is the same as any previously described *Baeomorpha* species. The distribution and possibly time of occurrence in the geological record (Taimyr amber is dated as Upper Cretaceous, 84–100 ma) also suggests that it is unlikely that *B. liorum* is the same as one of the previously described species of *Baeomorpha* from western Canada (Medicine Hat area, Alberta) or Taimyr amber.

Gumovsky et al. (2018) noted the unusual variation in number of funicular and claval segments among the fossil *Baeomorpha*. While this meristic variation among species within a given genus is uncommon, it occurs widely among families of extant Chalcidoidea, notably, in females and sometimes in males, in several genera of Mymaridae, the most ancestral lineage of Chalcidoidea (Heraty et al. 2013). Thus, the meristic differences seen among the various *Baeomorpha* species are not particularly unusual. In the male of *B. liorum* the size of  $fl_4$  differs between the antennae, a bilateral variation that occurs not infrequently in individuals of Mymaridae. Given this sort of variation we question whether Gumovsky et al. (2018) have not over split the species of *Baeomorpha* so far found in Taimyr amber.

Mymaridae is the most ancestral lineage of Chalcidoidea followed by Rotoitidae and then the remaining Chalcidoidea (Heraty et al. 2013). Mymaridae are well known in the fossil record, with the earliest species occurring in 99 my old Burmese amber (Poinar and Huber 2011) and the family is worldwide and especially well represented in generic diversity in the Southern Hemisphere. In contrast, Rotoitidae, as old as Mymaridae based on the age of *B. liorum*, are now restricted as extant species to New Zealand and southern Chile.

Gumovsky et al. (2018) proposed that Rotoitidae originated in Laurasia, based on the fossil evidence then available. This contrasts with Gibson and Huber (2000) who hypothesized a Gondwanan origin of Rotoitidae. Huber (2017) suggested that Chalcidoidea, or at least Mymaridae, originated in the Jurassic and perhaps the latter taxon was





**Figure 5.** *Baeomorpha liorum*, allotype male, habitus.

already present even earlier and possibly was widespread in Pangaea. If so, the distribution of Mymaridae and Rotoitidae, both as mid-Cretaceous fossils in northern Laurasia and in Burmese amber, and the present day distribution of both families as extant genera, either worldwide (Mymaridae) or in remnants of Gondwana (Rotoitidae), would then be explained simply as their expected distribution after the breakup of Pangaea began 200



**Figures 6, 7.** *Baeomorpha liorum*, allotype antenna. **7** *Baeomorpha liorum*, allotype metasoma.

million years ago. The distribution of *B. liorum* disproves the hypothesis that Rotoitidae originated in North Laurasia, specifically in their “*Baeomorpha* Realm” (Gumovsky et al. 2018, fig. 22) but does not exclude the possibility that *B. liorum*, perhaps together with other Burmese amber fossils, originated partly or entirely from somewhere in the southeast Laurasia mainland before or during the mid-Cretaceous. Rasnitsyn and Ölm-Kühnle (2018) supported the theory that the mid-Cretaceous Burmese biota, which includes *B. liorum*, was of a long-standing insular nature, the area having been separated from the rest of Laurasia for up to 140 ma according to one hypothesis (but not two other hypotheses) before the collision between the West Burma plate and Proto-Southeast Asia mainland. They proposed that the Burmese amber fossil assemblage reflects a pre-collision rather than post-collision date. Geologists such as Acharyya (1998, 2010), Audley-Charles et al. (1988) and Metcalfe (2017) discussed the complex of areas that broke off from Gondwana and drifted north to collide eventually with the main Laurasian landmass. Audley-Charles (1988, fig. 2) showed the position of Burma as separated by ocean from mainland Laurasia in the early Cretaceous. Metcalfe (2017) showed the collision and accretion of the Sibumasu plate (which includes Burma) to the Laurasian mainland in the Carboniferous-Permian. This is much earlier than the mid-Cretaceous, suggesting that the Burmese amber fossil assemblage reflects a post-collision date. Regardless, the close similarity of *B. liorum* to the Taimyr *Baeomorpha* species suggests that it probably derived from somewhere in Laurasia north of the southeastern area formed by accretion of the various land areas to form the area that is present day Indochina.

It is notable that *Archaeoteleia* (Scelioninae, Platygasteridae) (Talamas et al. 2016) has a very similar distribution to Rotoitidae, being present as an extant genus only in South America and New Zealand and as an extinct genus (with some morphological differences from extant species) in mid-Cretaceous Burmese amber. Incidentally, this is yet another example in Hymenoptera in which a given genus appears to have existed from the mid-Cretaceous to the present; the others belong to Chrysidoidea (Ross 2019, Martynova et al. 2019). The most parsimonious and, we believe, the best explanation for the extinct and extant distribution of Rotoitidae, *Archaeoteleia*, Mymaridae and perhaps the other, unrelated, taxa as well, is to assume they all evolved earlier than currently thought, perhaps sometime in the Jurassic and were widespread across Pangaea in suitable habitats. For example, hosts of *Archaeoteleia* are members of Macropathinae (Orthoptera: Rhaphidophoridae), thought to have originated prior to the tectonic separation of the supercontinent Gondwana (Beasley-Hall et al. 2018).

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# *Hybrizon* Fallén (Hymenoptera, Ichneumonidae, Hybrizontinae) in China

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## Abstract

The species of the genus *Hybrizon* Fallén (Hymenoptera: Ichneumonidae: Hybrizontinae) from China are reviewed, with special reference to Shandong (North China). Two new species (*Hybrizon hei* **sp. nov.** and *H. xui* **sp. nov.**) are described and illustrated. A key to the East Palaearctic species of *Hybrizon* is included.

## Keywords

Ichneumonidae; *Hybrizon*; Palaearctic; China; Shandong; endoparasitoids; ant larvae; key

## Introduction

*Hybrizon* Fallén, 1813, belongs to the small subfamily Hybrizontinae Blanchard, 1845 (= Paxyloommatinae Foerster, 1863, Hybrizoninae of some authors; Wharton and van Achterberg 2000) and contains endoparasitoids of ant larvae carried by workers outside their nest (Gómez Durán and van Achterberg 2011). Most likely the subfamily belongs to the family Ichneumonidae (Rasnitsyn 1980; Yu and Horstmann 1997), but was often associated with Braconidae (van Achterberg 1976) or considered to be a separate family (He 1981, Tobias 1988). The structure of the connection of

the second and third metasomal tergites and the venation of the hind wing, both indicate a closer relationship with the family Ichneumonidae (Sharkey and Wahl 1987; Wahl and Sharkey 1988) than with the Braconidae. According to the analysis of 28S ribosomal RNA Hybrizontinae are at a basal position of the Ichneumonidae-lineage (Belshaw et al. 1998; Quicke et al. 2000; Belshaw and Quicke 2002), but Gillespie et al. (2005) documented the unusual structure of 28S in *Hybrizon*, which makes proper alignment difficult. Quicke et al. (2009) and Broad et al. (2018) placed *Hybrizon* as derived subfamily within the ophoniformes-group of the Ichneumonidae. In the most recent overview (Bennett et al. 2019) Hybrizontinae are also included in the ophoniformes and grouped with part of the Ctenopelmatinae if all morphological and molecular data are combined. When only the molecular data are used Hybrizontinae cluster with Tersilochinae, Cremastinae, part of Mesochorinae and Sisyrus-tolinae. Hybrizontinae can be most easily separated by their aberrant venation of the fore wing (Figs 10, 17, 24), the antenna of both sexes with only 13 segments and the enlarged hind basitarsus. Only Neorhacodinae show a similar fusion of veins SR and M (= vein 3-SR+M) of the fore wing (as a result no vein r-m is present) and have also antenna with 13 segments, but Neorhacodinae lack the enlarged hind basitarsus of Hybrizontinae. Neorhacodinae are not considered to be closely related, but are grouped also in the ophoniformes (Bennett et al. 2019). *Hybrizon* is known from the Holarctic region and the NE part of the Oriental region (van Achterberg et al. 2013). Only three other extant genera are known, of which two are very similar: *Eurypterna* Foerster, 1863 (= *Ogkosoma* Haupt, 1913) and *Ghilaromma* Tobias, 1988 (Tobias 1988; van Achterberg 1999). The third extant genus is described very recently from Japan (*Neohybrizon* Hisasue & Konishi, 2019) with only the type species (*N. mutus* Hisasue & Konishi, 2019) known. *Neohybrizon* differs from the other extant genera by the extremely reduced mouth parts, the longer mesoscutum, the absence of the prepectal carina, the depressed medio-posterior area of the mesoscutum, the larger parastigma, the slenderer pterostigma, the straight vein 1-SR+1-M of the fore wing, and the longer hind femur (more than  $5.5 \times$  as long as the hind trochanter, about 4 times in *Hybrizon*) (mainly after Hisasue and Konishi 2019).

## Material and methods

The collecting site is the Forestry Protection Station in Jinan (NE China, Shandong Prov., Shanghe County) and the collecting was done with Malaise traps. Images were acquired by using a KEYENCE VHX-5000 Digital Microscope imaging system and processed with Photoshop CC software.

For references to East Palaearctic genera and species of Hybrizontinae, see Yu et al. (2016) and for morphological terminology, see van Achterberg (1988). The specimens are deposited in the Institute of Insect Sciences, Zhejiang University, Hangzhou (ZJUH), Department of Life Sciences, Northwest University, Xi'an (NWUX) and Naturalis Biodiversity Center, Leiden (RMNH). An asterisk indicates new to the fauna.

## DNA extraction

Genomic DNA was extracted from female adult specimens by using DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) and following a non-destructive DNA extraction protocol as described in Taekul et al. (2014). Voucher specimens after extraction were washed by 100% alcohol and restored in Zhejiang University (Hangzhou, China).

## PCR amplification and COI, 28SrRNA sequencing

The barcode region of the mitochondrial cytochrome oxidase subunit I (*COI*) was amplified using the LCO1490/HCO2198 primer pair: (F) (LCO1490) GGT-CAACAAATCATAA AGATATTGG; (R) (HCO2198) TAAACTTCAGGTGAC-CAAAAAATCA (Folmer et al. 1994). The nuclear 28S rRNA D1–2 (28S) was amplified using the primer part: (F) (3665) AGAGAGAGTTCAAGAGTACGTG; (R) (4068) TTGGTCCGTGTTTCAAGACGGG (Belshaw et al. 1998). PCRs were carried out using Tks Gflex DNA Polymerase (Takara) and conducted in a T100 Thermal Cycler (Bio-rad). PCR protocols followed the studied listed above for each molecule. Amplifications were sequenced by Sanger method on an Applied Biosystems (ABI) 3730XL by Sangon Biotech (Shanghai, China). All the amplified sequences were uploaded into GenBank (accession numbers in descriptions). The *COI* sequence of *H. buccatus* (KU753286) and 28S sequences of *H. buccatus* (KU753494) and *H. ghilarovi* (EU378579) were downloaded from GenBank. Sequences of *Lathrolestes nigricollis* (Thomson, 1883) (GQ325436.1) and *Perilissus rufoniger* (Gravenhorst, 1820) (KR880228) were used as out-groups to root the *COI* trees. Sequences of *Perilissus rufoniger* (Gravenhorst, 1820) (EU378529) was used as out-group to root the 28S rRNA tree.

## Data analysis

The preliminary alignment was carried out by using MAFFT v.7.388 by the G-INS-I strategy for *COI* and Q-INS-I strategy for 28S (Kato and Standley 2013). Alignments were checked and corrected manually, and the final alignments of *COI* and 28S were 635bp and 697bp, respectively. The alignments were then analyzed using RAxML as implemented in Geneious 11.0.3.

## Results

The results of the RAxML analysis are presented in Figures 30, 31. The ML phylogenetic tree both of *COI* and 28S rRNA revealed that all species from Shandong province based on morphological characters were also supported by molecular differences. The

pairwise percentage identity of *COI* sequences between the three in-group species was 81.072% to 85.93%, with out-group *Lathrolestes nigricollis* and *Perilissus rufoniger*, was 76.717% to 78.559%, and 64.992% to 67.504%, respectively.

### Genus *Hybrizon* Fallén, 1813

Figs 1–29

*Hybrizon* Fallén, 1813: 19; Bennett et al. 2019: 68; Hisasue and Konishi 2019: 241; for earlier references see van Achterberg et al. (2013) and Yu et al. (2016).

Syn.: *Paxylomma* de Brébisson, 1817; *Paxyloma* Stephens, 1835; *Paxylomme* Wesmael, 1835; *Paxyllomma* Curtis, 1837; *Paxylloma* Blanchard, 1840; *Pachylomma* Ratzeburg, 1848; *Plancus* Curtis, 1833; *Eupachylomma* Ashmead, 1894.

### Key to East Palaearctic species of the genus *Hybrizon* Fallén

- 1 In lateral view length of hind basitarsus 4.0–5.0 times its maximum width (Figs 2, 3, 11); mesoscutum with pair of anteriorly broad bands of distinct punctures (Fig. 14), rarely punctures largely absent or obsolescent; vein 1-M of fore wing paler than vein 2-CU1 of fore wing (Fig. 10); basal cell of fore wing largely glabrous, with about 15 setae (Figs 1, 10), rarely more; scutellum (except sometimes laterally) dark brown as mesoscutum medio-posteriorly (Fig. 14); [length of fore wing 2–3 mm; propodeum largely smooth or granulate, except for medial carinae]; Mongolia, Russia, Japan (Kyushu, Shikoku), South Korea, China (Jilin; ?Heilongjiang; \*Shaanxi; \*Shandong).....***H. buccatus* (de Brébisson, 1825)**
- In lateral view length of hind basitarsus 5.4–7.0 times its maximum width (Figs 5, 18, 25); mesoscutum usually smooth, at most with narrow bands of punctures or notaulic area granulate (Figs 21, 28); vein 1-M of fore wing as dark as vein 2-CU1 of fore wing or nearly so (Figs 17, 24); basal cell of fore wing variable, **if** largely glabrous, then scutellum (except medio-anteriorly) ivory and contrasting with mesoscutum medio-posteriorly (Figs 26, 28).....**2**
- 2 Basal cell of fore wing largely glabrous or sparsely setose, with 10–24 setae (Fig. 24); disco-submarginal cell of fore wing about as high as subdiscal cell (Fig. 24); ivory scutellum (except medio-anteriorly) distinctly contrasting with dark brown mesoscutum medio-posteriorly (Figs 26, 28), rarely both dark brown; anteriorly notaulic area of mesoscutum ivory or brownish (Figs 26, 28), rarely dark brown; scutellum strongly shiny and smooth (Fig. 28); maximum width of face 1.3–1.4 times its minimum width (Fig. 27); length of fore wing 2.6–3.7 mm; China (Shandong), South Korea ..... ***H. xui* sp. nov.**
- Basal cell of fore wing (except basally) more or less evenly setose (Figs 4, 6, 17); disco-submarginal cell of fore wing 1.4–1.9 times as high as subdis-

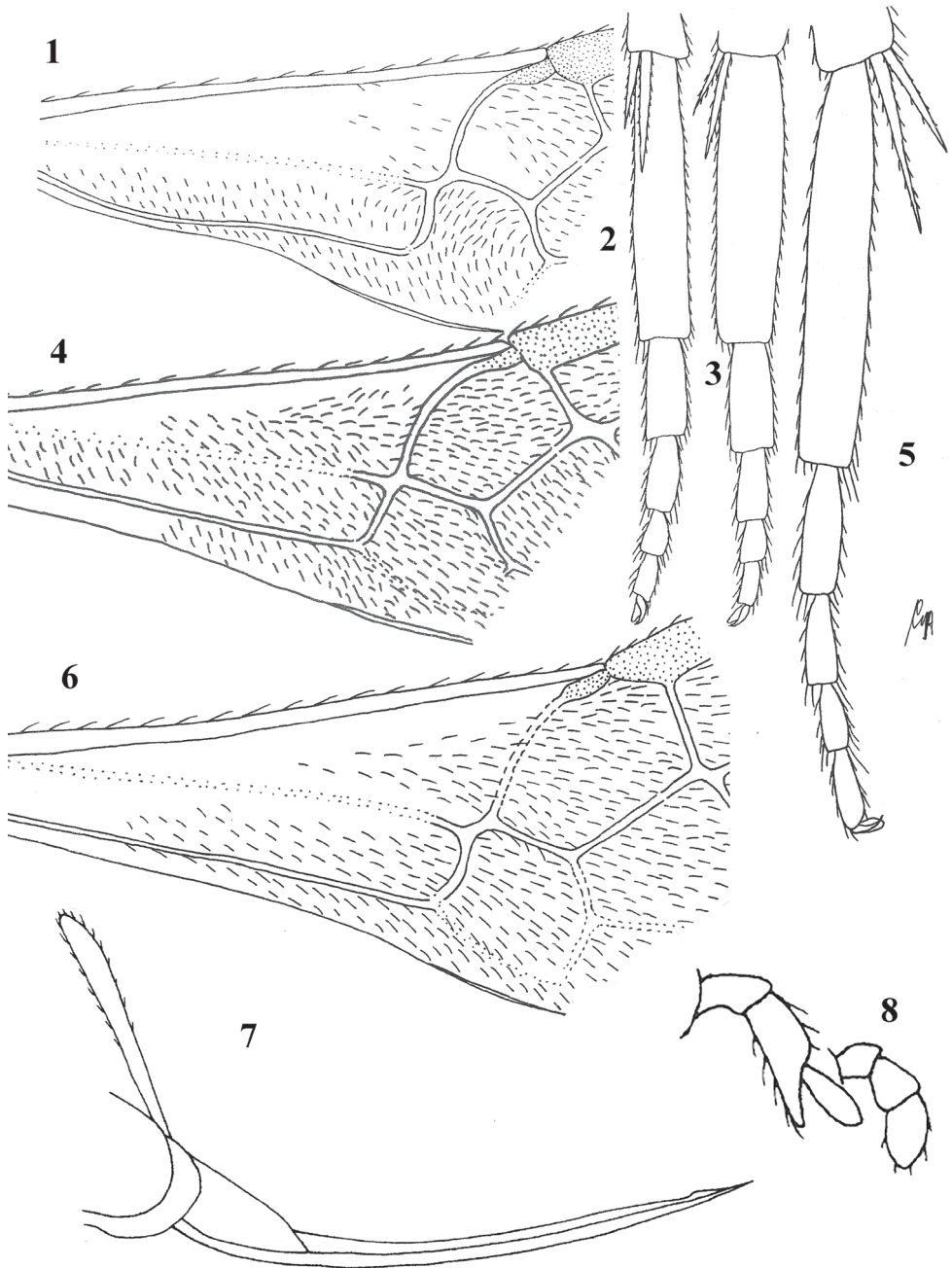
- cal cell (Figs 4, 6, 17); scutellum and mesoscutum medio-posteriorly usually similarly dark brown, but sometimes intermediate (Fig. 21); anteriorly notaulic area often dark brown; scutellum moderately shiny and more or less granulate (Fig. 21); maximum width of face 1.2–1.4 times its minimum width (Fig. 20); length of fore wing 2.1–3.1 mm.....**3**
- 3 Eyes distinctly setose; vein 1-M of fore wing straight anteriorly or nearly so (Fig. 6); ovipositor long and setose part of ovipositor sheath 0.5–0.7 times as long as second metasomal tergite (Fig. 7); scutellum and notaulic area of mesoscutum distinctly granulate; vein r of fore wing issued rather far from base of pterostigma (Fig. 6); pedicellus about as wide as scapus; [ventrally pedicellus yellowish or brown; ventral half of metapleuron coarsely rugose to densely rugulose]; Russia (Far East); Japan (Hokkaido), China (Hunan, Jilin, \*Shaanxi), South Korea.....***H. ghilarovi* Tobias, 1988**
- Eyes glabrous (Fig. 21); vein 1-M of fore wing weakly curved anteriorly (Figs 4, 17), rarely nearly straight; ovipositor shorter and setose part of ovipositor sheath 0.2–0.4 times as long as second tergite (Figs 15, 16, 29); scutellum and mesoscutum smooth or superficially granulate (Fig. 21); vein r of fore wing issued close to base of pterostigma (Figs 4, 17); pedicellus slightly wider than scapus.....**4**
- 4 Face yellow; vein r of fore wing nearly vertical (Fig. 4); maximum width of face 1.1–1.2 times its minimum width; ventral half of face less shiny and more or less granulate; pedicellus brown ventrally, darker than yellowish scapus; Russia (Far East); China (Hunan) ..... ***H. flavofacialis* Tobias, 1988**
- Face at least partly dark brown or brown (Fig. 20); vein r of fore wing distinctly oblique (Fig. 17); maximum width of face 1.3–1.4 times its minimum width (Fig. 20); ventral half of face distinctly shiny and largely smooth; pedicellus and scapus ventrally similarly yellowish or pedicellus somewhat darker (Figs 16, 19, 21); [ventral half of metapleuron and of mesopleuron granulate]; China (Shandong).....***H. hei* sp. nov.**

### Species occurring in China

#### *Hybrizon buccatus* (de Brébisson, 1825)

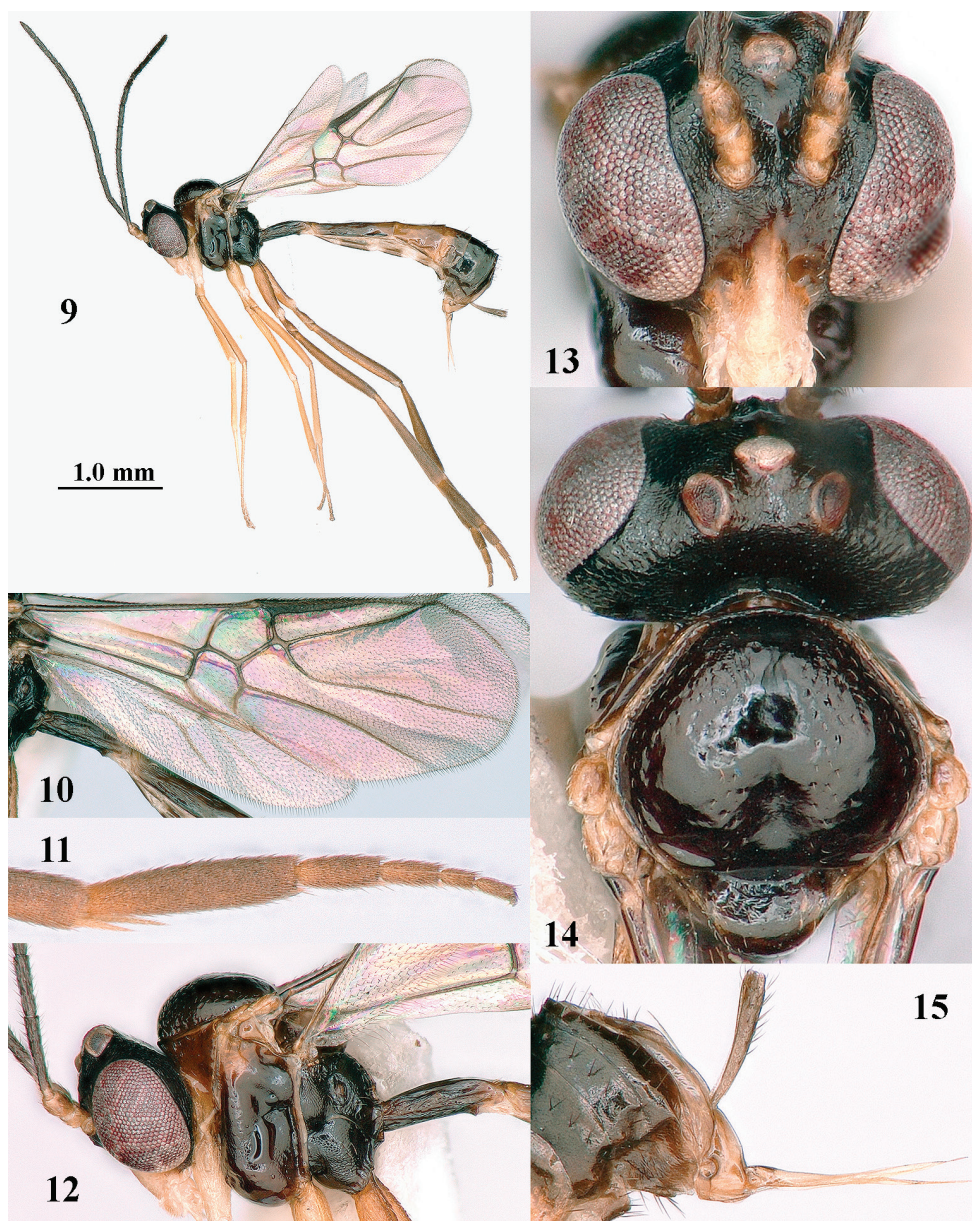
Figs 1–3, 9–15

**Material.** 1 ♀ (ZJUH), “NE China: Shandong, Shanghe County, Ji’nan, Xushang, Dong Balizhuang, 36°16'4"N, 117°9'10"E, Malaise trap, 24–30.ix.2018, Jia-He Yan & Qi-Meng Yang”; 2 ♀ (NWUX), “NW China: Shaanxi, Xunyangba, Ningshaan, 1481 m, Y[ellow] & G[reen] [Malaise] trap, 33°54'N, 108°55'E, 1.vii–17.viii.2016, Tan JL & Tan QQ, NWUX”. Reported from North China by He (1981: Heilongjiang, Jilin) and by Konishi et al. (2012: Jilin). The figured specimen in He (1981) probably belongs to *H. xui* sp. nov. The listed material could not be retrieved, but



**Figures 1–8.** 1–3 *Hybrizon buccatus* (de Brébisson) ♀, Bulgaria, Brodilovo, but 3 of ♀ from Netherlands, Nunspeet 4, 5 *H. flavofacialis* Tobias, female, China, Hunan, Yuanjiang 6, 7 *H. gblarovi* Tobias: 6 of ♀, China, Hunan, Yuanjiang and 7 of ♀, Bulgaria, Brodilovo 8 *H. juncoi* (Ceballos), ♀, Spain, Estepona 1, 4, 6 basal half of fore wing 2, 3, 5 hind basitarsus lateral 7 ovipositor and sheath lateral 8 palpi anterior. From van Achterberg (1999) and van Achterberg et al. (2013).





**Figures 9–15.** *Hybrizon buccatus* (de Brébisson), ♀, China, Shandong **9** habitus, lateral aspect **10** wings **11** hind tarsus, lateral aspect **12** head and mesosoma, lateral aspect **13** head, anterior aspect **14** head and mesosoma, dorsal aspect **15** ovipositor and ovipositor sheath, lateral aspect.

the figure shows a slender hind basitarsus (about 6 times as long as wide) and vein r of fore wing connected somewhat distally from base of pterostigma, what does not fit with *H. buccatus*.

**Differentiating diagnosis.** Easily to separate from other Chinese species because of the largely glabrous basal cell of fore wing, combined with dark brown scutellum, less slender hind basitarsus and lesser body size (length of fore wing not exceeding 3 mm).

***Hybrizon flavofacialis* Tobias, 1988**

Figs 4, 5

**Material.** Series from S. China (Hunan) listed by van Achterberg et al. (2013).

**Differentiating diagnosis.** Differs from other Chinese species by the long and robust ovipositor, the granulate mesoscutum and scutellum, and the nearly vertical vein r of fore wing.

***Hybrizon ghilarovi* Tobias, 1988**

Figs 6, 7

**Material.** 1 ♀ (NWUX), “NW China: Shaanxi, Panda valley, Foping, black Mal[aise] trap, 1411 m, 33°67'N, 107°97'E, 29.v.–19.vi.2016, Tan JL & C. v. A[chterberg], NWUX”. Series from S. China (Hunan) listed by van Achterberg et al. (2013). Konishi et al. (2012) reported this species from NE China (Jilin).

**Differentiating diagnosis.** Differs from other Chinese species by the distinctly setose eyes, vein 1-M of fore wing straight anteriorly or nearly so (Fig. 8) and long setose part of ovipositor sheath (0.6–0.7 times as long as second metasomal tergite).

***Hybrizon hei* van Achterberg & Liu, sp. nov.**

<http://zoobank.org/AF9727B5-5B3F-471F-9026-539BBFC0B781>

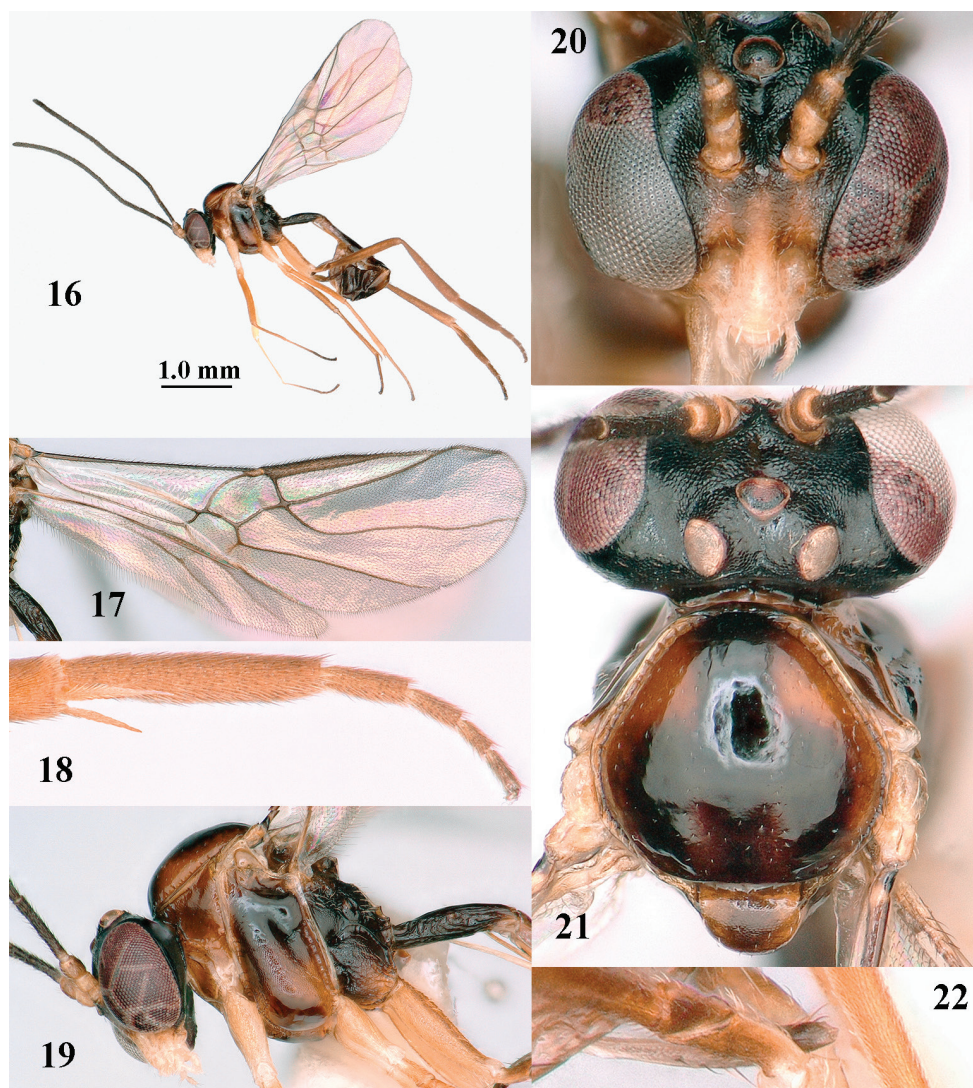
Figs 16–22

**Type material.** Holotype, ♀ (ZJUH), “NE China: Shandong, Shanghe County, Ji’nan, Xushang, Dong Balizhuang, 36°16'4"N, 117°9'10"E, Malaise trap, 24–30.ix.2018, Jia-He Yan & Qi-Meng Yang”, “20190119” (the molecular sequences originate from this specimen). Paratypes (ZJUH, RMNH): 10 ♀, same data as holotype.

**Differentiating diagnosis.** The West Palaearctic *H. pilialatus* Tobias, 1988, is very similar to the new species, but *H. pilialatus* has vein r of fore wing distinctly removed from base of pterostigma and less oblique (Fig. 15 in van Achterberg 1999; vein r issued virtually at base of pterostigma and distinctly oblique in *H. hei*), disco-submarginal cell of fore wing 1.1 times higher than subdiscal cell (1.5–1.9 times in *H. hei*) and vein 1-R1 (= metacarp) of fore wing about 0.4 times length of pterostigma (about 0.6 times in *H. hei*). According to the molecular analyses it is distinctly separated from *H. xui* and *H. buccatus* (Figs 30, 31); unfortunately, molecular data of its most closely relative (*H. pilialatus*) are yet unknown.

**Molecular data.** MN168094 (28S) and MN125615 (COI).





**Figures 16–22.** *Hybrizon bei* sp. nov., ♀, paratype **16** habitus, lateral aspect **17** wings **18** hind tarsus, lateral aspect **19** head and mesosoma, lateral aspect **20** head, anterior aspect **21** head and mesosoma, dorsal aspect **22** ovipositor and ovipositor sheath, lateral aspect.

**Description.** Holotype, ♀, length of body 3.6 mm, of fore wing 2.6 mm.

**Head.** Antenna with 13 segments and 0.9 times as long as fore wing, length of third segment 1.3 times fourth segment, length of third, fourth and penultimate segments 6.5, 5.0 and 3.0 times their width, respectively; pedicellus slightly longer and wider than scapus; apical segment of maxillary palp rather elongate (compared to width of penultimate segment; Fig. 19); face rugulose-granulate medio-dorsally and remainder largely smooth (Fig. 20); maximum width of face 1.4 times its minimum width (Fig. 20); frons granulate and rather shiny, near antennal sockets depressed and

rugulose; length of eye 3.8 times temple in dorsal view; temples directly narrowed behind eyes; vertex shiny and very superficially granulate; OOL:diameter of ocellus:POL = 3:3:6; length of malar space 2.5 times basal width of mandible, concave, anteriorly smooth and posteriorly granulate.

**Mesosoma.** Length of mesosoma 1.1 times its height; mesoscutum strongly shiny, smooth (except for some superficial punctulation) and without notauli (Fig. 21); scutellum convex and moderately shiny, superficially granulate (Fig. 21); ventral half of mesopleuron rather matt and granulate; mesosternal sulcus narrow and smooth; metapleuron shiny and granulate; metanotum slightly and obtusely protruding dorsally; propodeum granulate, but medially and posteriorly areolate with interspaces largely smooth.

**Wings.** Fore wing: marginal cell comparatively slender (Fig. 17); basal cell of fore wing largely and evenly setose (Fig. 17); vein r issued at base of pterostigma and distinctly oblique (Fig. 17); vein 1-M moderately curved and medium-sized, with disco-submarginal cell 1.5 times higher than subdiscal cell.

**Legs.** Hind coxa granulate; in lateral view length of femur, tibia and basitarsus of hind leg 8.3, 7.6 and 5.6 times their width, respectively; spurs of hind tibia 0.3 and 0.4 times hind basitarsus.

**Metasoma.** Length of first tergite 3.1 times its apical width, shiny, smooth except some aciculae, laterally rugose (Fig. 19), subapically parallel-sided and its spiracles slightly protruding; basal half of second tergite with some weak striae; remainder of metasoma smooth and shiny; hypopygium with bristly setae; second tergite with sharp lateral crease; length of setose part of ovipositor sheath 0.08 times fore wing and 0.26 times second metasomal tergite (Fig. 22); ovipositor needle-shaped.

**Colour.** Dark brown or brownish black; mouthparts (including mandible) and clypeus largely white; scapus, pedicellus ventrally, tegulae, legs and anterior half of fourth tergite yellowish brown; scutellum (except medially), pronotum, mesosternum, mesopleuron (except dorsally) and metasoma (except first tergite) mainly brown; remainder of antenna largely dark brown; veins and pterostigma largely brown; vein 1-M of fore wing paler than vein 2-CU1 of fore wing; wing membrane subhyaline.

**Variation.** Length of body (2.3–)3.4–4.1 mm, of fore wing (2.1–)2.6–2.9 mm; maximum width of face 1.3–1.4 times its minimum width; in lateral view length of hind basitarsus 5.4–5.8(–6.3) times its maximum width; disco-submarginal cell of fore wing 1.4–1.7(–1.9) times higher than subdiscal cell; scutellum sometimes rather flat and not reaching level of mesoscutum, but in most specimens convex and protruding above level of mesoscutum, dark brown to largely pale yellowish; face dark brown or partly pale brown, frequently with ivory stripe medially; mesoscutum dark brown or brown antero-laterally.

**Distribution.** China (Shandong).

**Etymology.** Named after Prof. Dr Jun-Hua He (Zhejiang University, Hangzhou) on the occasion of his 90<sup>th</sup> birthday for his numerous contributions to the systematics of Chinese Hymenoptera for more than 45 years.

***Hybrizon xui* van Achterberg & Liu, sp. nov.**

<http://zoobank.org/4AA0A64B-BA65-43EA-9249-7A9EF3EE05AA>

Figs 23–29

*Hybrizon juncoi*: Konishi et al. 2012: 21, 22.

**Type material.** Holotype, ♀ (ZJUH), “NE China: Shandong, Shanghe County, Ji’nan, Xushang, Dong Balizhuang, 36°16'4"N, 117°9'10"E, Malaise trap, 24–30.ix.2018, Jia-He Yan & Qi-Meng Yang”, Paratypes (ZJUH, RMNH): 40 ♀, same data as holotype, of which 1 ♀ (ZJUH) additionally labelled “201901120”, because the molecular sequences originate from this specimen.

**Differentiating diagnosis.** The new species is similar to the SW Palearctic *H. juncoi* (Ceballos, 1957), because of the largely glabrous basal cell of the fore wing, vein 1-M of fore wing as dark as vein 2-CU1 of fore wing, ivory scutellum (except medio-anteriorly), larger body size and anterior notaulic area of mesoscutum more or less ivory or brownish. Konishi et al. (2012) included Korean specimens of this species under *H. juncoi*, but *H. juncoi* has the hind basitarsus about 4.5 times longer than wide (both sexes; 5.6–6.8 times in *H. xui*), vein r of fore wing issued comparatively far removed from base of pterostigma (distance to base of pterostigma about equal to length of vein r; much less so in *H. xui*), propodeum distinctly rugose-granulate (granulate and partly smooth in *H. xui*), vein 1-M comparatively short (fig. 41 in van Achterberg 1999), resulting in a transverse disco-submarginal cell lower than subdiscal cell (vein 1-M medium-sized, resulting in a disco-submarginal cell as high as subdiscal cell in *H. xui*) and penultimate segment of maxillary palp enlarged (Fig. 8; small in *H. xui*). According to the molecular analyses it is distinctly separated from *H. hei* and *H. buccatus* (Figs 30, 31); unfortunately, molecular data of its most closely relative (*H. juncoi*) are yet unknown.

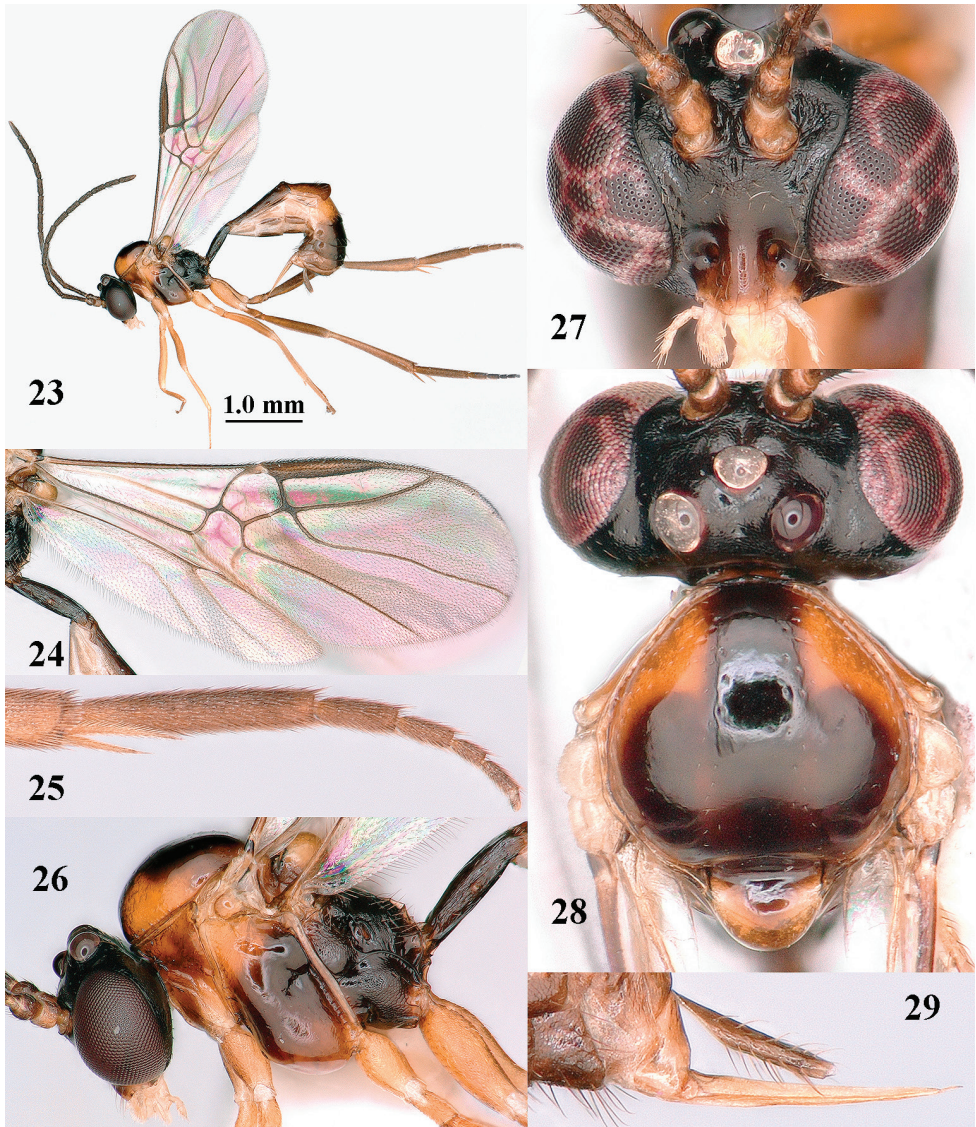
**Molecular data.** MN168195 (28S) and MN260327 (*COI*).

**Description.** Holotype, ♀, length of body 4.2 mm, of fore wing 3.1 mm.

**Head.** Antenna with 13 segments and 0.9 times as long as fore wing, length of third segment 1.4 times fourth segment, length of third, fourth and penultimate segments 5.3, 3.8 and 3.3 times their width, respectively; pedicellus slightly shorter than and as wide as scapus; penultimate segment of maxillary palp small compared to apical segment (Fig. 26); face rugulose-granulate medio-dorsally and remainder largely smooth; maximum width of face 1.4 times its minimum width (Fig. 27); frons smooth and shiny but near antennal sockets depressed and rugulose; length of eye 6.8 times temple in dorsal view; temples directly narrowed behind eyes; vertex shiny and superficially granulate; OOL:diameter of ocellus:POL = 3:5:7; length of malar space 1.3 times basal width of mandible, concave and largely smooth, posteriorly granulate.

**Mesosoma.** Length of mesosoma 1.2 times its height; mesoscutum strongly shiny and smooth, only anteriorly with few punctures and notauli absent (Fig. 28); scutellum strongly convex (protruding up to dorsal level of mesoscutum or above) and shiny, smooth (Figs 26, 28); mesopleuron shiny and largely smooth; mesosternal sulcus nar-

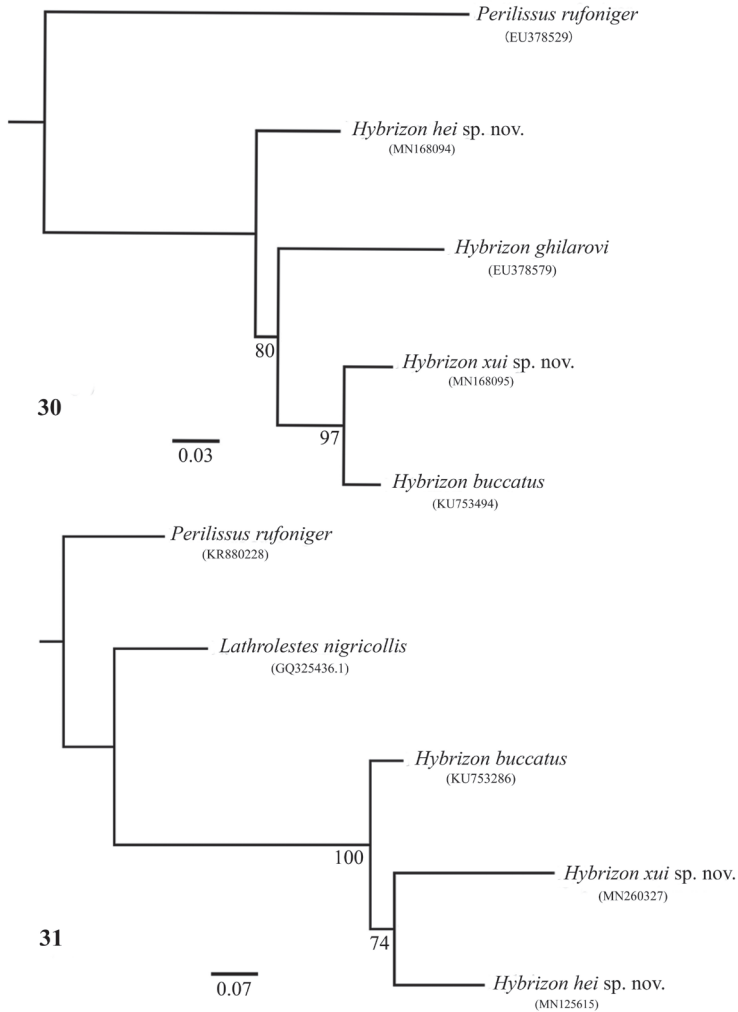




**Figures 23–29.** *Hybrizon xui* sp. nov., ♀, paratype **23** habitus, lateral aspect **24** wings **25** hind tarsus, lateral aspect **26** head and mesosoma lateral aspect **27** head, anterior aspect **28** head and mesosoma, dorsal aspect **29** ovipositor and ovipositor sheath, lateral aspect.

row and smooth; metapleuron shiny and granulate; metanotum obtusely protruding dorsally; propodeum granulate, but medially and posteriorly with some rugae or carinae and interspaces largely smooth.

**Wings.** Fore wing: marginal cell comparatively wide (Fig. 24); basal cell of fore wing largely glabrous, with 18 setae (Fig. 24); vein r nearly vertical and issued comparatively close to base of pterostigma (Fig. 24); vein 1-R1 0.6 times length of pterostig-



**Figures 30, 31.** RAXML result analysis of 28S and COI sequences. Numbers in parentheses are GenBank numbers.

ma; vein 1-M moderately curved and medium-sized, resulting in a disco-submarginal cell as high as subdiscal cell.

**Legs.** Hind coxa finely granulate; in lateral view length of femur, tibia and basitarsus of hind leg 6.9, 6.8 and 5.6 times their width, respectively; spurs of hind tibia 0.35 and 0.40 times hind basitarsus.

**Metasoma.** Length of first tergite 3.4 times its apical width, shiny, smooth (also laterally), medially with shallow elongate depression, subapically widened and its spiracles slightly protruding; second tergite with spaced striae basally and some superficial micro-sculpture medially; remainder of metasoma smooth and shiny; hypopygium

with long bristly setae (Fig. 29); second tergite with sharp lateral crease; length of setose part of ovipositor sheath 0.08 times fore wing and 0.26 times second metasomal tergite.

**Colour.** Dark brown; mouthparts (including mandible) and tegulae white; scapus, and scutellum (except medio-anteriorly) ivory; scutellum distinctly contrasting with dark brown mesoscutum medio-posteriorly (Fig. 28); mesoscutum antero-laterally, pronotum, mesosternum, mesopleuron dorsally and ventrally, anterior half of fourth tergite and legs yellowish brown; pedicellus entirely brown and distinctly contrasting with pale scapus (Figs 26, 27), remainder of antenna largely dark brown; veins and pterostigma largely dark brown; vein 1-M of fore wing as dark as vein 2-CU1 of fore wing or nearly so; wing membrane subhyaline.

**Variation.** Length of body (3.2–)3.6–4.5 mm, of fore wing 2.6–3.7 mm; maximum width of face 1.3–1.4 times its minimum width; basal cell of fore wing with 10–24 setae; anteriorly notaulic area of mesoscutum ivory or brownish yellow, rarely dark brown; in lateral view length of hind basitarsus 5.4–6.6 times its maximum width; pedicellus entirely brown or dark brown, rarely pale yellowish ventrally; apical half of fourth tergite dark brown to brownish yellow; hind leg brownish yellow to brown. One paratype has a transverse groove subbasally on the second tergite.

**Distribution.** China (Shandong).

**Etymology.** Named in commemoration of the much too early deceased hymenopterist Prof. Dr Zai-Fu Xu (South China Agricultural University, Guangzhou; ix.1965 – vi.2017) for his great contributions to our knowledge of the Chinese Hymenoptera.

## Discussion

There are five species (including the two new species in present study) recognized from the Chinese fauna (van Achterberg et al. 2013, Konishi et al. 2012). The three species of *Hybrizon* from Shandong province are separated by the morphological characters and supported by the genetic distance between *COI* sequences as well. Unfortunately, molecular data of most closely relative species (*H. pilialatus* Tobias, 1988 and *H. juncoi* (Ceballos, 1957) are not yet known. But all these species can be distinguished based on the morphological characters alone. Konishi et al. (2012) included the Korean specimens under *H. juncoi* (Ceballos, 1957), but based on the ratio of length to width of hind basitarsus, we consider it should be a misidentification and include it under *H. xui* sp. nov. Based on the pairwise percentage identity of *COI* sequences of the three species from China are also significantly different, the genetic distance between species from the same locality is also very high.

The specimens of *Hybrizon hei* sp. n and *H. xui* sp. nov. collected in the Malaise trap in Shandong province all are female, there are 11 individuals of *H. hei* sp. nov. and 41 individuals of *H. xui* sp. nov. Only a single female specimen of *H. buccatus* was found in the same locality. Biologically, species of Hybrizontinae are known to be associated with ants (Donisthorpe and Wilkinson 1930, Gómez Durán and van Achterberg 2011, Hisasue and Konishi 2019), it is highly likely that the new species from Shandong also emerged from some ant nest near the Malaise trap.

## Acknowledgements

We are deeply grateful to Mr. Jia-He Yan (Forestry Protection Station of Shanghe County, Shandong Province) for his help to collect the specimens, Prof. Xue-Xin Chen (Zhejiang University) for his encouragement during the research, thanks to Prof. Ming-Yi Tian (South China Agricultural University) for access to the digital camera and Dr. Hua-Yan Chen (Sun Yat-Sen University) for his kind help in molecular analysis. This project was supported by the National Basic Research Program of China (No. 2013CB127600) for JXL.

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# Evolution of glandular structures on the scape of males in the genus *Aphelinus* Dalman (Hymenoptera, Aphelinidae)

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## Abstract

The pores and associated glands on male antennae in species of Hymenoptera are involved in mate recognition and are diverse and widespread among taxa. However, nothing has been published about these structures in species of *Aphelinus* (Chalcidoidea: Aphelinidae), a genus of parasitoid wasps with a long history in biological control. Images from scanning electron microscopy (SEM) and transmission electron microscopy (TEM) of *Aphelinus varipes* revealed pores on the ventral side of the male scape that were connected to glands. A survey of the scapes of male antennae in 16 species in six species complexes of *Aphelinus*, as well as two outgroup species, *Aphytis melinus* and *Centrodora* sp., showed that pores were present in all except *Centrodora* sp. The pores varied in several characters: the shape of the structures that carried them, pore size, elevation of the cuticle surrounding the structures, the extent of a carina delimiting the area around the structures, and the number and position of pores. The shape of the pore-bearing structures, the elevation of cuticle around these structures, and the extent of the carina around them map well onto a molecular phylogeny of these *Aphelinus* species. Combinations of pore characters are diagnostic of species complexes, and in some cases, species of *Aphelinus*.

## Keywords

*Aphelinus*, antennal morphology, scanning electron microscopy, scape, sexual dimorphism, mate recognition, glands

## Introduction

Successful mating depends on discriminating between individuals of the same versus different species, as well as between potential mates that will yield progeny with high versus low fitness. Communication with pheromones that attract conspecifics and provide cues for their recognition is often a key component in the quest for mates by insects in general and Hymenoptera in particular (for review, see Ayasse et al. 2001). However, more or less elaborate courtship behavior may also be needed to secure mates (for reviews, see Brown 1999, Spieth 1974, Yuval 2006). In parasitic Hymenoptera, courting males often move their antennae in specific patterns and touch females directly with them (for review, see Gordh and DeBach 1978). Such behavior, usually called antennation, often occurs after a male has approached a female, she has stopped walking, and he has climbed on her back so that their bodies are parallel with his head above hers. Starting at this point, males perform various behaviors that may include head-bobbing, antennal waving and stroking, as well as other behaviors, like leg sweeps. Although male antennation during courtship was described at least as early as 1910 (Girault and Sanders 1910), Barrass (1960) in research on *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae) provided perhaps the first quantitative analysis of courtship behavior, which included quantitation of male antennation. In one of a series of papers on reproductive isolation among closely-related species of *Aphytis* Howard (Hymenoptera: Aphelinidae), Rao and Debach (1969) described antennation behavior in Aphelinidae. Gordh and DeBach (1978) later used a quantitative analysis of differences in courtship behavior, including antennation, to distinguish among cryptic species of *Aphytis* in the *lingnanensis* species complex.

The well-documented role of antennation in courtship triggered investigations into the morphology of antennae. Based on scanning electron microscopy (SEM) of antennae, Goodpasture (1975) suggested that the numerous pores on the scapes of males of some species of *Monodontomerus* Westwood (Hymenoptera: Torymidae) might secrete a pheromone. Dahms (1984a) found pores on the ventral surface of male scapes in *Melittobia australica* Girault (Hymenoptera: Eulophidae), for which he had described antennation a decade earlier (Dahms 1973). He proposed that these pores released a pheromone involved in mate recognition, rather than being sensory organs, as had been previously conjectured. This discovery prompted more studies on morphology of male antennae in parasitic Hymenoptera, using SEM and transmission electron microscopy (TEM). Bin et al. (1989) found three types of glands in antennae of *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygasteridae), and they suggested roles in courtship and mate recognition. On the ventral side of the fourth antennomere of *Amitus spiniferus* (Brèthes) (Hymenoptera: Platygasteridae), Isidoro and Bin (1995) found numerous pores on an elevated plate, and these pores were attached internally to a complex of glandular cells. They suggested that this structure released and spread a mate-recognition pheromone during courtship, and Isidoro et al. (1996) suggested that such structures be called release-and-spread structures (RSS). Research has continued to delineate the taxonomic distribution and morphological diversity of these structures (Bin et al. 1999, Romani et al. 2010).

RSS and their associated glands have been found on male antennae in other chalcids: *Trichogramma australicum* Girault (Hymenoptera: Trichogrammatidae) (Amorn-

sak et al. 1998), *Leptomastix dactylopii* Howard, *Rhopus meridionalis* (Ferrière), and *Asitus phragmitis* (Ferrière) (Hymenoptera: Encyrtidae) (Guerrieri et al. 2001). They have also been found in parasitoids in other superfamilies: *Trissolcus basalis* (Wollaston) (Hymenoptera: Platygasteridae) (Bin and Vinson 1986), a variety of species of Cynipidae and Figitidae (Cynipoidea) (Isidoro et al. 1999), *Trichopria drosophilae* (Perkins) (Hymenoptera: Diapriidae) (Sacchetti et al. 1999), and *Pimpla turionellae* (Linnaeus) (Hymenoptera: Ichneumonidae) (Bin et al. 1999). In the last two species, the RSS and glands were shown to be necessary for successful courtship and copulation (Bin et al. 1999, Romani et al. 2008).

Observations on courtship behavior in several species of *Aphelinus* Dalman (Hymenoptera: Aphelinidae) showed that males antennate during courtship (Kazmer et al. 1996, Rhoades 2015), but nothing has been published on pores and glands on the antennae of *Aphelinus*. However, antennal pores and glands have been reported on the antennal clubs of males of *Aphytis melinus* DeBach (Romani et al. 1999), which is closely related to *Aphelinus* (Kim and Heraty 2012). Furthermore, observations of slide-mounted *Aphelinus* specimens using differential interference contrast microscopy (DICM) showed that RSS are widespread in the genus, and that the arrangement and shape of RSS differed among species complexes. Here we report results of an investigation of the glandular ultrastructure underlying RSS in scapes of male *Aphelinus varipes* (Förster) using TEM, and a survey of variation in the RSS in 16 species in six species complexes of *Aphelinus* using SEM, DICM, and macrophotography that documents their diversity and shows that they are taxonomically and phylogenetically informative.

## Materials and methods

We follow the species complex classification of Hayat (1998), with one modification: we treat the *daucicola* species complex as distinct from the *mali* complex (Hopper et al. 2012).

With TEM, we studied the structure of the cells underlying the pores in the male scape of *A. varipes*. With SEM, we studied male scapes of two to three specimens each from nine species of *Aphelinus* in six species complexes, along with species in two other genera of Aphelininae: *Aphytis melinus* Debach and an undetermined species of *Centrodora* Förster (Hymenoptera: Aphelinidae) (Table 1). With DICM, we studied male scapes of specimens from an additional seven species of *Aphelinus* in two species complexes (Table 1). Prior to preparation for imaging, the material was stored in molecular-grade ethanol.

For TEM, specimens were immersed in a solution of glutaraldehyde (2.5 ml/25 ml solution) and paraformaldehyde (1 g/25 ml solution) in 0.1M cacodylate buffer +5% sucrose, pH 7.2–7.3. The scape was removed from the rest of the antenna and cooled at 4 °C for 3 h. The specimens were placed in 0.1M cacodylate buffer +5% sucrose, pH 7.2–7.3, overnight at 4 °C, then the specimens were post-fixed in 1% OsO<sub>4</sub> (osmium tetroxide) for 1 h at 4 °C and rinsed in the previous buffer. Dehydration in a graded ethanol series from 60% to 99% was followed by embedding in Epon-Araldite with propylene oxide as bridging solvent. Thin sections were made with a diamond knife DiATOME ultra 45° (DiATOME AG, Biel, Switzerland) on a LKB Bromma ultramicrotome (LKB®, Sweden), and mounted on formvar-coated, 50-mesh grids. The

sections were stained with uranyl acetate (20 min, room temperature) and lead citrate (5 min, room temperature). Finally, the sections were investigated with a TEM Philips EM 208 (Thermo Fischer Scientific, Hillsboro, Oregon, USA). Digital images with 1376×1032 pixels, 8 bit, uncompressed greyscale in TIFF files were obtained using a high-resolution digital camera MegaViewIII (SIS) connected to the TEM.

For SEM, specimens were critical-point-dried (CPD) using a Tousimis Samdri-790 (Tousimis Research Corporation, Rockville, Maryland, USA), following the manufacturer's protocol. After CPD, two to three males from each accession (Table 1) were mounted onto standard 12.7mm Ted Pella pin stubs using black carbon tape. Specimens were then gold sputter-coated using a Technics Hummer I (Anatech Ltd, Battle Creek, Michigan, USA), following the manufacturer's protocol. Gold was sputtered on specimens for a total of five minutes, in one-minute intervals separated by one minute. All antennomeres on both the left and the right antennae were examined on each specimen. SEM images were acquired using a Tescan Vega 3 microscope (Tescan USA, Warrendale, Pennsylvania, USA) with secondary electron-emission in high vacuum and beam-acceleration voltages ranging from 15 kV to 30 kV. The beam intensity was either 3 or 5 (range is 1–20), and the scan speed was either 6 or 7 (corresponding to 32 or 100 msec/pixel). For DICM, specimens were slide-mounted in Canada balsam using a protocol modified from Noyes (1982) and observed with an Olympus BH2 compound microscope equipped with differential interference contrast and planapochromat objectives. DICM images were captured with a Jenoptik ProGres CT5 digital camera using Image Pro Plus 7.0. Macrophotographic (MP) images were taken of card-mounted specimens using a Macropod Pro setup (<https://macroscopicsolutions.com/>) consisting of Mitutoyo long-working distance 50× and 100× planapochromat objectives, a Canon 200 mm prime lens, and a Canon EOS 5D Mark III camera. DICM and MP images were focus-stacked using Zerene Stacker 1.04 and final preparation of images from SEM, DICM, and MP was done in Adobe Lightroom. Sample size for specimens examined by DICM and MP varied from a few specimens to ten specimens, or more in cases in which abundant material was available.

Voucher specimens of material examined have been deposited in the Texas A&M University Insect Collection with Voucher #733. Voucher numbers in Table 1 refer to specimens deposited in the Beneficial Insect Introduction Research Laboratory (USDA/ARS), as voucher specimens of the original collections from which colonies were founded.

Five morphological traits of the RSS were recorded for 14 species of *Aphelinus*, as well as for *Aphytis melinus* (Table 2). Eight of these 14 species of *Aphelinus* were studied using SEM, the remainder were studied using DICM. The data were entered into mx, an open-source, web-based database management system (code and documentation available at <http://mx.phenomix.org>), and the results were also exported as a Nexus file. Diagnostics (Consistency Index and Retention Index) were calculated for each trait using PAUP\* with the traits mapped onto a molecular phylogeny from Heraty et al. (2007), modified with additional unpublished data. PAUP\* (4.a build 159; Swoford 2002) and the Trace Character History algorithm using the Parsimony Ancestral States in Mesquite (Maddison and Maddison 2018) provided the most parsimonious reconstructions of character state changes on the phylogeny.

**Table 1.** Collection information and imaging technique for *Aphelinus* species (SEM = scanning electron microscopy, DICM = differential interference contrast microscopy, MP = Macropod macrophotography).

Species complex	Species	Year collected	Country	Host	Host plant	Collector	Permit, voucher	Imaging
<i>subflavescens</i>	<i>A. perpallidus</i> Gahan	2009	USA	<i>Monelliopsis pecanensis</i>	<i>Carya illinoensis</i>	A. Dickey	TAMUIC voucher 733	SEM
	<i>A. asychis</i> Walker	2000	France	<i>Diuraphis noxia</i>	<i>Triticum</i> sp.	N. Ramualde, D. Coutinot, J. Lopez	P526P-15-04274, AFR00_Dn	SEM
	<i>A. sinensis</i> Shirley & Woolley	2002	China	<i>Aphis glycines</i>	<i>Glycine max</i>	K. Hoelmer, K. Chen, W. Meikle	P526P-01-53096, AChAg	SEM
<i>abdominalis</i>	<i>A. abdominalis</i> (Dahlman)	2014	USA	–	–	Syngenta Bioline	P526P-15-04767, AbUSA_14	SEM
	<i>A. daucicola</i> Kurdjumov	2012	USA	<i>Aphis helianthi</i>	<i>Daucus carota</i>	C. Dieckhoff	P526P-15-04767, DUSA12_DE	SEM
	<i>A. coreae</i> Hopper & Woolley	2009	Korea	<i>Aphis glycines</i>	<i>Glycine max</i>	K. Hoelmer	P526P-08-02142, MKor09_M	SEM
<i>mali</i>	<i>A. glycinis</i> Hopper & Woolley	2007	China	<i>Aphis glycines</i>	<i>Glycine max</i>	K. Hoelmer	P526P-01-72318, MCh04_Bj	DICM
	<i>A. rhamni</i> Hopper & Woolley	2005	China	<i>Aphis glycines</i>	<i>Rhamnus</i> sp.	K. Hoelmer	P526P-01-72318, MCh07_Bj	DICM
	<i>A. mali</i> Haldeman	1985	Australia	<i>Eriosoma lanigerum</i>	–	M. Carver, H.J. Banks	ANIC database no. 32 064862	MP
<i>varipes</i>	<i>A. atriplicis</i> Kurdjumov	2000	Republic of Georgia	<i>Diuraphis noxia</i>	<i>Triticum</i> sp.	D. Coutinot	P526P-15-04274, VGg00_Dn	DICM
	<i>A. certus</i> Yasnosh	2001	Japan	<i>Aphis glycines</i>	<i>Glycine max</i>	R. O'Neil, D. Voegtlin	P526P-01-53096, VJp01_TU	SEM
	near <i>A. certus</i>	2009	Korea	<i>Aphis glycines</i>	<i>Glycine max</i>	K. Hoelmer	P526P-08-02142, VKor09_M	DICM
	<i>A. hordei</i> Kurdjumov	2011	France	<i>Diuraphis noxia</i>	<i>Triticum</i> sp.	G. Mercadier, M. Roche	P526P-15-04274, VFr11_Dn	DICM
	<i>A. kurdjumovi</i> (Kurdjumov)	2000	Republic of Georgia	<i>Rhopalosiphum padi</i>	<i>Triticum</i> sp.	D. Coutinot	P526P-13-02503, VGg00_Rp	DICM
	<i>A. nigrinus</i> Howard	2015	USA	<i>Melanaphis sacchari</i>	<i>Sorghum bicolor</i>	–	P526P-15-04767, VUSA14_TX	DICM
	<i>A. varipes</i> (Förster)	2000	France	<i>Rhopalosiphum padi</i>	<i>Triticum</i> sp.	N. Ramualde, D. Coutinot, J. Lopez	P526P-13-02503, VFr00_Rp	SEM

**Table 2.** Characters of release and spread structure on male scapes of *Aphelinus* species and *Aphytis melinus*.

Species complex	Species	Pore			Pore region		
		Number	Size <sup>a</sup>	Shape <sup>b</sup>	Location <sup>c</sup>	Carina <sup>d</sup>	Elevation <sup>e</sup>
N.A.	<i>Aphytis melinus</i>	2	small	flat	proximal	complete	none
	<i>subflavescens</i>	2	large	crenulated ridge	proximal	complete	depressed
	<i>asychis</i>	4	small	flat	midpoint	none	elevated
	<i>A. sinensis</i>	5	small	flat	midpoint	none	elevated
	<i>abdominalis</i>	3	small	cone, round top	distal	complete	depressed
	<i>daucicola</i>	5	large	cone, flat top	proximal	complete	depressed
	<i>mali</i>	2	large	cone, flat top	midpoint	complete	depressed
	<i>A. glycinis</i>	2, 3, 5	large	cone, flat top	midpoint	complete	depressed
	<i>A. rhamni</i>	2, 3	large	cone, flat top	midpoint	complete	depressed
	<i>varipes</i>	3	large	cone, flat top	proximal	half	depressed
	<i>A. certus</i>	3	large	cone, flat top	midpoint	half	depressed
	<i>A. near certus</i>	3	large	cone, flat top	midpoint	half	depressed
	<i>A. hordei</i>	3	large	cone, flat top	midpoint	half	depressed
	<i>A. kurdjumovi</i>	3	large	cone, flat top	midpoint	half	depressed
	<i>A. nigrinus</i>	3	large	cone, flat top	midpoint	half	depressed
	<i>A. varipes</i>	3	large	cone, flat top	midpoint	half	depressed

<sup>a</sup> small = diameter of setae base (Fig. 2A–C, E); large, diameter >2× setae base (Figs 2D, 3A–F)  
<sup>b</sup> flat = not raised above surrounding cuticle (Fig. 2A, B, E); cone, flat top = on cones, truncated and flat on top (Figs 1A, 3A–F); cone, round top = on cones, rounded on top (Fig. 2C); crenulated ridge (Fig. 2D)  
<sup>c</sup> distal = most proximal pore distal to scape midpoint; proximal = most proximal pore proximal to scape midpoint; midpoint = most proximal at scape midpoint  
<sup>d</sup> complete = carina completely surrounds pores (Figs 2C–E, 4A); half = at proximal end of pores only (Fig. 4B); no carina around pores (Figs 2A, B, 4C)  
<sup>e</sup> none = neither depressed or elevated relative to surrounding cuticle (Fig. 2E); elevated = elevated relative to surrounding cuticle (Fig. 2A, B); depressed = depressed relative to surrounding cuticle (Figs 2C, D, 3A–F)

Results

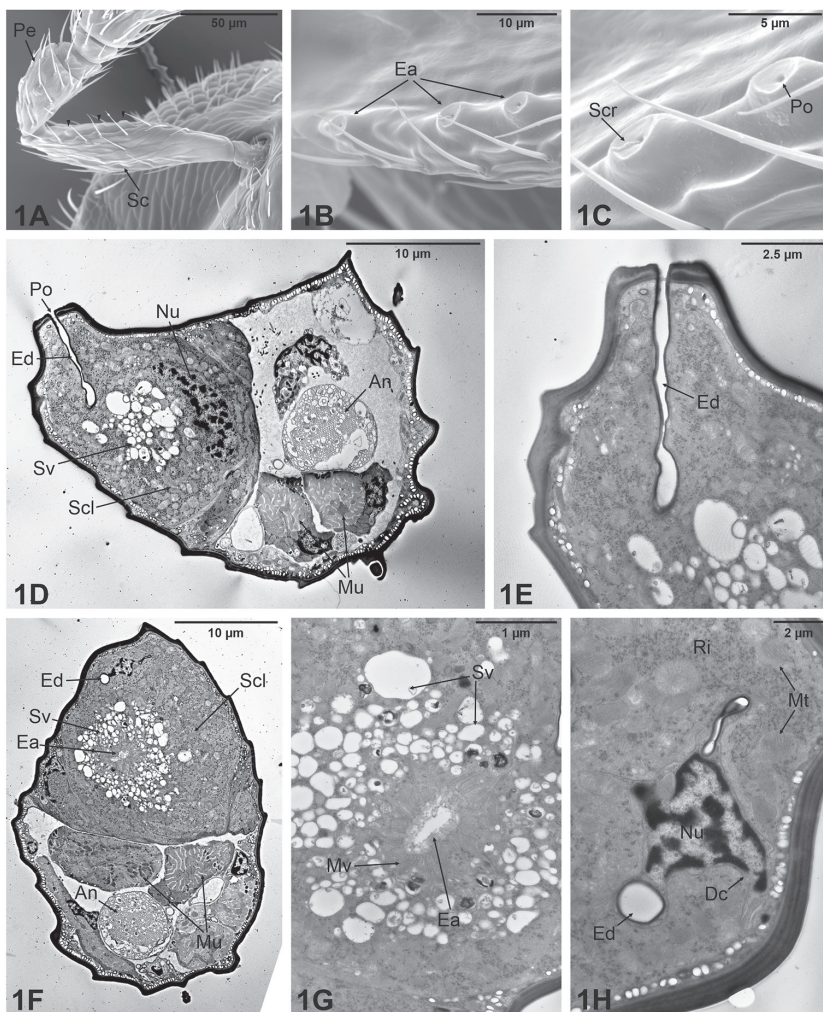
The male scape in *A. varipes* is characterized by the presence of cuticular modifications located on the ventral side, defining a specialised area (Fig. 1A). The ventral margin presents three subconical elevated areas with truncated and slightly concave tops that carry single pores and which are surrounded by a depressed region delimited by a carina (Fig 1B). In some specimens, a secretion oozing from the pore can be observed accumulating on top of the flattened area (Fig. 1C). Internal observations revealed the presence of a large cell that occupies about half of the whole internal scape volume behind each pore (Fig. 1D). This cell has a large nucleus located in the basal region, a cluster of electron-lucid vesicles located in the middle region, and a straight evacuating duct connected with the external pore (Figs 1D, E). The antennal muscles located within the scape are not connected with the glands, and they are located in the remaining half of the internal scape volume together with the antennal nerve (Fig. 1D, F). Sections taken in a different plane show the presence of a well-developed end apparatus located in the middle region of the cell and characterized by an aporous structure surrounded by microvilli (Fig. 1F, G). Large clumps of electron-lucid vesicles surround the end apparatus (Fig. 1G). The cytological features of the cell are those typical of



intensively active cells, i.e. the presence of a large nucleus and cytoplasm showing the presence of abundant mitochondria and ribosomes (Fig. 1H). The cuticular evacuating duct is connected to the end apparatus and is produced by an associated duct cell with very reduced cytoplasm and a small nucleus (Fig. 1H). The secretion gathered at the level of the end apparatus flows through the evacuating duct and reaches the external pore where it is released.

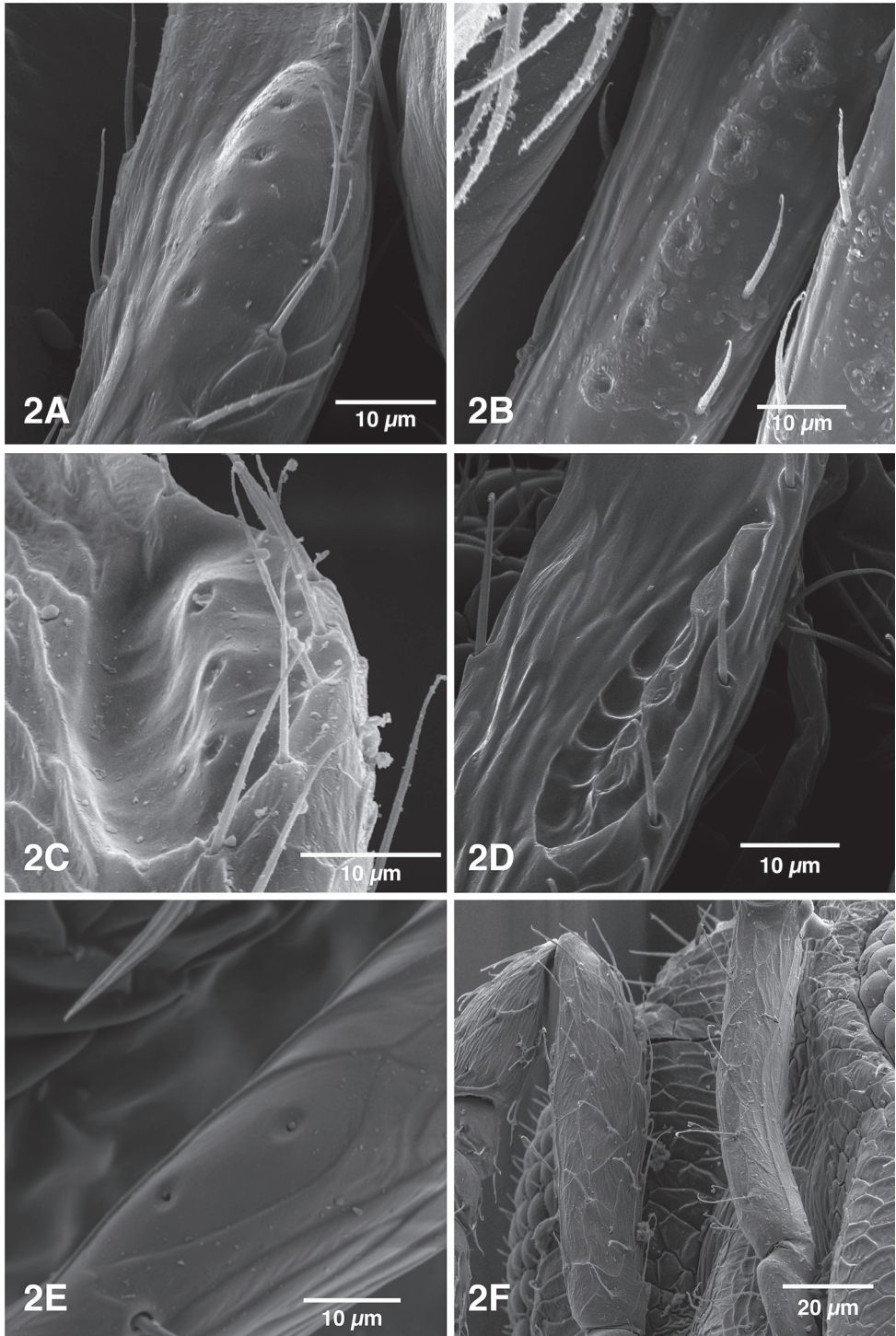
The morphology of these release-and-spread structures varies among *Aphelinus* species and *Aphytis melinus* (Figs 2, 3; Table 2). The pores in the *asychis* complex are sessile, i.e. not raised above surface of surrounding cuticle, and are on a convex region not surrounded by a carina (Fig. 2A, B). In the other species complexes of *Aphelinus*, the pores are in a depressed region of the cuticle, but individual pores are on elevated structures (Figs 2C, D, 3A–E), which vary from smoothly rounded (Fig. 2C), to crenulated ridges (Fig. 2D), or truncated and volcano-like (Fig. 3A–F). In the two outgroup species, pores are present and sessile in *Aphytis melinus* (Fig. 2E), and absent in *Centrodora* sp. (Fig. 2F).

Mapping six characters of the release-and-spread structures (Table 2) onto a molecular phylogeny of these *Aphelinus* species and *Aphytis melinus* revealed two broad phylogenetic patterns for different sets of characters; one set had shared states for the *mali* and *varipes* complexes and different states in the other species complexes, and the other set had different states in all the species complexes (Fig. 5). For the shape of the structure bearing each pore (Fig. 5A) and the elevation of the region around the pores (Fig. 5C), consistency and retention indexes are 1.0, indicating no homoplasy and potentially useful phylogenetic signal. States for these characters are the same in the *mali* and *varipes* complexes, as well as *Aphelinus daucicola* Kurdjumov, the shape being raised, conical, truncated, and flat or slightly concave on the top with the region around these structures being depressed. The shape varies among the other species, with *Aphelinus abdominalis* (Dalman) having raised structures that are rounded on top, and *Aphelinus perpallidus* Gahan having pores on a crenulate ridge, in both cases surrounded by a depressed region. Species in the *asychis* complex, as well as *Aphytis melinus* have sessile pores, suggesting that sessile pores might be ancestral. However, the surrounding region is elevated in the *asychis* complex, but neither depressed nor elevated in *Aphytis melinus*. Pore size (Fig. 5B) is also the same in the *mali* and *varipes* complexes, as well as *A. daucicola*, and the same in the *asychis* complex, *A. abdominalis* and *Aphytis melinus*, but the consistency index is 0.5 and the retention index is 0.67 because of parallel increase in pore size in *A. perpallidus* and in the lineage consisting of *A. daucicola* through *Aphelinus certus* Yasnosh. For the carina around the pores (Fig. 5D), the consistency and retention indexes are 1.0, indicating no homoplasy and strong phylogenetic signal. However, the state of the carina differs between the *varipes* complex and *mali* complex. Species in the *varipes* complex have a carina around the proximal end of the pores, whereas species in the *mali* complex, as well as *A. daucicola*, *A. perpallidus*, and *Aphytis melinus* have a carina completely surrounding the pores, suggesting that a complete carina is ancestral in *Aphelinus*, although it is absent in the *asychis* complex. Both the number (Fig. 5E) and location of pores (Fig. 5F) have consistency and retention indexes less than 1 (0.6 and 0.5 for pore number; 0.4 and 0.25 for pore location), indicating a fair amount of

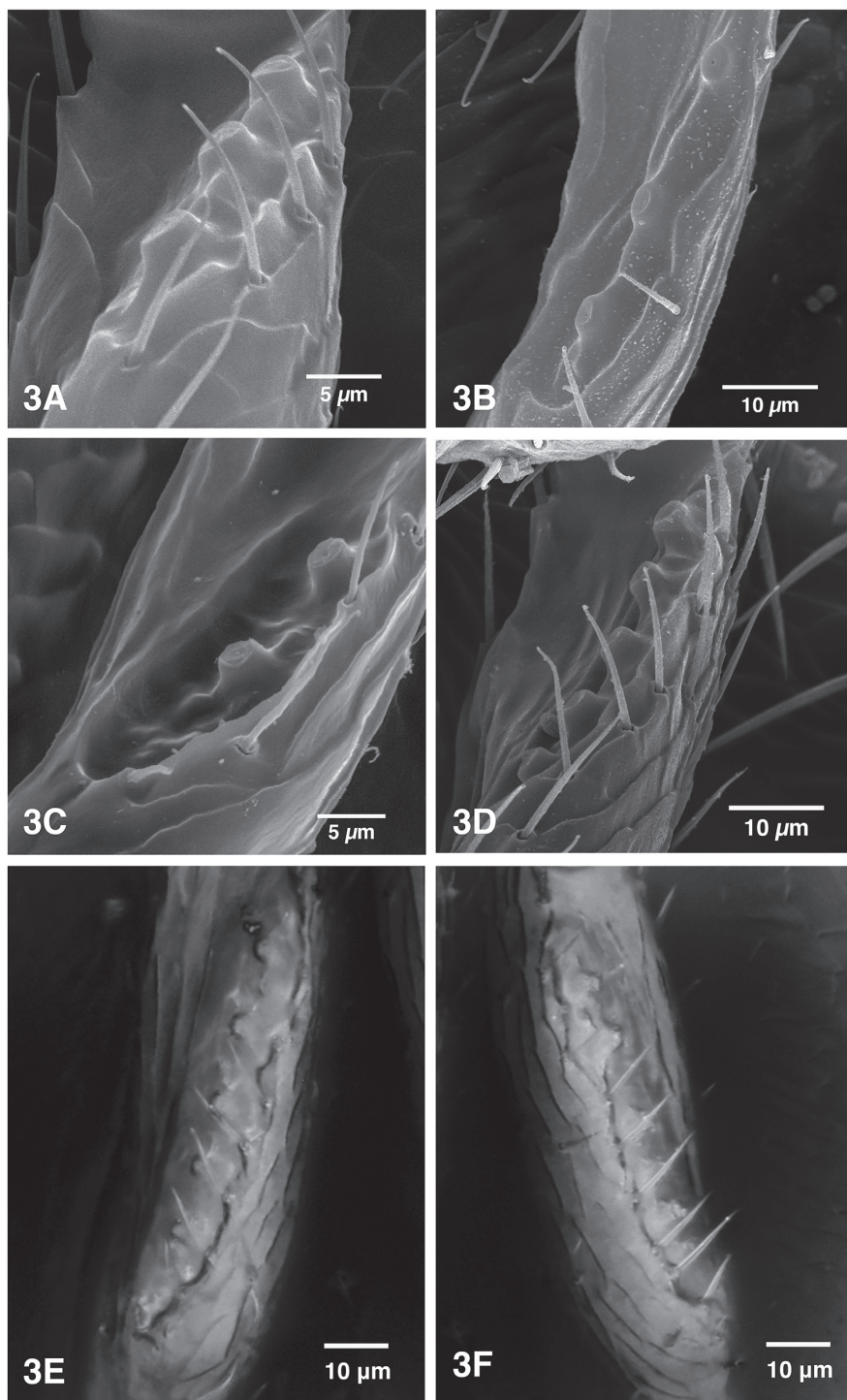


**Figure 1.** Structure of the male scape in *Aphelinus varipes*. **A–C** Scanning electron microscope images showing in **A** the modified male scape (Sc) with the presence of a ventral carina on which three specialized structures (arrowheads) are observed **B** detail of the carina revealing three elevated areas (Ea) **C** close up of the previous in which a single apical pore (Po) per Ea is clearly visible, as well as secretion (Scr) oozing from the pore itself. **D–H** Transmission electron microscope images showing internal ultrastructural features of the male scape **D** cross section of the scape taken through one of the elevated areas, showing the secretory cell (Scl) that occupies about half of the scape internal volume; Scl has a large nucleus (Nu) located basally, a central cluster of electron-lucid secretory vesicles (Sv) and a straight evacuating duct (Ed) connected with the external pore (Po); the rest of the scape volume is occupied by muscles (Mu) and the antennal nerve (An) **E** close-up view of the previous image, showing the cuticular evacuating duct (Ed) running straight towards the external pore **F** cross section of the scape taken in a different view, showing the large secretory cell (Scl) with a centrally positioned end apparatus (Ea) surrounded by numerous secretory vesicles (Sv); the evacuating duct (Ed), muscles (Mu), and antennal nerve (An) can be seen **G** detail of the end apparatus (Ea), which appears perforated and surrounded by microvilli (Mv); secretory vesicles (Sv) are above **H** detail of the duct cell (Dc) characterised by a very reduced cytoplasm and a small nucleus (Nu); the duct cell is surrounded by the cytoplasm of the secretory cell, that reveals the presence of ribosomes (Ri) and mitochondria (Mt); the evacuating duct (Ed) is visible in cross section. Scale bars: 50  $\mu\text{m}$  (**A**); 10  $\mu\text{m}$  (**B**, **D**, **F**); 5  $\mu\text{m}$  (**C**); 2.5  $\mu\text{m}$  (**E**); 1  $\mu\text{m}$  (**G**); 2  $\mu\text{m}$  (**H**).



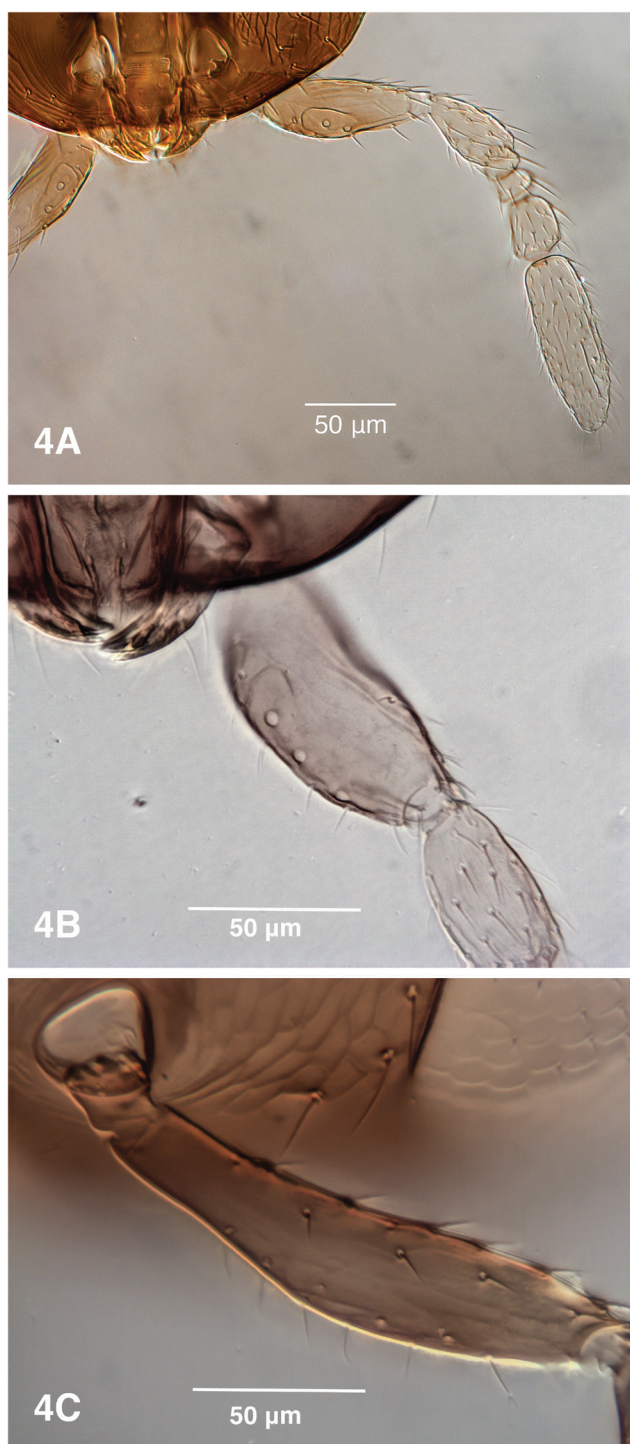


**Figure 2.** Scanning electron microscope images of the ventral surfaces of male scapes in four *Aphelinus* species and two outgroup species. **A** *A. asychis* **B** *A. sinensis* **C** *A. abdominalis* **D** *A. perpallidus* **E** *Aphytis melinus* **F** *Centrodora* sp.

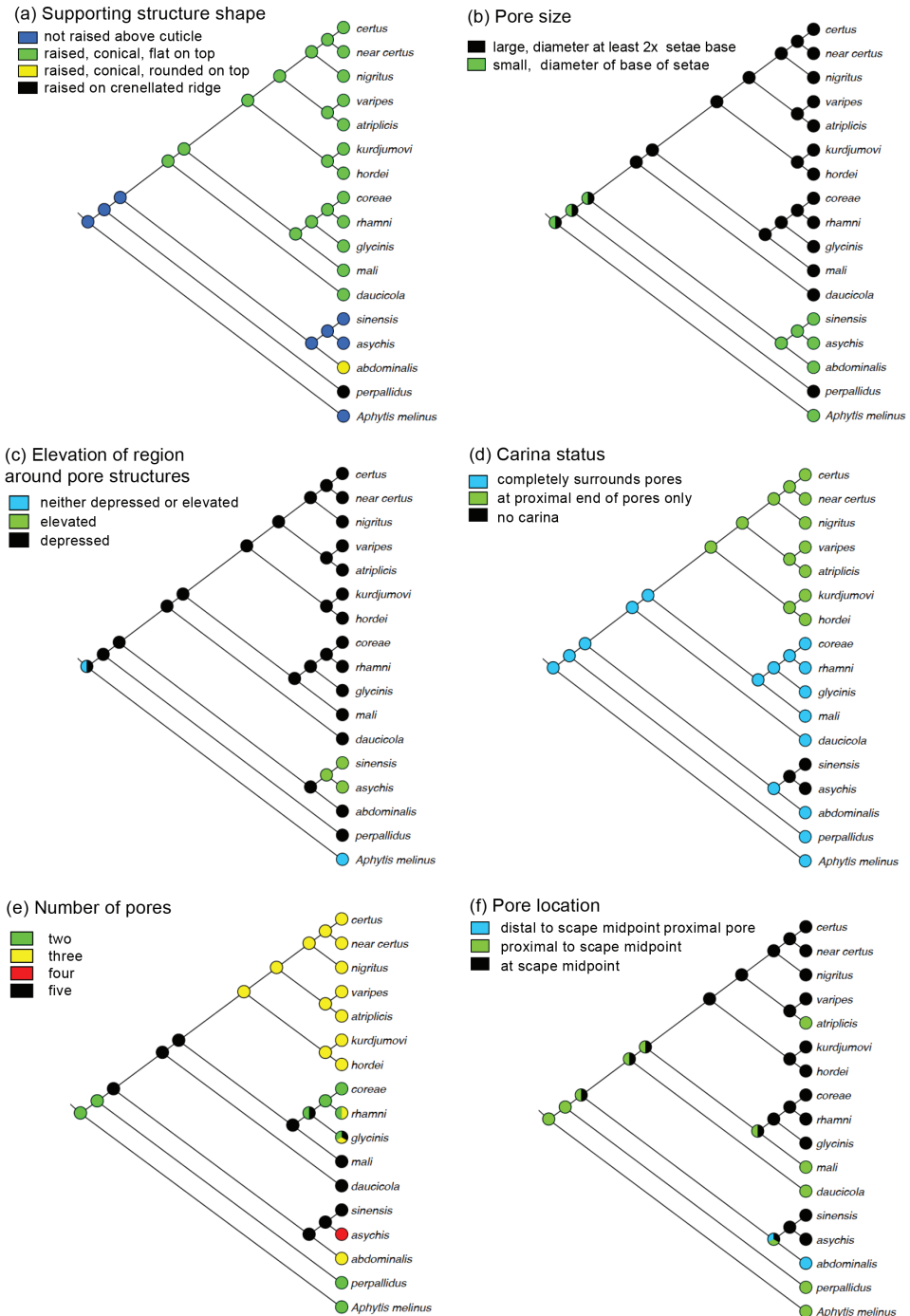


**Figure 3.** Scanning electron microscope (A,B,C,D) and macrophotographic (E,F) images of the ventral surfaces of male scapes in five *Aphelinus* species. **A** *A. albipodus* **B** *A. varipes* **C** *A. coreae* **D** *A. daucicola* **E,F** *A. mali*.





**Figure 4.** Three states of character representing form of carina on *Aphelinus* male scapes, lateroventral view.  
**A** Pores completely surrounded by carina **B** carina at proximal end of pores only **C** no carina around pores.



**Figure 5.** Characters of release-and-spread structures mapped onto molecular phylogeny of *Aphelinus* plus *Aphytis melinus*. **A** Supporting structure shape **B** pore size **C** elevation of region around pore structures **D** carina status **E** number of pores **F** pore location.



homoplasy for these characters. The *varipes* complex is consistent in pore number with all species having three pores. Nine species in the *varipes* and *mali* complexes have the most proximal pore at the scape midpoint. However, *Aphelinus atriplicis* Kurdjumov, *Aphelinus mali* (Haldeman), and *A. daucicola*, have the most proximal pore proximal to the scape midpoint. For *A. mali* and *A. daucicola* this may have arisen because they both have five pores, which might force the most proximal pore further towards the head. Species in the *asychis* complex have four or five pores, but like most species in the *varipes* and *mali* complexes, the most proximal pore is at the scape midpoint. However, species in the *asychis* complex have small, sessile pores that are close together, which may allow them to fit more distally than found in *A. mali* and *A. daucicola*. On the other hand, both *A. perpallidus* and *Aphytis melinus* have only two pores but have the most proximal pore proximal to the scape midpoint, suggesting that fit to the available length may be not be important for pore placement.

## Discussion

There is considerable variation among *Aphelinus* species in the characters of the release-and-spread structures on male scapes. Although three characters show some homoplasy with CI values of 0.50 to 0.75 (pore number, size, and location), three characters have CI = 1.0 (supporting structure, elevation of cuticle, and extent of carina). Combinations of characters are diagnostic for species complexes of *Aphelinus* (Table 2), and some combinations are diagnostic for species within complexes. Furthermore, the morphologically distinctive aspects of the male scape in these *Aphelinus* species mapped reasonably well onto the molecular phylogeny. It is intriguing that pores were found on the male scapes of one outgroup taxon, *Aphytis melinus*, but were absent from the male scapes of *Centrodora* sp. Along with *Aphelinus*, both outgroups are members of Aphelininae, but *Aphytis* and *Centrodora* are in the subtribe Aphytini (Hayat 1998) and are closely related members of a clade separate from the lineage containing *Aphelinus* in the morphological phylogeny of Kim and Heraty (2012). A different RSS structure on the antennal club (terminal antennomere) of *Aphytis* males may also play a role in male antennation during courtship (Romani et al. 1999). A broader survey of RSS structures on male antennae in Aphelinidae would be worthwhile.

*Aphelinus varipes* males have specialized secretory structures on the scape, which are connected with the external pores. The glandular units have secretory cells releasing secretions in electron-lucid vesicles. These vesicles surround an end apparatus connected with the cuticular evacuating duct (produced by a duct cell) that allows the external release of the secretion. These features are typical of secretory cells belonging to class III, according to the classification of insect epidermal glands proposed by Noirot and Quennedey (1974, 1991) and Quennedey (1998). Male antennal glands in this class have been reported for other groups of Hymenoptera, including Symphyta and Aculeata (Bin and Vinson 1986, Bin et al. 1999, Isidoro et al. 1999, Romani et al. 2005, Romani et al. 2008), and functionally, these structures have been related in most cases with courtship behavior by males.

However, despite the numerous cases reported, occurrence of male antennal glands on the scape is relatively uncommon. Dahms (1984a) described the presence of antennal glands on the profoundly modified scape of males of *Melittobia australica*, which are related to stereotyped antennal movements during courtship involving the scape itself.

Dahms (1984b) used differences among structures on the ventral area of male scapes in a revision of the genus *Melittobia* Westwood (Hymenoptera: Eulophidae). Dahms compared his work on *Melittobia* with that of van den Assem et al. (1982) on *Melittobia* and noted that both antennation and morphology of the structures on male scapes varied among *Melittobia* species groups. The species group that did not have extensively modified structures did not antennate as strongly in its courtship as the species groups that had more modified male scapes.

In Aphelinidae, male antennal glands have been reported in *Encarsia asterobemisiae* Viggiani and Mazzone (Hymenoptera: Aphelinidae), *Encarsia aurantii* (Howard) and *Encarsia opulenta* (Silvestri) (Pedata and Isidoro 1993), however, in these species RSS are located on the flagellar segments, not the scape. The functional significance of RSS on the scapes of *Aphelinus* and *Aphytis* (and perhaps other Aphelinidae) presents an intriguing problem in functional morphology associated with mate recognition. By demonstrating the diversity in forms of RSS and by placing this diversity in a phylogenetic context, our results are a first step in unraveling this puzzle. Knowledge of these structures may help in understanding mate selection in this genus, as well as adding to the knowledge about sex glands in parasitic Hymenoptera in general.

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# A new genus and three new species of Neotropical sawflies (Hymenoptera, Tenthredinidae) from Costa Rica, with host plants and life history notes

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## Abstract

Descriptions, host plants, and biological notes are given for three species of Tenthredinidae from Costa Rica. *Waldheimia saurauia* Smith & Nishida, **sp. nov.** (Blennocampinae) feeds on *Saurauia montana* Seem. (Actinidiaceae). *Leseha* Smith, **gen. nov.** (Selandriinae), includes two species that feed on ferns: *Leseha vespa* Smith & Nishida, **sp. nov.**, feeds on *Phlebodium pseudoaureum* (Cav.) Lellinger (Polypodiaceae) and *L. carranzae* Smith & Nishida, **sp. nov.**, feeds on *Elaphoglossum bellermannianum* (Klozsch) T. Moore, and *E. lingua* (C. Presl) Brack. (Dryopteridaceae). *Stromboceros cruralis* Konow, 1899 from Peru, *Dochmioglène cubitalis* Malaise, 1954 from southern Brazil, *Siobla joergenseni* Schrottky, 1913 from northern Argentina, *Selandria limbata* Kirby, 1882 from Brazil, and *Strongylogaster strigatus* Enderlein, 1920 from southern Brazil, are all transferred to *Leseha* (**combs. nov.**).

## Keywords

*Blechnum*, Blennocampinae, *Elaphoglossum*, *Phlebodium*, *Saurauia*, Selandriinae, taxonomy, *Waldheimia*

## Introduction

A number of host plants and life histories of Central American sawflies were given in the publications by Kimsey and Smith (1985), Smith and Janzen (2003a, b), and Smith et al. (2013); however, there remains much to be discovered. Field work in Costa Rica by KN has provided the host plants and life histories of three additional species. All three species were previously undescribed, and two belong to a new genus. Two species belonging to the subfamily Selandriinae were reared from larvae feeding on ferns, *Elaphoglossum* sp. (Dryopteridaceae) and *Phlebodium pseudoaureum* (Cav.) Lellinger (Polypodiaceae). The other, a new species of *Waldheimia* of the subfamily Blennocampinae, was feeding on the tropical tree *Saurauia montana* Seem. (Actinidiaceae). Such discoveries are significant, and here we describe these sawflies and give notes and illustrations on their biology.

## Materials and methods

The hosts and biology of the three species treated were studied in the field and under rearing conditions in area of the main building of Estación Biológica Monteverde (EBM), Puntarenas Province, Costa Rica, in between May and October in 2008, 2017 and 2018. EBM is a private biological research station with ca. 120 hectares of secondary and primary cloud forest preserve (Fig. 9), located on the Pacific slope of Tilarian Mountain Range. The coordinates of the study site are 10°19'07"N, 084°48'29"W, and the elevation approximately 1530 m. The climatic conditions of the area, according to Herrera Soto and Gómez Pignataro (1993), are tropical temperate humid with 3 to 4 months of dry season. The life zone ecology is considered lower mountain wet forest, with a mean annual rainfall of ca. 4000 mm and mean annual temperature of 17 °C (Bolaños and Watson 1993). The rainy season with typical afternoon thunder showers lasts from mid-May to November. December through February is a transition to the dry season with strong trade winds carrying drizzle rain and mist. Late February to mid-April becomes very dry (A. Pounds, pers. comm. 2014; KN personal observations 2013–2018). The general vegetation type is 'perpetually dripping cloud forest,' characterized by diverse and abundant epiphytes and epiphylls, dense understory shrubs, tree saplings, and large herbs (Haber et al. 2000; KN personal observations 2013–2018). The habitat of the study site is open with a gradient of rich native vegetation (man-modified native plant garden) with a few exotic plant species, surrounded by protected secondary forests.

Studied host plants are: *Saurauia montana*, *Phlebodium pseudoaureum* [syn. *P. areolatum* (Humb. & Bonpl. Ex Willd.) J. Sm.], *Elaphoglossum bellermannianum* (Klotzsch) T. Moore, *Elaphoglossum hammelianum* A. Rojas, and *E. lingua* (C. Presl) Brack. (Dryopteridaceae).

Eggs, larvae, and adults were collected and placed in translucent plastic bags (655 mm long by 430 mm wide) with their host plants. To rear, the plastic bags were brought inside the laboratory of KN at EBM. The tops of the plastic bags were tied in a twisted fold, clamped with a clothespin and hanged from a rope clamped with another



clothespin. Larvae were supplied with fresh leaves attached to stems and with or without roots and soil. To provide pupation sites for the larvae, dioramic aquarium chambers were prepared by putting a layer of soil (2–3 cm deep), pieces of rocks, and fallen dry tree branches and leaves. Host plants with mature last instar larvae were transferred to the dioramic aquariums. The dioramic aquariums were covered/enclosed with fine mesh fabric to provide airflow, control humidity, and to minimize entering and escaping of insects and other arthropods, and placed outside in ambient temperature under the roof. The soil inside the aquariums was kept relatively moist by spraying water. The plastic bags and aquariums were reviewed at least once a day. Emerged adults were kept alive for some days refrigerated in vials and then preserved in 95% ethanol. Some mature, last feeding instar larvae were preserved in 75% ethanol. Measurements of immature stages were made by digital caliper.

Life histories of each species (Figures 1, 9–16, 24–38, and 45–50) were recorded with the following digital cameras: Olympus Tough TG-5, OM-D E-M1 Mark II with 60 mm macro lens, Canon EOS 7D Mark II with 100 mm macro lens, and Sony DSC-RX100IV. Images were processed and edited by Adobe Lightroom Classic and Photoshop software.

Figures 2–8, 17–23, 39–44, and 51–55 were acquired by DRS through an EntoVision micro-imaging system. This system included a Leica M16 with and JVC KY-75U 3-CCD digital video camera or a GT-Vision Lw11057C-SC1 digital camera attached that fed image data to a notebook or desktop computer. The program Cartograph 6.6.0 was then used to merge an image series into a single in-focus image.

Morphological terminology follows Huber and Sharkey (1993).

Depositories for specimens are as follows. Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (**LP**); The Natural History Museum, London, England, UK (**BMNH**); Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica (**MZUCR**); National Museum of Natural History, Smithsonian Institution, Washington, DC (**USNM**); Naturhistoriska Riksmuseet, Stockholm, Sweden (**NHRS**); Polska Akademia Nauk, Instytut Zoologii, Warszawa, Poland (**PAN**); Senckenberg Deutsche Entomologische Institut, Müncheberg, Germany (**SDEI**); Museo Nacional de Costa Rica, Sede e Santo Domingo de Heredia (former collection of INBio (INBio = **MNCRA**)). Most of the larvae and parasitoid flies and wasps reared are deposited at MZUCR.

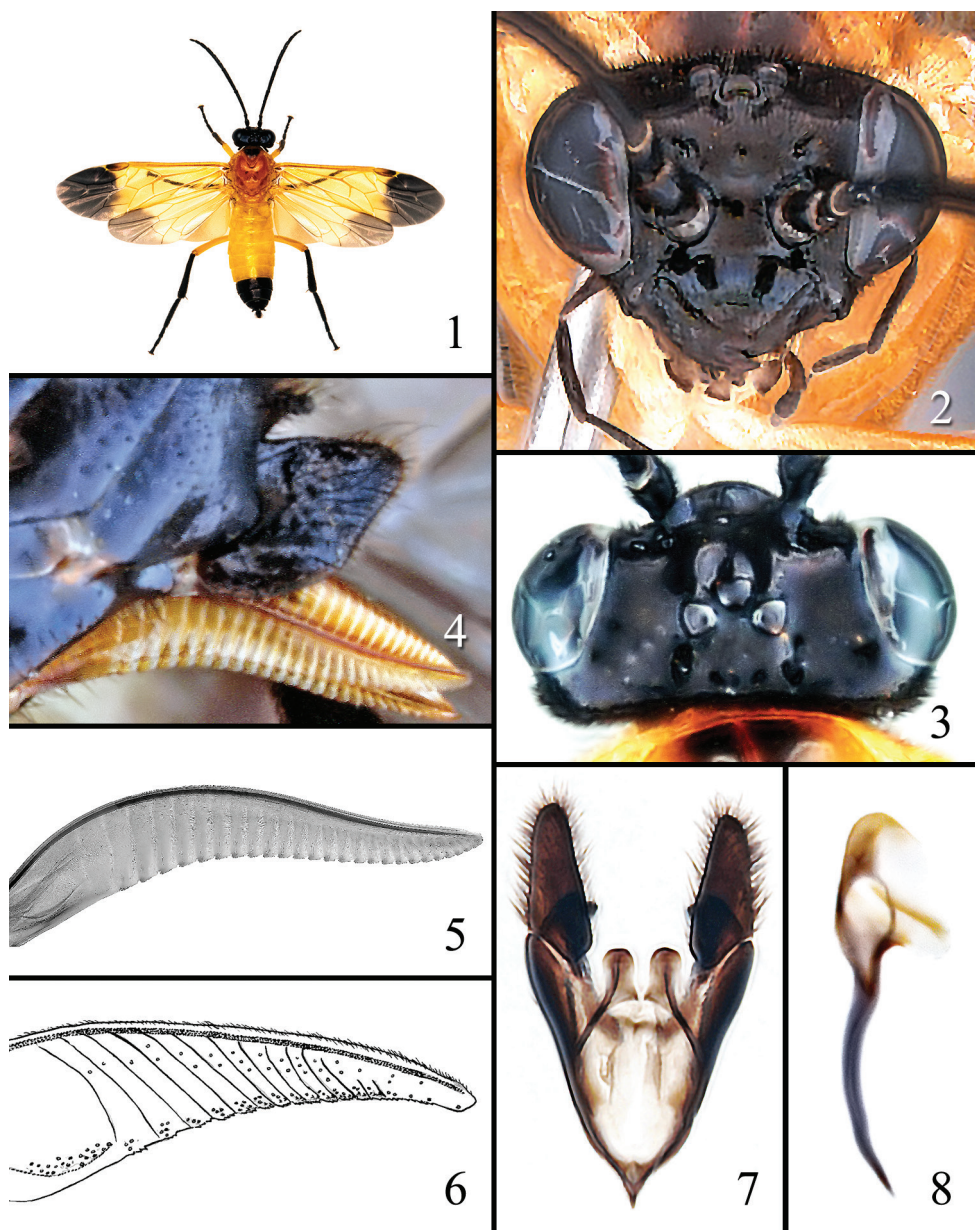
## Results

### *Waldheimia saurauia* Smith & Nishida, sp. nov

<http://zoobank.org/F8C3251E-EDF8-4EDC-86F8-D0B45E54B29A>

Figs 1–15

**Diagnosis.** Head black; legs with coxae, trochanters, and femora orange, tibiae and tarsi black; wings yellow with apex from stigma black; abdomen orange with apex black; lancet (Fig. 5) elongate, gradually tapering from base to apex; annuli straight.



**Figures 1–8.** *Waldheimia saurauia* (except 6) **1** dorsal view, female **2** head, front **3** head, dorsal **4** female sheath, lateral **5** female lancet **6** female lancet of *W. laeta* **7** male genital capsule **8** male penis valve.

**Description. Female** (Fig. 1): Length 8.5 mm. Antenna, head, and mouthparts black. Thorax orange with large black spot on mesoscutal middle lobe. Legs with coxae, trochanters, and femora orange, tibiae and tarsi black. Abdomen orange with apical three segments and sheath black. Forewing yellow infuscated with apex from base of stigma black; veins yellow in yellow part, black in black part; stigma mostly black with

extreme base orange. Hindwing yellow with apex from about apex of stigma black; veins yellow in yellow part, black in black part; stigma mostly yellow. *Head* (Figs 1–3): Antenna long, slender,  $2.4\times$  head width; 1<sup>st</sup> and 2<sup>nd</sup> antennomeres each longer than broad; 3<sup>rd</sup> antennomere subequal in length to 4<sup>th</sup>; 5<sup>th</sup> antennomere  $0.7\times$  length of 4<sup>th</sup>; apical 4 antennomeres about subequal in length, together about  $1.3\times$  length of 3<sup>rd</sup>; apical 4 antennomeres with elongate, pale sensory pits the length of each antennomere except for the basal quarter of the 6<sup>th</sup>. Malar space about as broad as diameter of front ocellus. Lower interocular distance  $1.1\times$  eye height. Distances between eye and lateral ocellus, between lateral ocelli, and between lateral ocellus and hind margin of head as 1.0:0.7:0.8; postocellar area  $1.6\times$  broader than long. *Thorax*: Hind basitarsus  $1.3\times$  longer than remaining tarsomeres combined; inner hind tibial spur  $0.3\times$  length of hind basitarsus. *Abdomen*: Sheath uniformly slender in dorsal view, with short, stiff hairs; in lateral view (Fig. 4) straight above, rounded below. Lancet (Fig. 5) long, gradually tapering from base to apex, annuli parallel and straight; with about 25 serrulae, serrulae flat with 4 or 5 small subbasal teeth.

**Male:** Length, 8.0 mm. Color and structure similar to holotype. Genitalia in Figs 7, 8; harpe elongate, about  $2.3\times$  longer than broad; valviceps of penis valve rounded at apex, with dorsal lobe.

**Larva** (Figs 12–15): Last feeding instar 15–25 mm long. Head black, width ca. 2.5 mm. Body white, second thoracic segment to abdominal segment 7 greenish internally; thoracic legs white, apically yellowish, claws black. Abdominal segments 1–7 with yellow tint more visible along spiracular to proleg area; anal plate white ( $n = 20$ ).

**Type material.** Holotype female, labeled “COSTA RICA, Puntarenas Province, Monteverde, Estación Biológica Monteverde, 1530 m,  $10^{\circ}19'08.5''\text{N}$ ,  $84^{\circ}48'32.0''\text{W}$ , larvae coll. 26.ix.2017, adult 14.i.2018, Kenji Nishida (USNM). Paratypes: Same data as for holotype (1 ♀ MZUCR); same data as for holotype except middle to late instar larvae collected 8.vii.2018, cocoons spun  $\pm 20$ .vii.2018, adult emergence 9–12. ix.2018, on *Saurauia montana*, Kenji Nishida (3 ♀, MZUCR, USNM); same except adult emergence 3.ix.2018 (2 ♂, USNM MZUCR); Est. Biol. Las Alturas, 1500m, Coto Brus, Prov. Punt., COSTA RICA, M. Ramirez, Set 1991, L-S-822500, 591800; Costa Rica, INBIO CR1000, 619428 (1 ♀, INBio); Est. La Casona Res. Biol., Monteverde, 1520m, Prov. Punt., COSTA RICA, N. Obando, Dic 1990, L-N-253250, 449700; Costa Rica, INBIO, CRI000, 664810 (1 ♀, INBio); Quebrada Segunda Ref. Nac. Fuana Silv. Tapanti, 1150m, Prov. Cartago, Costa Rica, G. Mora, Abr 1992, L-N 194000, 560000; Costa Rica, INBIO, CR1000, 727881 (1 ♀, INBio).

**Variation.** One paratype is about 8.5 mm long, the others are about 10.0 mm long. One paratype has the mesoscutal middle lobe, spot on the posterior corner of the mesoscutal lateral lobes, center of mesoscutellum, upper two-thirds of mesepisternum and mesepimeron blackish. Another paratype has similar black marks on the mesonotum, but the underthorax is completely orange.

**Etymology.** The name is the generic name of the host plant.

**Host, life history.** Larvae feed on *Saurauia montana* (Actinidiaceae). First to last feeding instar larvae were found on 45 cm to ca. 3 m tall trees growing along open trails contiguous to valley or stream (Fig. 10) ( $n = 10$  trees, 8 cohorts/groups). Eggs





**Figures 9–15.** *Waldheimia saurauia* **9** general habitat of Estación Biológica Monteverde **10** habitat at open trail along valley, arrow pointing at young *Saurauia montana* tree where young larvae were found **11** oviposition scar-swellings on secondary veins with larva-exited holes **12** middle stage first instar larvae, ca. 4 mm long, on underside leaf near oviposition site; some oviposition swellings are visible **13** early to middle instar larvae intermingled and resting **14** last feeding instar larva, lateral **15** last feeding instar larva, dorsolateral.



are unknown, but remains of eggs (egg shells) were found. Swellings from oviposition were noticed along the primary and secondary veins of young and soft leaves near apical shoots ( $n = 7$ ) (Fig. 11). Each swelling was ca.  $2.5 \times 1.5$  mm. By dissecting the swelling, a single egg shell (or a dead larva) was found in each. Apparent oviposition scar as old hole of ca. 0.5 mm was observed on the side of the secondary veins on underside leaf (abaxial) ( $n = 30$ ). The first instar larva in the egg apparently made an exit orifice of ca. 0.5 mm on upperside leaf (adaxial) ( $n = 30$ ). Early to late stage first instar were feeding gregariously, skeletonizing leaf along or near the oviposition site on abaxial (Fig. 12). Thirty and 33 first instar larvae were counted in each single cohort ( $n = 2$ ). Also under natural conditions in the field, early to middle instar larvae were intermingled and resting together ( $n = 1$  group) (Fig. 13). Middle to late instars were also found together resting and feeding on abaxial of relatively young leaves located at apical growth of the plant ( $n = 4$  groups). The larvae did not feed on the secondary veins of mature, hard leaves, but readily fed on the secondary veins of relatively young leaves. Under natural and rearing conditions, last feeding instars were scattered along different leaves, found either solitary or in groups of two to four larvae ( $n = 30$  larvae). Neither early nor late instar larvae fed on leaf buds or mature old leaves. The last feeding instar larvae molted and went under soil. Soil-covered ovoid cocoons ( $11\text{--}13 \times 6\text{--}7$  mm,  $n = 7$ ) were located at the bottom surface of the dioramic aquarium. A parasitoid, an unidentified fly ( $n = 1$ ) (Diptera: Tachinidae), emerged from a cocoon of *W. saurauia*.

Summary of collecting and rearing records is as follows: Middle to large instar larvae 26.xi.2017, most went into soil 4.xii.2017, adult emergence 4.i.2018; middle to late instar 8.vii.2018, cocoon spun 20.vii.2018, adult emergence 9–12.ix.2018; first instar 6.viii.2018, late to last feeding instar 20.ix.2018, went into soil 25.ix–6.x.2018. First instar larvae 25.ix.2018, middle instar larvae 15.x.2018. Early instar larvae 10.x.2018.

**Remarks.** At adult stage, this species is almost identical in color to *Waldheimia laeta* (Cameron) known from Central America and northern South America, but *W. laeta* usually has the clypeus white, areas around the antennal insertions orange, the mesonotum entirely orange, the apical four antennomeres shorter with the 6<sup>th</sup> and 7<sup>th</sup> only about as broad as long, the sheath shorter and rounded at its apex and by the lancet. The lancet of *W. laeta* (Fig. 6) is elongate but abruptly tapering to a rounded apex and has slanted annuli.

The host plant, *Saurauia montana*, is a relatively small tree 3–10 m high, leaves become up to ca. 8 by 30 cm, and distributed between Honduras and Panama. In Costa Rica, it has been recorded from 200–2600 m elevations on both Pacific and Atlantic (Caribbean) slopes, and in Monteverde area it is found commonly up to 1550 m in open habitat (Haber et al. 2000, Missouri Botanical Garden 2018).

Hosts for other *Waldheimia* are *Cissus pseudosicyoidea* Croat (Vitaceae) for *W. fascipennis* (Norton) (Smith and Janzen 2003b); *Cissus rhombifolia* Vahl (Vitaceae) for *W. suturalis* (Cameron) (Smith and Janzen 2003b); *Cissus alata* Jacq (Vitaceae) for *W. laeta* (Cameron (Smith et al. 2013)), *Davilla nitida* (Vahl) Kubitzki (Dilleniaceae) for *W. lucianocapellii* Smith (Smith et al. 2013); *Hamelia patens* Jacq. (Rubiaceae) for *W. interstitialis* (Cameron) (Kimsey and Smith 1985, Smith and Janzen 2003b).

***Leseha* Smith, gen. nov.**

<http://zoobank.org/F8C3251E-EDF8-4EDC-86F8-D0B45E54B29A>

**Type-species.** *Leseha vespa* Smith & Nishida

**Description.** Antenna with scape and pedicel each longer than broad. Mandibles evenly curved, each with one subapical tooth. Clypeus truncate to very shallowly emarginate. Malar space less than half diameter of an ocellus. Genal carina absent. Eyes large, converging below, lower interocular distance subequal to or slightly less than eye height. Head from above narrowing behind eyes; distance behind eyes half or less eye length. Epicnemeum elongate, flat, on same level as mesepisternum and separated by a fine suture. Anal cross vein of forewing absent. Anal cell of hindwing sessile. Tarsal claws with one inner tooth about as long and broad as outer tooth and located near outer tooth; basal lobe absent.

**Etymology.** The genus name is an arbitrary combination of letters; the gender is feminine.

**Remarks.** *Leseha* is separated from other genera of Selandriinae by the bifid tarsal claw without a basal lobe (Fig. 53), mandibles each with one inner tooth, absence of a genal carina, and elongate, flat epicnemeum. It is similar to *Adiaclema*, but *Adiaclema* has simple mandibles. The claws and epicnemeum are similar to *Liliacina*, but *Liliacina* has a deeply circularly emarginated clypeus and mandibles are long and bent at almost a right angle. In existing keys (Smith 2006) it will key to *Andeana* in couplet 22; however, the following will separate *Leseha* from *Andeana* (characters in parentheses): tarsal claws (Fig. 53) with long inner tooth, about as long and broad as outer tooth and situated next to outer tooth (inner tooth small, less than half length of outer tooth and situated near center of claw, as in Fig. 54); eyes large (Figs 17, 39), lower interocular distance subequal to or slightly less than eye height (small, lower interocular distance greater than eye height, as in Fig. 51); head in dorsal view (Figs 18, 40) narrowing behind eyes with distance behind eyes less than half eye length (head in dorsal view straight behind eyes, distance behind eyes more than half eye length, as in fig. 52); anal cell of hindwing sessile, as in Fig. 1 (anal cell of hindwing with short petiole, as in Fig. 55).

Hosts recorded for other Selandriinae are *Entodontopsis leucostega* (Brid.) W.R. Buck and Irel. (Stereophyllaceae) for *Adiaclema chigiyae* Smith (Smith and Janzen 2003b); *Blechnum occidentale* L. (Blechnaceae) for *Dochmioglène* sp., and *Lomariopsis vastita* E. Fourn. (Lomariopsidaceae) for *Dochmioglène crassa* (Cameron) (Smith et al. 2013).

**Species included.** In addition to the two new species described here, the following four South American species also belong in this new genus.

***Leseha cruralis* (Konow), comb. nov.**

*Stromboceros cruralis* Konow 1899: 296. ♀. “Peru (Callanga, Cuzco)”; Konow 1905: 98; Oehlke and Wudowenz 1984: 376 (holotype); Taeger et al. 2010: 532.

**Material.** Bolivia, Ecuador, Peru.

**Notes.** Two females at SDEI are labeled as types: the one labeled “Callanga, Cuzco, Peru,” “Coll. Konow,” “TYPE,” “*Stromboceros cruralis* Knw., Peru” is here designated lectotype. The other specimen from “Pachitea Peru” is not part of the type series since the locality was not mentioned by Konow.

***Leseha cubitalis* (Malaise), comb. nov.**

*Dochmioglene cubitalis* Malaise 1954: 283. ♀, ♂. no locality in original description; Taeger et al. 2010: 487.

**Material.** Brazil (Santa Catarina).

**Notes.** Malaise (1954) did not designate a holotype; he stated “(10 ♀♀, numerous ♂♂)”, so the exact number of specimens he had is unknown. The lectotype, here designated, is labeled “Brasilien, Nova Teutonia, 27°11'B., 52°23'L, Fritz Plaumann,” “11 Mar. 1942,” “TYPUS,” “*Dochmioglene cubitalis* sp. nov., R. Malaise det. 1952,” “31 71,” “Riksmuseum Stockholm” (NHRS).

***Leseha joergenseni* (Schrottky), comb. nov.**

*Stromboceros joergenseni* Jörgensen 1913: 274. ♀, ♂. nomen nudum.

*Siobla joergenseni* Schrottky 1913: 702. ♀, “♂”? “Bompland”; Taeger et al. 2010: 540; Abrahamovich et al. 2010: 67 (two syntypes, male and female, at LP).

**Material.** Argentina, Brazil.

**Notes.** Jörgensen’s mention of this species predates Schrottky’s description, but Jörgensen gave no description, only “Junto con la especie anterior, pero acaso no tan comun.” Schrottky stated “♀♂,” “22-IX-09, Bompland (Jorgensen Nr. 3).” DRS saw three females from La Plata (LP), no males. There are two females on the same pin with a label “Argentina, Bonpland, 22-IX-1909, P. Jorgensen,” “*Siobla joergenseni* Schrottky, C. Schrottcky det. 1012.” The lectotype, here designated, is the top specimen on this pin. The other female DRS saw has a different date, 20-IX-1910, and even though labeled as *joergenseni*, it belongs to the genus *Plaumanniana*.

***Leseha limbata* (Kirby). comb. nov.**

*Selandria limbata* Kirby 1889: 141. ♀, ♂. “Theresopolis, Brazil”; Dalla Torre 1894: 143; Taeger et al. 2010: 540.

*Stromboceros limbatus*: Konow 1905: 98.

**Material.** Brazil (Rio de Janeiro, Santa Catarina).

**Notes.** The holotype, at BMNH, is a male labeled “Type H.T.,” “B.M. Type Hym. 1.303,” “B. M. Type Hym., *Selandria limbata* (Kirby 1889),” “limbata type,” “27/987,” “Theresopolis, 88–137.” DRS could not find the female.

***Leseha strigata* (Enderlein), comb. nov.**

*Strongylogaster strigatus* Enderlein 1920: 363. ♀. “Südbrasilien, Santa Catarina; Brasilien, Espiritu-Santo”; Taeger et al. 2010: 537.

**Material.** Brazil (Santa Catarina).

**Notes.** Enderlein saw two females, one from each of the localities, but DRS saw only one female from Santa Catarina. It is labeled “S. Catarina, Lüderwaldt,” “Type,” “*Stromboceros strigatus* Endl., type F, Dr. Enderlein det 1918,” Muz. Zool. PAN Warszawa 12/75” and is here designated the lectotype.

***Leseha vespa* Smith & Nishida, sp. nov.**

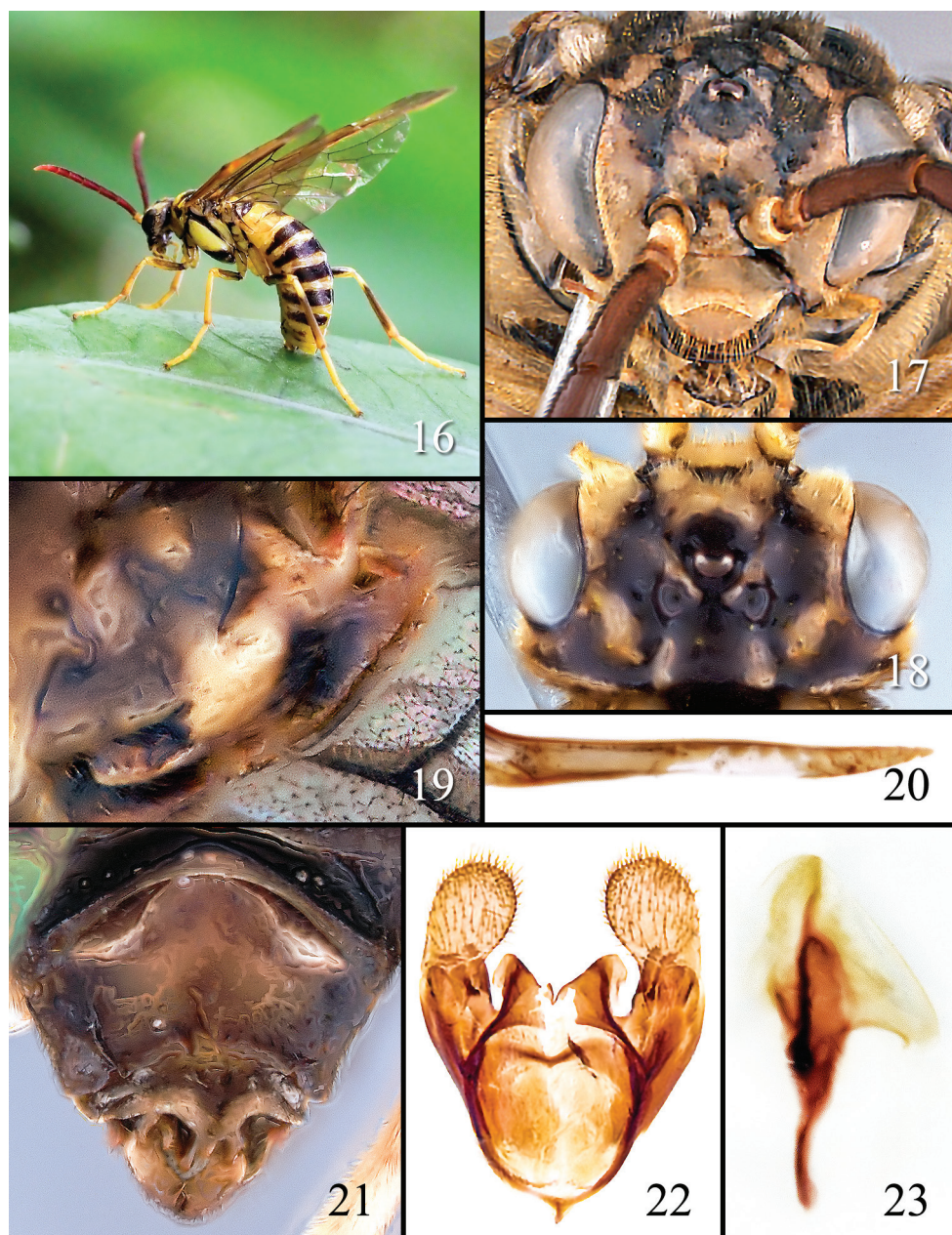
<http://zoobank.org/9475C9CD-04F9-4F14-AB49-4273FA8F885E>

Figs 16–37, 53

**Diagnosis.** Largely black with reddish-brown to yellow spots on head, thorax, and transverse stripes on abdomen (Fig. 16). Lancet (Fig. 20) very short, without distinct serrulae or annuli. Male with concave area on apical tergite.

**Description. Female** (Fig. 16): Length 9.5 mm. Antenna with scape yellow, pedicel and flagellum reddish brown, 4<sup>th</sup> antennomere to apex sometimes darker brown than pedicel and 3<sup>rd</sup> antennomere. Head mostly yellow with black marks; black on postocellar area, broad stripes from lateral ocelli almost to antennal insertions, area surrounding front ocellus, spot on occiput above each eye, spot above interantennal area, narrow bands surrounding antennal sockets. Thorax mostly yellow with black marks on center of mesoscutal middle lobe, lateral lobes except sides, downturned lateral sides of lateral lobes, mesoscutellar appendage, area between cenchri, mesosternum, line separating epicnemium, and spot on lower margin of propleuron. Legs yellow with black stripe on outer surface of hind femur. Abdomen with first 2 segments mostly yellow, segments 3 to apex mostly black above, apical 3 or 4 segments black. Sheath reddish brown at apex, black at base. Wings lightly, uniformly hyaline, costa and stigma yellow, other veins black. Head and thorax shiny, without sculpture, abdomen dull densely microsculptured. **Head** (Figs 17, 18): Antennal length 2.0× head width; scape and pedicel about as long as broad, 3<sup>rd</sup> antennomere slightly longer than 4<sup>th</sup>, as 1.0:0.8; antennomeres 4 to apex slightly decreasing in length, slightly thickened at antennomeres 5–7. Clypeus with shallow, circular emargination. Malar space less than half diameter of front ocellus. Lower interocular distance slightly longer than eye height, as 1.0:0.9. Distances between eye and lateral ocellus, between lateral ocelli, and between

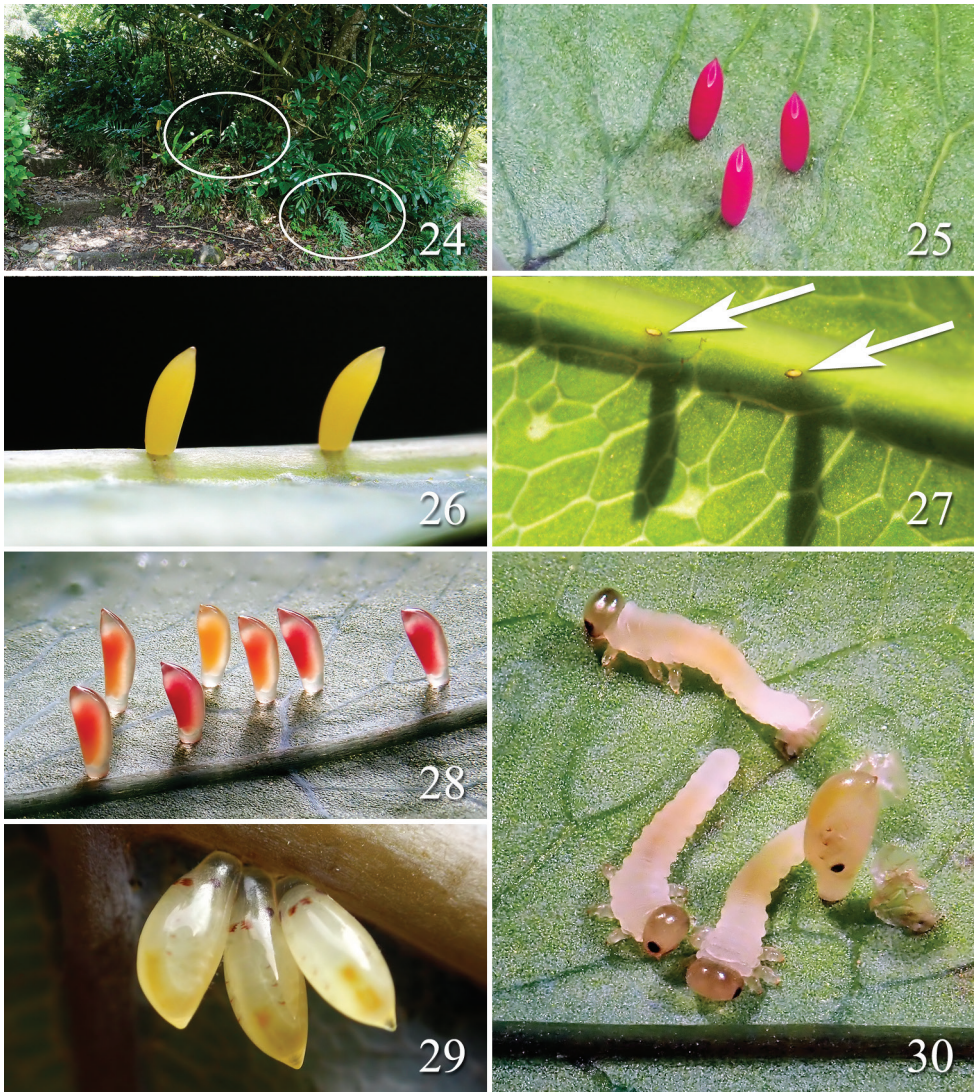




**Figures 16–23.** *Leseha vespa* **16** adult female, ovipositing **17** head, front **18** head, dorsal **19** sheath, lateral **20** female lancet **21** apical tergite of male **22** male genital capsule **23** male penis valve.

lateral ocellus and hind margin of head as 1.0: 0.6:1.0; postocellar area about 1.6× broader than long. *Thorax*: Hindbasitarsus subequal in length to remaining tarsomeres combined; hind tibial spurs subequal in length, about as long as width of hind tibia at apex. *Abdomen*: Sheath (Fig. 19) in lateral view narrow, slightly turned up at apex,





**Figures 24–30.** *Leseha vespa* **24** habitat where host plants occur (circles) **25** three freshly laid purple eggs on abaxial of mature old frond **26** freshly laid yellow eggs on abaxial of young frond of soft primary vein (note: frond was flipped upside-down for photography) **27** adaxial of Fig. 26 showing pierced holes of oviposition (arrows), ca. 0.2 mm **28** middle stage (3-day old) purple orange and yellow eggs **29** clustered mature yellow eggs showing developing larva in each (note: mandibles stemmata, and thoracic legs are seen in reddish brown **30** just hatched first instar larvae (2.6–2.7 mm long, n=30), an egg with developed larva inside (black stemmata), and remaining shrunk egg shells.

dorsal margin slightly concave, ventral margin rounded, tapering to narrowly rounded apex; in dorsal view broad at base, tapering to narrow rounded apex, with long, fine hairs. Lancet (Fig. 20) very short; serrulae and annuli barely discernable.





**Figures 31–37.** *Leseha vespa* **31** early stage first instar larva on abaxial blade and feeding scar as hole(s) on young frond (note green internal color of larva) **32** early stage first instar larvae scrape-feeding on abaxial blade of mature frond **33** middle instar larva feeding on sorus on mature tough frond (note brown internal color of larva) **34** last feeding instar larva, lateral view **35** last feeding instar larvae, dorsal view **36** cocoon (ca. 12 mm long) spun on surface of dry, mossy branch (enclosed in oval circle) **37** pupa in situ (cocoon is cut to show pupa).

**Male:** Length, 8.0 mm. Color similar to female. Apex of abdomen (Fig. 21) with deep, oval concavity dorsally; 7<sup>th</sup> tergite emarginate and with ridge at apex, 8<sup>th</sup> tergite deeply concave. Genitalia in Figs 22, 23; harpe rounded; parapenis rounded at apex, slanted laterally; valvices of penis valve with long, narrow apical lobe and long narrow dorsal lobe.

**Larva:** Last feeding instar (Figs 34, 35): Length 18–24 mm. Head black, width ca. 2.2 mm. Body pale green with yellowish tint, yellowish tint more visible on thoracic segments 2 and 3, and abdominal segments 7–10 and abdominal tergum 1 yellow, lateral lobes of thoracic segments 2–3 yellow, thoracic legs black, spiracular to proleg area of abdominal segments 1–10 creamy white ( $n = 7$ ).

**Type material.** Holotype female, labeled “COSTA RICA, Puntarenas Province, Monteverde, Estación Biológica Monteverde, 1530 m, 10°19'08.5"N, 84°48'32.0"W, larvae 15.v.2017, adults 22–25.vi.2017, *Phlebodium pseudoaureum*, Kenji Nishida (USNM). Paratypes: Same data as for holotype (2 ♀, 2 ♂, MZUCR, USNM); same data as for holotype except mid-May 2018, in flight and perched on leaves (1 ♀, MZUCR); adult emerged 26.viii.2018, *Phlebodium areolatum* (5 ♀, 2 ♂, USNM, MZUCR); larvae 15.viii.2018, emerged 17.viii.2018, *Phlebodium areolatum* (1 ♀, MZUCR); collected on *Phlebodium areolatum*, 14.vi.2018 (1 ♀, MZUCR); adult emerged 10.viii.2018, *Phlebodium areolatum* (3 ♀, USNM, MZUCR); adult emerged 21.viii.2018, *Phlebodium areolatum* (1 ♀, USNM); Costa Rica, S. J., San Antonio de Escazu, 1325 m, W. G. Eberhard, 12.VIII.2018, vouchers study of W. Eberhard (1 ♀, 2 ♂, USNM).

**Etymology.** The name *vespa* is Latin for wasp. This species resembles a commonly seen yellow and black striped paper wasp, an *Agelaia* sp. (Vespidae), at the same habitat of the study site in Monteverde.

**Host, life history.** The larvae feed on *Phlebodium pseudoaureum* (Polypodiaceae). In the native plant garden of EBM, *P. pseudoaureum* ferns were growing in patches (Fig. 24). Between May and June of 2017 and 2018, vigorous growths of new shoots and young fronds were observed. In May 2017 and 2018, some yellow and black striped paper wasp-looking sawfly females were observed walking on the host fern. Between 10:12 AM and 10:55 AM, the females laid ca. 1.5 mm long purple or yellow eggs (Figs 25, 26, 28, 29) on the abaxial of the blade ovipositing from the adaxial, i.e., oviposited piercing the ovipositor through blade tissue ( $n = 3$ ) (Figs 16, 25–29). On young, soft and succulent fronds, eggs were laid mostly on leaf veins ( $n = 12$  fronds) and on old and tough fronds, were laid on the blade ( $n = 10$  fronds). Pierced holes of oviposition were visible from adaxial. The females oviposited in small clusters of 2–7 eggs ( $n = 7$  clusters). In a few cases singly laid eggs and eggs positioned on adaxial blade were observed. Under captive conditions, a female laid up to 58 eggs in 10 days. Regarding the color variation of the eggs, in the first days of oviposition the eggs were yellow and then became orangish, and last days became purple. The eggs became translucent and enlarged in 2–3 days, and formation of the larvae was visible inside (Figs 28, 29). A commonly seen earwig (*Ancistrogaster spinax* or *A. scabiosa*: Dermaptera) placed in a petri dish quickly devoured 3 recently laid *L. vespa* eggs. Very recently hatched larvae were creamy-colored with light brown head and black stemmata (Fig. 30). The light brown head became black and as the larvae fed on the blade tissue the body became greenish internally. The early instar larvae fed on soft and succulent blades making small holes (Fig. 31) and grazed on tough blades (Fig. 32). Early instar larvae on very old and tough fronds fed on sori, and the body color was pale brown (Fig. 33) ( $n = 3$ ). Late instar larvae fed on the entire blade leaving tough vein areas. In the

dioramic chamber, pupation occurred under rocks and branches spinning dark brown ovoid cocoons ( $n = 18$ ) (Figs 36, 37). Relatively mature pupae were greenish ( $n = 2$ ) (Fig. 37). Some of the dissected cocoons contained prepupal larvae which apparently were in diapause ( $n = 3$ ).

A summary of collecting and rearing records is as follows: Eggs, early to late instar larvae on maturing fronds 12–16.vi.2008. Middle to late instar larvae on young fronds 15.v.2017, all went under soil 8–10.vi.2017, adult emergence 22–25.vi.2017; a female laid eggs 14.vi.2018, first instar hatched 22.vi.2018, last feeding instar 15–30.vii.2018, adult emergence 21.viii.2018; recently laid eggs 26–27.vii.2018, first instar hatched 4.viii.2018, middle to late instar larvae 27.viii.2018, adult emergence 22–30.ix.2018.

**Remarks.** *Phlebodium pseudoaureum* is an epiphytic or terrestrial fern with up to ca. 30 pinnae or 2 cm width growing to ca. 1 m tall. Fronds are soft and succulent when young, when mature it becomes tough (crunchy). Abaxial of frond is thinly covered with a white, waxy substance. It is distributed between Mexico (vicinity of Topic of Cancer) to northern Argentina, including the Caribbean (Dominican Republic and Jamaica). In Costa Rica it has been recorded from near sea level to 2500 m elevations on both slopes (Moran 2009; Missouri Botanical Garden 2018; KN personal observation 2017 – 2018). The species of the genus *Phlebodium* are closely related to *Polypodium* (Tejero'Díez et al. 2009).

Eggs ( $n = 7$ ) and some late-instar larvae were also found at 14°2'4"N, 87°4'29"W, ca. 1625 m elevation, in Reserva Biológica Monte Uyuca in Zamorano, Honduras (KN personal observation 2019). Although adults were not reared, these are most likely those of *L. vespa* based on the observation and the host plant.

The morphology, enlargement, and plant tissue association of the egg of this species are currently being studied by KN and Kondo Laboratory of Pattern Formation, Graduate School of Frontier Biosciences, Osaka University.

### ***Leseha carranzae* Smith & Nishida, sp. nov.**

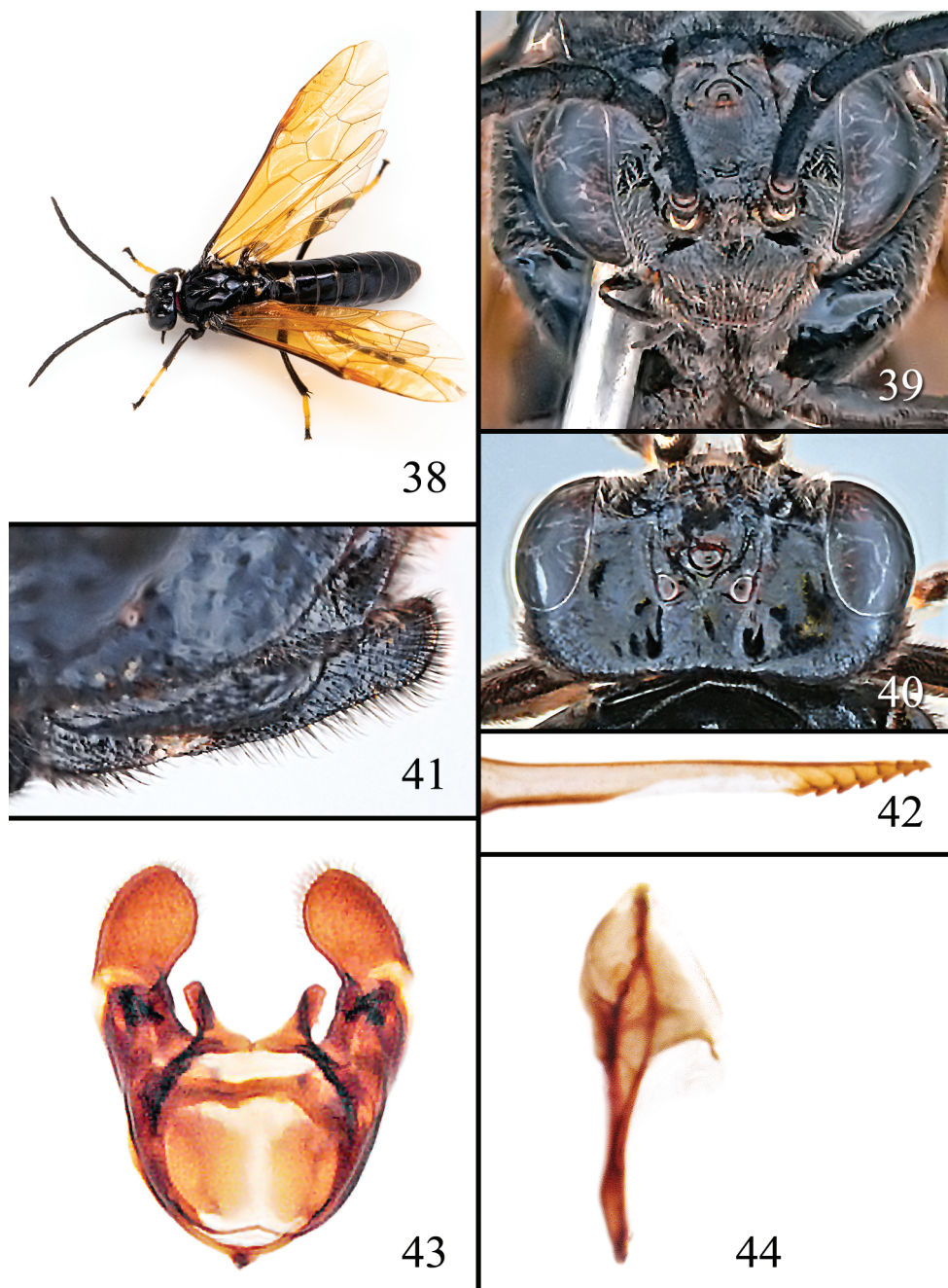
<http://zoobank.org/AFC92EC4-0D39-4D78-B776-11FDD9477395>

Figs 38–50

**Diagnosis.** Black with contrasting white basal 3 tarsomeres. Wings a contrasting bright yellow. Female lancet (Fig. 42) short, but with distinct serrulae and annuli at apex.

**Description. Female** (Fig. 38): Length, 10.0 mm. Black, small mark on outer surface of scape and basal 3 tarsomeres white. Wings, with veins and stigma, completely golden yellow. Head and thorax shiny, without sculpture, abdomen dull and densely microsculptured. *Head* (Figs 39, 40): Antenna 2.1× head width; scape and pedicel each slightly longer than broad; 3<sup>rd</sup> antennomere slightly longer than 4<sup>th</sup>, 4<sup>th</sup> to 9<sup>th</sup> antennomeres gradually decreasing in length. Malar space less than half diameter of front ocellus; clypeus with shallow, circular emargination. Lower interocular distance subequal to eye height. Distances between eye and lateral ocellus, between lateral ocelli, and between lateral ocellus and hind margin of head as 1.0: 0.5:1.2;

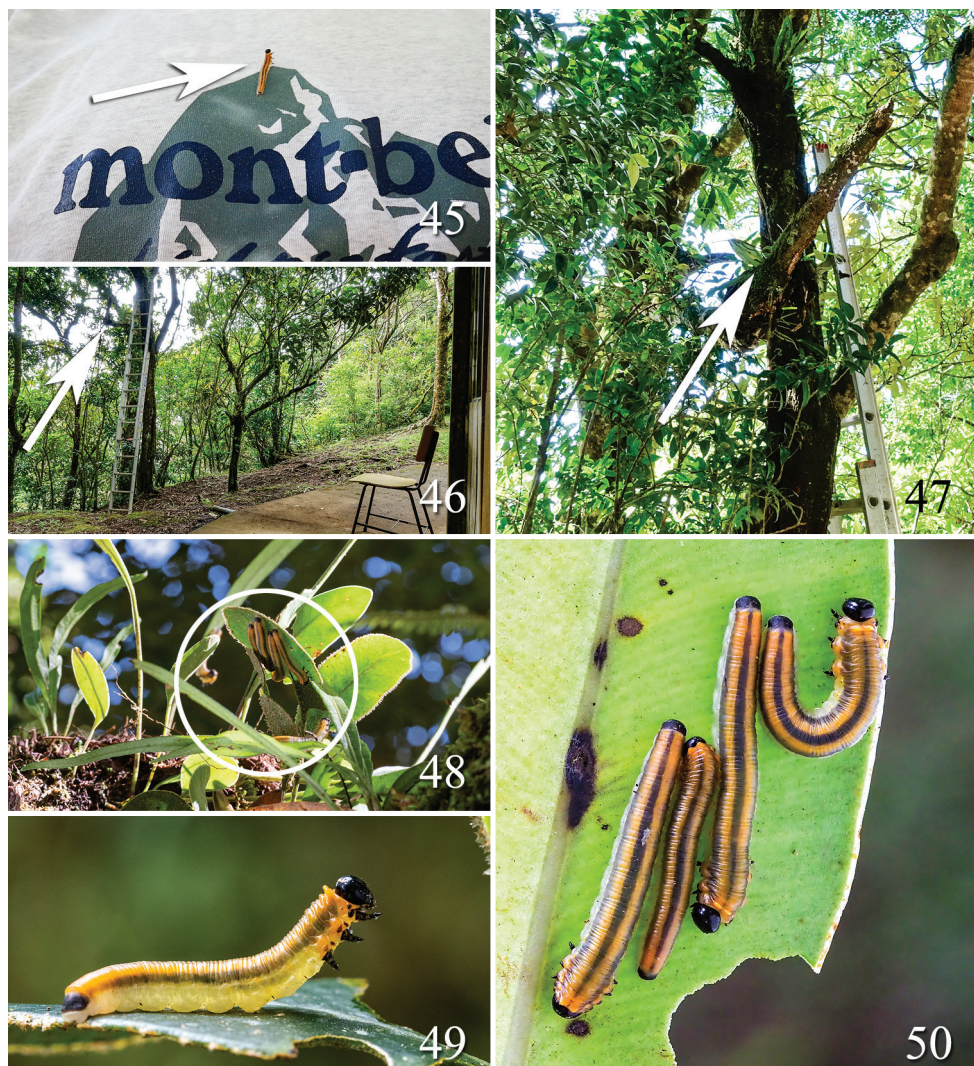




**Figures 38–44.** *Leseha carranzae* 38 female, dorsolateral view 39 head, front 40 head, top 41 female sheath, lateral 42 female lancet 43 male genital capsule 44 male penis valve.

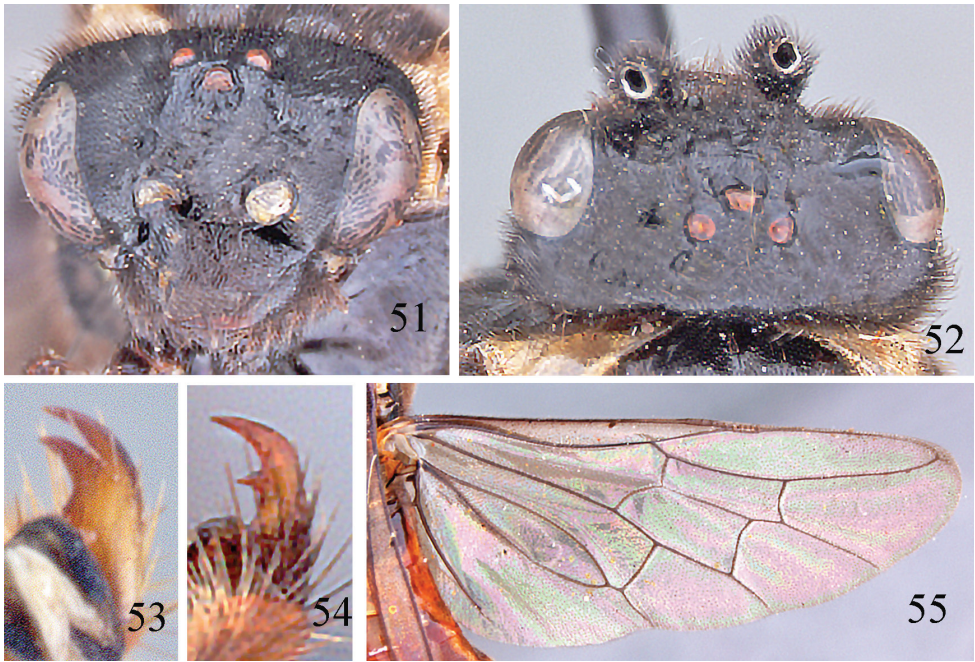
postocellar area almost quadrate, very slightly broader than long, with deep lateral grooves. *Thorax*: Hind basitarsus slightly longer than length of remaining tarsomeres combined, as 1.0:0.8; apical hind tibial spurs sub equal in length, length slightly less





**Figures 45–50.** *Leseha carranzae* **45** wandering last feeding instar larva (arrow) on shirt of KN **46** habitat with chair where wandering larva appeared (arrow pointing at location of host plants with larvae) **47** closer view of habitat (arrow pointing at host plants where larvae were present) **48** six last feeding instar larvae shown in indicated white circle, four last feeding instar larvae resting on abaxil of *Elaphoglossum bellermannianum* and two other larvae ‘in search of food plant’ **49** last feeding instar (lateral view) reaching for next frond **50** three last feeding instar and one penultimate feeding instar (dorsal view) resting abaxial of *Elaphoglossum lingua*, fed area shown on lower right.

than width of hind tibia at apex. Hind tibia and hind basitarsus slightly flattened, each with longitudinal groove. Tarsal claw with long inner tooth, very slightly shorter than outer tooth. *Abdomen*: Sheath (Fig. 41) short and rounded at apex in lateral view; in dorsal view, uniformly wide with stiff, straight hairs at apex. Lancet (Fig. 42) short, with few annuli and serrulae.



**Figures 51–55.** 51, 52, 54, 55 *Andeana* sp. 53 *Leseha vespa* 51 head front 52 head dorsal 53 trsal claw 54 tarsal claw 55 hindwing.

**Male:** Length 8.5–9.5 mm. Color and structure as for female. Genitalia in Figs 43, 44; harpes oval, slightly longer than broad; parapenis very narrow, elongate, apex slanted laterally; valviceps of penis valve rounded at apex, with narrow dorsal lobe directed posteriorly.

**Larva:** Last feeding instar (Figs 45, 48–50): Ca. 20 mm long. Head black; width ca. 2.5 mm. Body reddish yellow with longitudinal 3 dark green to dark gray stripes (one mesially on dorsum, other two above lateral lobes). Thorax laterally reddish yellow with black spots, thoracic legs black, spiracular to proleg area of abdominal segments 1–10 creamy white. Abdominal segment 10 and anal plate black ( $n = 7$ ).

**Type material.** Holotype female, labeled “COSTA RICA, Puntarenas Province, Monteverde, Estación Biológica Monteverde, 1530 m, 10°19'08.5"N, 84°48'32.0"W, larvae collected 4.xii.2017, adults 1.i.2018 to 27.i.2018, *Elaphoglossum* spp., Kenji Nishida” (USNM). Paratypes: Same data as for holotype (4 ♀, 2 ♂, MZUCR, USNM), on leaf, 6.viii.2018 (1 ♀, MZUCR); Costa Rica, San José, Zurquí Moravia, 1600 m, iii.1999, P. Hanson (1 ♀, MZUCR), same except iv.1995 (1 ♀, MZUCR), same except viii.1995 (1 ♀, USNM).

**Etymology.** Named after Melanie Carranza who started to have a passion for insects and helped with the rearing of this species and getting the adults.

**Host, life history.** Larvae were feeding on *Elaphoglossum hellermannianum*, *E. lingua* (under natural conditions) and *E. hammelianum* (under rearing conditions)



(Dryopteridaceae). On a windy afternoon of 4.xii.2017, while KN was sitting on a chair outside in front of the laboratory of EBM, a sawfly larva climbed on to his shirt (Fig. 45). KN had not seen this larva before and started to search for the host plant in the surrounding environment. The larva was placed in a translucent plastic bag with leaves of ca. 10 plant species, e.g., *Myrsine coriacea* (Myrsinaceae), *Myrcia splendens* (Myrtaceae), *Cornus disciflora* (Cornaceae), *Quercus insignis* and *Q. cortesii* (Fagaceae); however, the larva did not feed on any of these plants. The larva under captive conditions appeared to walk/move upwards to a higher position, and KN searched for other plants that grow on the higher part of trees, such as epiphytic ferns. KN collected *Elaphoglossum hammelianum* that was growing 4–5 m from the ground and placed in the plastic bag. The larva readily fed on the fern. KN searched for more larvae on *Elaphoglossum* ferns growing on trees in front of the laboratory, and found eight more larvae in a patch of *Elaphoglossum* species growing on a dead branch (Figs 46, 47). The larvae were feeding on thick and tough blades of *E. lingua* (Fig. 48). When finished devouring a blade the larvae walked around and settled on abaxial of *E. bellermannianum* and started to feed on it eventually. The larvae were collected and placed in the plastic rearing bag along with the *Elaphoglossum* spp. patch attached to the soil. Additionally, a small patch of *E. lingua* was added for rearing. The larvae fed on all three species of *Elaphoglossum* under rearing conditions. From 9.xii.2017 the larvae started to disappear from fronds little by little until 17.xii.2017. The larvae probably spun cocoons within the attached soil, rhizome, and roots, and pupated. Adult emergence occurred between 1.i.2018 and 27.i.2018. Part of the life history data and additional information were published online (Nishida 2017). See Type Material section and above for collecting and rearing records.

**Remarks.** *Elaphoglossum bellermannianum* is a scaly blade (leather like) epiphytic fern, with elongate oval shaped blade of 6–17 cm long by 1.5–4 cm wide, relatively thick and dark green on adaxial. The species has been recorded from Dominican Republic, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, and Bolivia (Vasco 2011, Missouri Botanical Garden 2018). In Costa Rica it is distributed between 1500 and 3100 m elevations. *Elaphoglossum hammelianum* is epiphytic, having relatively thin, narrow and long blade (up to 20–30 cm) with wavy margin. Pale brown scales are present scattered along the blade (KN personal observation 2017, 2018). It has been recorded from elevations between 900 and 3100 m from Costa Rica through western Panama (Missouri Botanical Garden 2018). *Elaphoglossum lingua* is an epiphytic or terrestrial fern with thick and crunchy tongue-shaped blades. The blade grows up to ca. 24 by 7 cm. It is found from Costa Rica, Antilles to Brazil at Tropic of Capricorn and recorded along the mountain ranges of Costa Rica between 1100 and 2700 m (Mickel 2009, Missouri Botanical Garden 2018, KN personal observation 2017, 2018).

Two other species of Selandriinae were reared from ferns at the same study site: a single specimen of a black and pink ‘firefly-mimicking’ species from *Elaphoglossum lingua* and more than 30 adults of another species from *Blechnum appendiculatum* (Blechnaceae). Also, unidentified sawfly larvae ( $n = 2$ ) were collected feeding on *Serpocaulon ptilorhizon* (Polypodiaceae); however, adults were not obtained.

## Acknowledgments

We thank Robbin Moran, Klaus Mehlreter, and Emily Holenbeck for identifications of the fern species, William A. Haber and Willow Zuchowski for identification of *Saurauia* species, Paul. E. Hanson for identification of the vespid wasp, Daniel Briceño Lobo for identification of the earwig, Museo de Zoología-Escuela de Biología, P. E. Hanson, Eddy Camacho, and Michael Gates for making sawfly specimens reach the hands of DRS, Melanie Carranza for assisting in the field work and rearing of sawflies, Elizabeth Heffington for reviewing of the draft, and EBM and Willow Zuchowski for letting KN study in the garden. William Eberhard, Smithsonian Tropical Research Institute and Escuela de Biología, Uiversidad de Costa Rica, also provided some specimens. E. Hollenbeck also provided literature. KN gives thanks also to F. Castañeda and N. Estrada for the field trip to Reserva Biológica Monte Uyuca. KN obtained research/collecting permit from Lourdes Vargas Fallas of MINAET-SINAC in San José. 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.

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# Outbreaks of *Tomostethus nigrinus* (Fabricius, 1804) (Hymenoptera, Tenthredinidae) on *Fraxinus angustifolia* ‘Raywood’ in Belgium

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## Abstract

In Western Europe the ash sawfly *Tomostethus nigrinus* is known to occur at low densities on *Fraxinus excelsior* and is uncommonly reported as a pest species. However, we show here that outbreaks can occur on non-endemic trees such as *F. angustifolia*, and that the species is able to spread quickly using city infrastructure. At the visited localities near the city of Ghent, foliage of *Fraxinus angustifolia* ‘Raywood’ emerged approximately one month earlier than on *F. excelsior*. At the same time, changed climatic conditions in the last decade, i.e. higher temperatures in March, caused adults to emerge earlier. Synchronicity of the potential hosts and *T. nigrinus* may therefore have altered, playing a crucial role in population dynamics. Future research should aim to confirm if the species dramatically declines in numbers after reaching its peak population level, an effect which was observed in previous studies, but for which there is still no satisfactory explanation.

## Keywords

sawfly, gregariousness, migration, phenology, ash, urban

## Introduction

The ash sawfly, or black sawfly, *Tomostethus nigrinus* (Fabricius, 1804) is widespread throughout the Palaearctic (e.g., Abe 1989 for Japan, Zhelochovtsev and Zinovjev 1996 for Russia, Taeger et al. 2006 for Europe). In the Low Countries it is known to occur at low densities on *Fraxinus excelsior* Linnaeus, 1753. It is considered to be uncommon, only a few observations are known from Belgium and The Netherlands (Bequaert 1912; Crèvecoeur and Maréchal 1938; Magis 1987; pers. comm. A. Mol). Outbreaks were not yet known from those countries. From 2016 onwards however, massive defoliation was increasingly observed in the city of Ghent (Flanders, Belgium) near the ‘Rabotpark’. In 2019 the defoliation event was observed more closely and some specimens were collected. In contrast to many outbreaks explicitly mentioned in the literature, defoliation in Ghent affected *Fraxinus angustifolia* Vahl, 1804 ‘Raywood’, whereas nearby trees of *F. excelsior* were largely ignored.

Based on our observations on this first report of serious outbreaks of *T. nigrinus* in the Low Countries, we want to re-evaluate the importance of host plant specificity. Furthermore we made some interesting observations on both adult and larval behaviour. Finally, we tried to identify possible factors determining and/or controlling the presence and ‘outbreak’ rates of the sawfly larvae.

## Material and methods

### Voucher specimens

BELGIUM • 1 ♀, 7 mm; Langemark, ‘t Bosseltje; 50°54'57"N, 2°53'31"E; 28 Apr. 2018, F. Verheyde leg.; F. Verheyde coll. 20180428-155545497 • 7 ♂♂ 2 ♀♀, 5 larvae; Gent, Rabotpark; 51°03'54"N, 3°43'01"E; 30 Apr. 2019; F. Verheyde leg.; F. Verheyde coll. 20190430-170021621

Apart from the single, previous finding at ‘t Bosseltje (above), which was on *Fraxinus excelsior*, nearly all subsequent observations were made in the city park ‘Rabotpark’, where outbreaks were reported for the first time (coordinates: see above), on *Fraxinus angustifolia* ‘Raywood’. The first author visited the site three times in 2019, on April 11 and 30 and on May 20. The second author, living in the immediate vicinity of the city park, made irregular observations of the ashes from 2016 onwards.

The city park mainly consists of one large avenue and/or bicycle path, with trees planted on both sides of the path. In the surroundings, next to a large building which stands directly before the path, younger trees are planted. Apart from *Fraxinus*, these include *Alnus* and *Robinia* species. Most trees were planted in 2008. In 2012 177 trees of *F. angustifolia* ‘Raywood’ were counted. Common ash or *F. excelsior* is also represented by 7 trees (Roskams and De Haeck 2012).

The adult specimens were identified using Benson (1952). As with most species of the subfamily Blennocampinae, *T. nigrinus* is mainly black, except for its at most piceous front legs. A useful character for recognition of *Tomostethus*, with only one



species in Central Europe, is that vein M of the fore wing runs subparallel with *Im-cu*. Furthermore, although fore wing vein 2A is reduced, as in other Blennocampinae, this basal part of the fore wing anal cell of *Tomostethus* has a unique shape: sinuately recurved towards vein 1A. The wing membrane has a specific pigmented line in the basal part of the cell, located where 2A is faintly expressed (Fig. 1). The complete wing membranes are more or less greyish, with the fore wings somewhat darker than the hind wings (Benson 1952; Mol 2002). Our collected specimens are mainly males, due to being mainly found on the stems, whereas females fly higher for oviposition. The collected male specimens are on average smaller, varying in body length between 5.5 and 7.0 mm, with females varying between 6.5 and 7.5 mm. Females are slightly more robust than males, with the abdomen and thorax somewhat wider.

Although their association with *T. nigrinus* adults seemed obvious, larval determination was checked with Lorenz and Kraus (1957). While morphological details described there are correct, it is important to note that their observations were based on a preserved sample in ethanol from the Natural History Museum, which may explain some errors related to coloration. The larval head for example is without doubt more greenish than yellowish, especially in the first larval instars. In these instars, the abdomen is more brownish coloured and thus contrasts more with the colour of the head (Fig. 2). The older larva becomes a lighter green, with whitish bands (fat bodies) clearly showing through dorsally (Fig. 3). After the last larval moult, the larva changes to an olive green colour just before descending from the tree and prior to spinning its cocoon (Matošević et al. 2003).

## Results

During the last week of March and the first two weeks of April 2019 many adults were seen near the ashes. Females were found resting and ovipositing on the edges of the leaves of *Fraxinus angustifolia* (Figs 4, 5). This happened at different heights and on trees of different age. Another part of the city park with approximately 2–3 years old trees was similarly colonized, although the numbers of sawflies were lower. Exceptionally, some (early) males were found feeding on yellow inflorescences of nearby herbs. This was only observed on Brassicaceae, while *Taraxacum* sp., although very abundant, was completely ignored. On most trees a few dozen adults were seen, reaching on an older tree an extrapolated total of approximately 75 adults.

Some other more general behavioural aspects are noteworthy. Firstly, many – especially male – adults were found warming up on the tree stems (Fig. 5). However, some of these adults, both males and females, were also found dead on the stems, still attached with their tarsi to the bark. Secondly, the flying behaviour of the sawfly was found to be quite characteristic and slow, with adults often ‘dropping’ from higher tree branches to the stem. No copulating sawflies were found. Possibly, copulation is brief and takes place higher in the trees. With the favourable weather conditions, the flight period was short, between two and three weeks. From the third week of April onwards, larvae started to hatch.



**Figure 1.** *Tomostethus nigrinus* F. ♂, leg. Janet Graham, North Wales, V. 2018 Janet Graham.



**Figure 2.** Younger larva of *Tomostethus nigrinus* on *Fraxinus angustifolia*, leg., det., coll., F. Verheyde, Ghent (BE), 30.IV.2019 Fons Verheyde.

The abundance of larvae made clear how severe the outbreak was. Half a meter around the foot of one tree, in all directions, the ground was covered with a layer of (+ 10.000) larvae, approximately 8 centimetres thick (Figs 6–9). The lowest larvae in this layer, closest to the ground, consisted of some dead or weakened individuals, a couple of them already darkening in colour. However, starvation rates in total seemed



**Figure 3.** Older larva of *Tomostethus nigrinus* on *Fraxinus angustifolia*, leg., det., coll., F. Verheyde, Ghent (BE), 30.IV.2019 Fons Verheyde.



**Figures 4, 5.** Adult females of *Tomostethus nigrinus* on *Fraxinus angustifolia*, resting on younger leaves (left); sunning on tree stems (right), Ghent (BE), 11.IV.2019 Fons Verheyde.





**Figures 6, 7.** Thousands of larvae of *Tomostethus nigrinus* on the stem of a tree (left) and a lamppost (right), Ghent (BE), 30.IV.2019 Fons Verheyde.

to be rather low. On another tree, not including the larvae on the ground near the foot, an extrapolated count of 550 larvae was obtained on only the stem (surface size being approximately 2.5 m<sup>2</sup>). All larval instars were observed, but predominantly the last two instars were found, possibly due to the dates of our visits.

In contrast to normal pupation strategies (Viitasaari 2002), larvae often dropped from the leaves or branches to the ground. Descending larvae on the stems of trees were seldom seen and may in fact be exceptional for some species in outbreaks (e.g. Larsson and Tenow 1984 for *Neodiprion sertifer* Geoffroy, 1785). This finding was confirmed by a citizen who attached five glue bands to a damaged tree in front of his house. The lower bands captured many more larvae. However, the larvae clearly also used this strategy to migrate from tree to tree. Migration happened en masse and in several directions. Near the trees with the most dense population, the bicycle path was coloured green by run over larvae, crossing the path to trees on the other side. Interestingly, larvae ascended everything on their way. A lamppost (Fig. 7), positioned next to the tree with its layer of larvae (Fig. 6), was visited by hundreds of larvae. Similarly visited were a bench, a trash can and a sign post.

The feeding habits of larvae are rather well-described in existing literature, and our observations mostly confirm what is known. The larvae were mainly found on the underside of the leaves (Fig. 11) and only the main veins of the leaves remained after defoliation by the last instars. However, there was a lot of variation in feeding





**Figures 8, 9.** Layer of larvae (thickness + 8 cm) of *Tomostethus nigrinus* near the base of the stem of *Fraxinus angustifolia*, Ghent (BE), 30.IV.2019 Fons Verheyde.

patterns. The majority of the defoliation, at our study site, started at around 2 to 3 meters above ground level, with the top of the tree only defoliated during a final stage (Fig. 10). However, this was not always the case, and this should be addressed more systematically to make any conclusive remarks. By mid-May, defoliation was complete,



**Figures 10, 11.** Defoliation of *Fraxinus angustifolia* by *Tomostethus nigritus*, Ghent (BE), 30.IV.2019  
Fons Verheyde.

and just before the end of May most larvae had disappeared. In June no more larvae were found, in contrast to other localities mentioned in literature, where larvae were still active even in the third week of June (e.g. Austara 1991; Stockan and Taylor 2014). Permanent damage appears to be rather limited, which corresponds with the reports in literature (notably Matošević et al. 2003). All ‘damaged’ trees were able to grow new shoots after defoliation.

## Distribution

Some efforts were made to find more localities with outbreaks of *T. nigritus*. The city of Ghent and local entomological associations were contacted. Two additional locations were found using social media. Both, sufficiently documented (and validated), dated from the first week of May and consisted of outbreaks on *Fraxinus angustifolia* ‘Raywood’.

The first location, situated on ‘Sint-Amandsberg’ (Ghent, 51°04'26.4"N, 3°45'36.0"E), is an average city lane, where *Fraxinus angustifolia* ‘Raywood’ is planted on both sides of the road. According to the observer (Wouter Chielens), it was the first time he saw the larvae at this location, having lived there for ten years at the time when he was interviewed. In a direct line, it is 3.1 km distant from the Rabotpark.

The second location, situated in Mariakerke (Ghent, 51°04'20.6"N, 3°41'11.1"E) consists of a square with several trees, five of them representing *Fraxinus* sp. According to

this observer (Kris Van der Stiggel), it was the second year he saw the larvae, but in 2018 they only visited three trees. In a direct line, it is 2.3 km distant from the Rabotpark.

Thirdly, the second author has also seen traces of defoliation on *Fraxinus* sp. near Wondelgem (51°05'13.2"N, 3°42'54.0"E), which is also close to Ghent and Rabotpark (2.3 km). Neither adults nor larvae could be found on this site.

Other smaller and confirmed locations, with at least feeding traces, are a playground near Citadelpark (51°02'16.4"N, 3°43'08.0"E), a playground near Rabotpark (51°03'41.4"N, 3°42'55.1"E) and trees near an intersection (51°04'22.1"N, 3°42'46.8"E). In total, including Rabotpark, seven locations are thus known at the moment, but in fact many more may be found. At the time of writing, the city of Ghent is making an overview of all known locations (pers. comm. Wim Moerdijk, groendienst Stad Gent).

## Discussion

The main reason for Ghent being a clear hotspot for the sawfly seems to be nothing more than the choice of *Fraxinus angustifolia* 'Raywood' for amenity tree planting in the city planning. Although we have no clear overview of the total number of trees planted at all locations, it was certainly planted many times between 2005 and 2015 in city parks, streets, squares, etc. The city infrastructure made the quick migration of the sawfly possible. As the species is native, originally it may have spread from the nearest local nature reserves (e.g. Bourgoyen-Ossemeersen, which is only on 2.3 kilometres from the city park). This movement from natural ash 'forests' to plantations is also proposed by Mitali (2012) to explain the dramatic increase of *T. nigrinus* in northern Italy. Another possibility is that it was imported with the root balls *Fraxinus*, but no evidence has been found for this, and the fact that trees were planted as early as 2008 speaks against it.

Excluding Italy (Mitali 2012), common ash (*Fraxinus excelsior*) has been mentioned as the most preferred host plant in literature (e.g., Taeger et al. 1998), both for populations at "normal" levels (low densities) or appearing at outbreak levels (high densities). These reports of outbreaks, however, deal with two main types: outbreaks in forests (mainly in eastern Europe), and outbreaks in urban environments (see Tab. 1). Factors influencing outbreak dynamics can be fundamentally different in each case. For example, floods have been identified as an important natural controlling factor in Croatian forests (Matošević et al. 2003).

Parasitism is difficult to assess without rearing, but no parasites were observed in situ. Parasitism rates reported in the literature are however rather high, fluctuating between 44% and 80% (Mrkva 1965; Matošević et al. 2003; Mitali 2012). The rate of predation, e.g. birds feeding on the larvae, is limited. Starlings, wood pigeons and tits were seen eating the larvae, but these were isolated and rare observations. Near London, a pair of blackbirds were seen feeding on the larvae (Cheke and Springate 1999).

Ironically, while our results are opposite (Fig. 12) to the findings of Matošević et al. (2003), who reported severe defoliation of *Fraxinus excelsior*, with *F. angustifolia* nearly untouched, her general hypotheses are confirmed. There is no preference among



**Table 1.** Reports of outbreaks of *Tomostethus nigrinus* mentioned in the literature.

Location	Date	Host	Environment	Reference
Armenia	?	?	?	Harutyunian (1987)*
Austria				
- Lower Austria: Marchfeld, Waldviertel; Styria: Liezen, Pöls;	1974, 1977, 1999	<i>F. excelsior</i> (and other species?)	Urban: alleys along streets	Pschorn-Walcher (1982)
- Upper Austria: Mühlviertel				Pschorn-Walcher and Altenhofer (2000)
Croatia (Zagreb)	1997	<i>F. excelsior</i>	Urban: streets	Matošević et al. (2003)
Czech Republic	1958–1960	<i>F. excelsior</i>	Forest	Martinek (1964), for southern Moravia
	1965			Mrkva (1965)
	1999–2000	Mixed		Liška and Holuša (2002)
England				
- London	V.1993	<i>F. excelsior</i>	Urban	Cheke and Springate (1999)
- Manchester	2010			Stockan and Taylor (2014)
- Shirley	VI.1952			Benson (1952)
- Telford	2014			
Germany (Lower Saxony)	1993–1994	<i>F. excelsior</i>	Forest	Taeger et al. (1998)
Iran (Kohkilouyeh and Boyer Ahmad province)	?	?	?	Moghadam and Abai (1993)*
Ireland	2016	<i>F. excelsior</i>	Urban	Jess et al. (2017)
Italy				
- Friuli Venezia Giulia	1999–2009	<i>F. angustifolia</i> & <i>excelsior</i>	Urban & forest	Zandigiacomo et al. (2006); Stergulec et al. (2009)
- Lombardia	1980–2007	<i>F. angustifolia</i>	Forest	Trematerra and Petralli (1987); Campanaro et al. (2007)
Norway:				
- Kragerø	1986–1992	<i>F. excelsior</i>	Urban: parks & streets	Fjeldalen (1993)
- Oslo	V–VI.1990			Austara (1991)
- Fredrikstad				
Scotland (Aberdeen)	V-VI. 2013–2014	<i>F. excelsior</i>	Urban: streets	Stockan and Taylor (2014)
Ukraine				
- Donetsk, Kharkov region	2002–2015	Mixed	Urban & forest	Meshkova et al. (2017)
- Molodezhny park of Kharkov	2013–2015			Zinchenko and Kukina (2015)

\*- reference not seen.

several ash species, although Pschorn-Walcher (1982) explicitly excluded *F. americana* as a larval host. The most important factor leading to outbreaks is synchrony in the phenology of the insect with that of its potential host plant (Matošević et al. 2003). At the localities we observed, foliage of *Fraxinus angustifolia* ‘Raywood’ emerged approximately one month earlier than on *F. excelsior*. At the same time, changed climatic conditions, i.e. the higher temperatures in March, April and May from 2010 onwards (on average 2 to 3 degrees higher compared to values for 1981–2010; numbers from KMI 2019), caused adults to emerge as early as the last week of March, and larvae were gone before the end of May. Synchronicity of the potential hosts and *T. nigrinus* may therefore have altered. Already Pschorn-Walcher (1982) noted that ash trees growing leaves comparatively early or comparatively late get infested by *T. nigrinus* at a comparatively low rate.





**Figure 12.** Defoliated *Fraxinus angustifolia* and untouched *Fraxinus excelsior*, Ghent (BE), 15.V.2019 Geert Sioen.

After migrating from a more natural environment, the sawfly might have responded to the different conditions in the urban setting (Matošević et al. 2003). Particularly important may be the absence of flooding, which is thought to cause high mortality in the cocoon stages (e.g. Mrkva 1965). Something which has received little to no interest in the case of *T. nigrinus* are the changes in gregariousness or group living. This is quite surprising in view of the vastly increased density of larvae living together within these urban environments. It was proven for the Australian sawfly *Perga affinis* how important these differences are in the development of the species. For grouped versus single larvae, the mortality risk was found to be lower, growth rates were faster (due to higher temperatures), and individual larvae from large groups had an increased weight in their final instar (Fletcher 2009).

There is one more aspect to consider: the state of health and age of the trees. In the invasive sawfly *Aprocero leucopoda* Takeuchi, 1939 (Argidae), elms are generally infested independent of their age and site characteristics (Blank et al. 2010). However, a severe outbreak was described from eastern Germany, where this species defoliated trees of *Ulmus* 'New Horizon', which were recently planted along a bicycle path (Blank et al. 2014) and supposedly in a physiologically suboptimal state. Meshkova et al. (2017) hypothesized that larger trees tend to be in better health, and although not statistically proven, that defoliation seemingly decreased with tree diameter. Interestingly, our locality, the Rabotpark, used to have many problems concerning the health conditions of its trees, which were planted in 2008. In a report from 2012 the bases

of the stem of 124 Ash trees (67% of the total) were found to be damaged, probably by collisions with mowing machinery. Generally, the condition of the trees planted in the Rabotpark was considered to be moderate to poor. Soil conditions are poor, due to strong soil compaction, disturbed hydrological conditions, large quantities of incorporated fresh organic material, and high salt concentrations. In addition, the ashes were largely planted too deep (Roskams and De Haeck 2012). However, since 2012, the trees have grown and now seem to be relatively healthy. Furthermore, the widespread and undifferentiated distribution of sawfly larvae on trees in and outside the Rabotpark suggests that tree health is not an important factor.

## Conclusion

We have shown that in Western Europe urban environments seem to be more suitable places than semi-natural habitats for *Tomostethus nigrinus* to reach a threshold in the numbers of larvae, above which it may be termed as ‘in outbreak’ or as a ‘pest’. Rates of parasitism (and possibly predation) are conceivably lower and environmental conditions (i.e. humidity) influencing the pupal stage are more stable. It is also possible that urban trees are, generally speaking, less healthy due to the soil and mowing conditions in their artificial environment. This may be a trigger to some extent, but should not be exaggerated. More importantly, higher temperatures are reached in cities, and are possibly stimulated by climatological changes. This inspires a faster development of the larvae. As a result, during the last decade the phenology of *F. angustifolia* was able to synchronize with the phenology of *T. nigrinus*. The city infrastructure supported quick migration and an increased density of the species.

When the threshold is reached after which an ‘outbreak’ of *T. nigrinus* occurs, it is possible that the close proximity of many larvae living together brings some the benefits mentioned by Fletcher (2009). From that point onwards, the increased chance of survival and increased fitness of individuals leads to increasing severity of the outbreaks each year until these climax. In the following year the population declines for some yet unknown reason (examples of ‘cycles’ or similar trends can be found in Mitali 2012 and Meshkova et al. 2017). Future research will have to explain this sudden decrease. In our case, it will thus be interesting to see if outbreaks remain equally severe in following years.

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# On the taxonomy of *Heterarthrus* (Hymenoptera, Tenthredinidae), with a review of the West Palaearctic species

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## Abstract

The sawfly genus *Heterarthrus* is naturally distributed in the Palaearctic, with a single described Oriental species. Their larvae mine in the leaves of trees and shrubs of Salicaceae, Betulaceae, and Sapindaceae (*Acer*). We here recognise twelve West Palaearctic species as valid, with the status of two additional nominal species group taxa in need of further study: *fruticicolum* Ermolenko, and *smithi* Ermolenko. A key to adults of the species occurring in the West Palaearctic is presented. Two new species are described: *Heterarthrus vikbergi* Liston, Mutanen & Viitasaari, **sp. nov.** from females and males reared from leaf-mines in *Populus balsamifera* collected in eastern Finland, and *Heterarthrus fiora* Liston, **sp. nov.** from females reared from *Acer pseudoplatanus*. The latter is a widespread European species, previously misidentified as *Heterarthrus aceris* (Kaltenbach, 1856). New junior subjective synonyms are *Phyllotoma aceris* Kaltenbach, 1856 of *Heterarthrus leucomela* (Klug, 1818), *H. aihinoensis* Haris, 2006 of *H. kamtchaticus* (Malaise, 1931) sp. rev., and *H. imbroensis* Schedl, 1981 of *H. wuestneii* (Konow, 1905). Lectotypes are designated for *Phyllotoma flavicollis* Gussakovskij, 1947, *P. kamtchatica* Malaise, 1931, and *Tenthredo ochropoda* Klug, 1818.

## Keywords

Sawflies, leaf-miners, new species, new synonyms, identification key

## Introduction

Twenty-two extant species of *Heterarthrus* were treated as valid by Taeger et al. (2010). These are naturally distributed only in the Old World: mainly in the Palearctic, with a single described Oriental species, *Heterarthrus birmanus* Malaise, 1961 (Malaise 1961). Two species, *Heterarthrus nemoratus* (Fallén, 1808) and *H. vagans* (Fallén, 1808), have been introduced to North America (Digweed et al. 2009, Humble 2010). Saini and Vasu (1999) wrote that six species occur in the Oriental Realm, citing Benson (1952) as the source of this information, but the latter work contains no such statement.

*Heterarthrus* larvae are leaf-miners of trees and shrubs of Salicaceae, Betulaceae, and Sapindaceae (*Acer*). Some species have been termed “pests” in various publications, particularly *H. nemoratus* and *H. ochropoda* (Klug, 1818). Although they have seldom been found in Europe to have a major impact on the health or growth of their hosts (Pschorn-Walcher 1982), heavy infestations in regions where they are invasive can cause significant increment losses (Peirson 1929). Also, at high population levels the mines render the affected trees unsightly, thus reducing their aesthetic value in urban environments and gardens (Digweed et al. 2009).

The examination of type specimens and other material, necessary for the identification of a species from Finland, here described as new to science, yielded some additional taxonomic results. These are presented, together with a key to the West Palearctic species.

## Material and methods

Morphological terminology follows Viitasari (2002). The following abbreviations are used for the names of institutions and collections:

<b>HNHM</b>	Hungarian Natural History Museum, Budapest, Hungary;
<b>MZLU</b>	Lunds universitet, Entomology Collection, Lund, Sweden;
<b>NHRS</b>	Swedish Museum of Natural History, Stockholm, Sweden;
<b>NMS</b>	National Museums of Scotland, Edinburgh, Scotland;
<b>SDEI</b>	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
<b>ZISP</b>	Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia;
<b>ZMHUB</b>	Naturkundemuseum, Berlin, Germany;
<b>ZMUO</b>	Zoological Museum, University of Oulu, Oulu, Finland.

Many specimens of *Heterarthrus* have been sequenced for the mitochondrial COI gene as part of the German Barcode of Life, and the Finnish Barcode of Life projects. The samples were sequenced at the Canadian Centre for DNA Barcoding (CCDB), Ontario, Canada, following the protocols described in deWaard et al. (2008). Partly, the 92 sequences used here were published in Schmidt et al. (2017), available at <http://www.barcodinglife.org>.

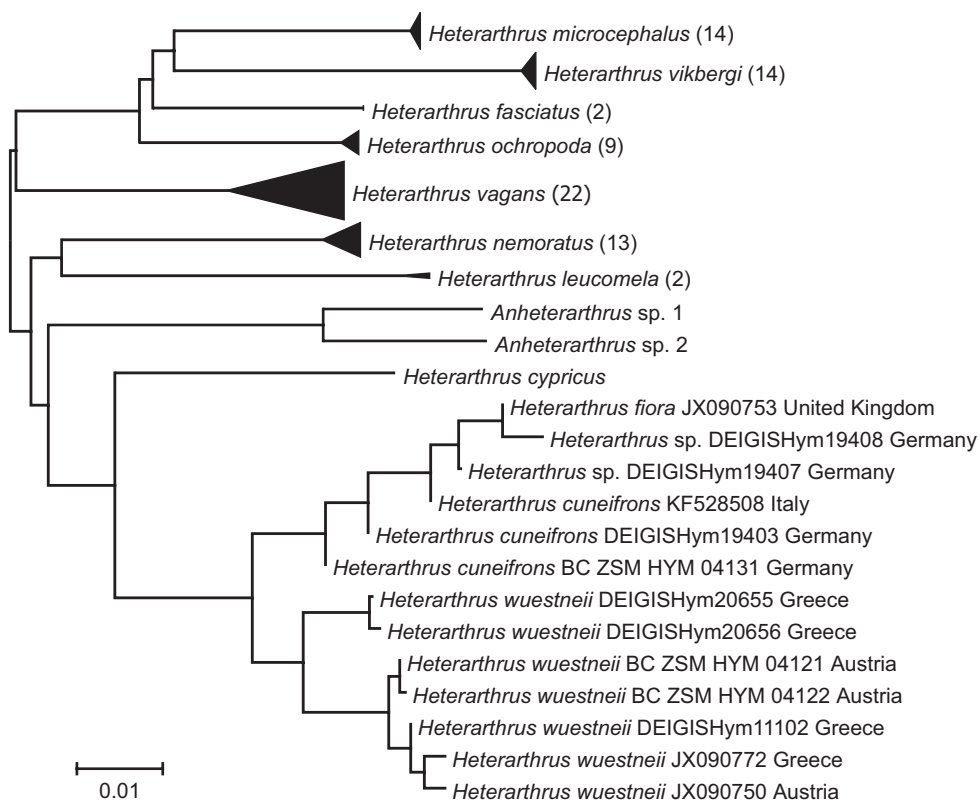


[ps://doi.org/10.5883/DS-RSYM](https://doi.org/10.5883/DS-RSYM), and Kirichenko et al. (2018), available at <https://doi.org/10.5883/DS-SALICLM>. The nucleotide divergences between the examined specimens and species were calculated with analytical tools in BOLD systems v. 4.0 (<http://www.boldsystems.org>) and to visualize the divergences between the species a neighbour-joining tree was constructed using the Kimura 2-parameter model in Mega 7.0.21 (Kumar et al. 2016) (Fig. 1). Details of voucher specimens, including voucher data and images, of newly published records are publicly available through the dataset DS-HETER at <http://www.boldsystems.org> and at <https://doi.org/10.5883/DS-HETER>.

## Results

### Character states

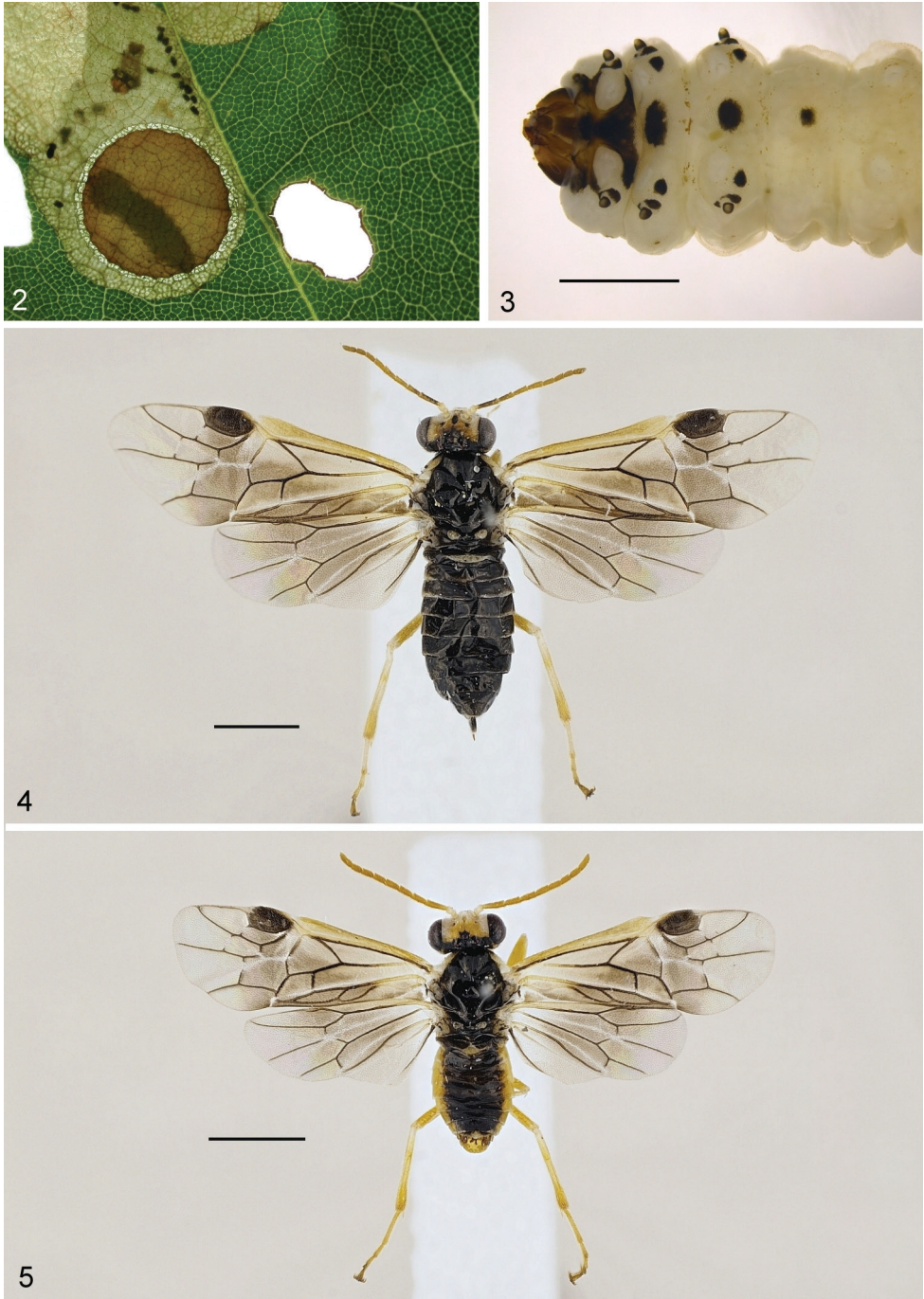
**The genus-level characters.** In the Palearctic, imagines of *Heterarthrus* are readily distinguished from the other genera of leaf-mining fenusine Blennocampinae by their fully developed fore wing anal cell, with vein 2A+3A complete for its entire length and joined to 1A by an oblique cross-vein (other genera: with vein 2A+3A basally incomplete and either curved up towards 1A to form a small basal loop, or more or less straight). Even in the field, they can usually be recognised by their distinctively shaped head: in dorsal view very wide in proportion to its length, with frontal grooves strongly developed, but frons seldom projecting beyond the anterior of the eyes. Other Fenusini have, in dorsal view, a more globose head: longer relative to its width, with shallower frontal grooves, and the frons usually projects beyond the eyes. Morphologically similar to *Heterarthrus* are *Anheterarthrus* Wei, Nie & Taeger, 2006 species, three of which have been described (Taeger et al. 2010). *Anheterarthrus* is a replacement name for *Anheterus* Wei, 1998 (primary homonym). They are so far known only from Chinese territories in the Oriental Realm. *Anheterarthrus* species differ from *Heterarthrus* species in: claw with weakly developed, obtuse basal lobe (*Heterarthrus* with large, acute basal lobe); inner spur of protibia simple (in *Heterarthrus* with bifid apex); metatibial spur longer than  $0.33 \times$  length of metabasitarsus (in *Heterarthrus* at most  $0.33 \times$  length of metabasitarsus); in dorsal view length of head of female behind eye longer than length of eye (in *Heterarthrus* length of head of female behind eye shorter than length of eye) (see Wei 1998; the holotypes of all three species were examined by Liston). We obtained COI barcode sequences for two unidentified *Anheterarthrus* specimens, possibly belonging to undescribed species, collected at high altitudes in Yunnan, China (Fig. 1). In a phylogenetic maximum likelihood analysis of available COI data for *Heterarthrus* and *Anheterarthrus*, and in trees rooted to either *Caliroa cerasi* (Linnaeus, 1758) (Blennocampinae: Caliroini) or *Fenusa pumila* Leach, 1817 (Blennocampinae: Fenusini), *Anheterarthrus* is deeply embedded within *Heterarthrus* (results not shown). Since the phylogenetic information content of COI at this phylogenetic level is low, the relationship of these genera requires further study.



**Figure 1.** Neighbour-Joining tree of West Palearctic *Heterarthrus* species based on the barcoding region of the mitochondrial COI gene of 92 specimens of *Heterarthrus* and *Anheterarthrus*. The height of the terminal triangles is proportional to the number of individuals (shown in parentheses), the depth of the triangles to variation within the lineage. For the species feeding on *Acer* spp. each specimen is shown as the species in this complex do not form clearly distinct clusters.

*Heterarthrus* larvae are distinguishable from those of other leaf-mining Palearctic sawflies, except some *Profenusa* species, by their strongly reduced thoracic legs: two-segmented in *Heterarthrus*, with claw minute or absent; three- to five-segmented and with well-developed claw in most other Fenusini, and five-segmented with well-developed claw in *Pseudodineura* (Nematinae) (Lorenz and Kraus 1957, Altenhofer 1980a).

*Heterarthrus* possesses one highly distinctive biological character, apparently not found in any other sawflies: the lens-shaped cocoon is spun inside the leaf and incorporates a circular portion of the upper leaf epidermis (Fig. 2). Other sawflies spin a more or less cylindrical cocoon with rounded ends, or make no cocoon at all, and other leaf-mining sawflies always leave the mine before making a cocoon. Altenhofer (1980b) described the construction of *Heterarthrus* cocoons in considerable detail, and distinguished two different behavioural groups: species in which the cocoon is detached from the leaf before leaf-fall takes place, and species in which the cocoon



**Figures 2–5.** **2** *Heterarthrus wuestneii* cocoon in mine on *Acer campestre*, Germany, Tübingen, 18.06.2004 (Photo J. Späth) **3** *H. vagans* mature larva, ventral, Sweden, Abisko National Park, 27.08.2018 **4** *H. vikbergi* sp. nov. holotype ♀ **5** *H. vikbergi* sp. nov. paratype ♂. Scale bar: 1mm.

remains within the leaf until after leaf-fall. Only the *Acer*-feeding species (with the exception of *H. leucomela*) have been thought to adopt the former strategy. According to Altenhofer (1980b), the different habits are possibly linked to the risk of desiccation during the cocoon stage, in which the species' phenology also plays a role. The cocoons of "detaching" species can be moved by rapid movements of their inhabitant, so that the cocoon eventually works its way into the upper layer of soil, where it is presumably less at risk of desiccation than in a leaf which is still on the tree. It is noteworthy that among the *Acer*-feeding species, the larva of *H. leucomela* takes much longer to develop than any other species, and so would not have to survive the hottest and driest part of the year in its cocoon which remains in the leaf. However, the differences in behaviour might have resulted from other types of selective pressure, such as predation.

**The species-level characters.** The external morphological characters used in our key to separate imagines at species level have mostly already been employed in keys or taxonomic treatments of *Heterarthrus* species (e.g. Benson 1952, Altenhofer and Zombori 1987), but the presence or absence of transverse grooves on the anterior part of the median mesoscutal lobes seems first to have been noticed by Hara (2012).

- Coloration. Previous keys to European *Heterarthrus* have all used abdomen colour as the entry character, e.g. Enslin 1914, Benson 1952, Muche 1977, Zhelochovtsev 1988. Although we also found that body colour in most species is stable within rather narrow limits, and that many colour characters are of high diagnostic value, this is not true for *H. vagans*, in which the coloration of the abdomen and head is highly variable. Specimens of this species, particularly males, therefore often key to the wrong species. Wing colour, particularly the colour of the fore wing costa relative to the pterostigma, and sometimes the colour of the wing membranes, is of high diagnostic value in some cases.
- Size of the compound eyes. Species with small eyes have a correspondingly long malar space. The exact points between which the malar space is to be measured are difficult to determine, so that some measurement error is inevitable. On the other hand, interspecific differences in this character are sometimes so great in this genus, that precise measurement is not essential. In some species, the size of the eyes and length of malar space differs significantly between the sexes.
- Shape of the head. In dorsal view the head behind the eyes shows interspecific variability in length and in how strongly it is narrowed towards the posterior. Neither character appears to be directly related to the size of the eyes. A significant practical problem with this character, is that even a slight alteration in viewing angle (i.e. rotation of the head around its transverse axis) greatly affects the perceived proportions (Figs 41, 42).
- Number of antennomeres, and length of antennae. The two characters are partly interdependent, although the presence / absence of a single antennomere in the same species is caused by subdivision, or lack thereof, of the apical flagellomere, and therefore does not affect antenna length. Although the number of antenno-



meres is quite variable in some species, there are sufficient interspecific differences between ranges to make the character useful.

- Median mesoscutal lobes. The transverse grooves on the anterior of the median mesoscutal lobes are strongly developed in all known *Acer*-feeding species except *H. leucomela*, in which they are weak and indistinct. All other West Palaearctic species have very weakly developed grooves, or apparently they are not developed at all, as in most *vagans* specimens.
- Hypopygium. Altenhofer and Zombori (1987) described and illustrated the female hypopygium of four of the *Acer*-feeding species. They indicated that large differences exist, to which they attributed high diagnostic value. We dissected several reared specimens and examined the hypopygia on microscope slides (Figs 22–24), but did not find the differences to be nearly so large as in their illustrations. The paired postero-median structures shown in the drawings by Altenhofer and Zombori (1987, figs 3–5) as discrete “prongs”, are in fact more or less weakly sclerotised bands on a transparent, membranous flap, which is extremely delicate and easily destroyed. The shape and extent of the sclerotised parts is very variable. Possibly of some diagnostic value is the outline of the posterior margin of the entire sternum, which in *H. cuneifrons* (Fig. 23) is medially more narrowly and deeply emarginate than in *H. flora* (Fig. 24) or *H. wuestneii* (Fig. 22), but this needs to be checked in a greater number of specimens. In any case, the differences which we observed are again much smaller than indicated by Altenhofer and Zombori (1987, figs 3–5). In pinned specimens, much apparent variability of the hypopygium, observed *in situ*, is presumably caused by distortion during drying.
- Valvulae 3. Particularly in dorsal view, the profile is often highly distinctive (see Figs 25–28), but in some individuals can be misleading, if the valvulae have been displaced during exposure of the lancet. The length and arrangement of setae on the valvulae are also sometimes helpful, and less prone to alteration by preparation.
- Lancet. The overall shape and structure of the lancet are rather uniform. Nevertheless, diagnostic differences in the shape of the saw teeth are apparent between all West Palaearctic species studied, except for *H. wuestneii* and *H. cuneifrons*.
- Penis valves. More so than the lancet, overall penis valve morphology is fairly uniform across the species studied. At the same time, an unusually high level of intraspecific variability occurs: compare, for example, the two penis valves of *imbro-sensis* (= *H. wuestneii*) illustrated by Schedl (1981), and valves of *H. wuestneii* and *H. cuneifrons* as Figs 69–73. It seems very likely that the markedly (compared with most other Tenthredinidae) three-dimensional valves distort greatly during preparation, and that differences in their angle of repose on the microscope slide exacerbate this. The level of apparent intraspecific variability is in our opinion so great, that examination of the penis valve is of little help in identifying specimens of this genus.
- Genetic data. COI mitochondrial barcodes appear to distinguish most species very clearly, with the exception of what might be called the *H. wuestneii* species complex, comprising *H. cuneifrons*, *H. flora* and *H. wuestneii* (Fig. 1). Thus, species whose imagines are rather easily identified using morphological characters, are also

those which are clearly identifiable by their barcodes. However, barcoding can be generally recommended as a method for the identification of *Heterarthrus* larvae (except the *H. wuestneii* complex), and particularly for the three species feeding on *Populus*, whose larvae are not adequately distinguished morphologically.

- Larvae. West Palaearctic *Heterarthrus* larvae exhibit rather minor interspecific morphological differences. Lorenz and Kraus (1957) describe mainly characters in the shape and arrangement of the dark, sclerotised body markings, and the structure of the anal prolegs. These characters, in conjunction with the identity of the host plant and features of the mine, enable the identification of most species (Altenhofer 1980a, Späth and Liston 2003). For accurate species level identification of larvae, barcoding is generally recommended (see above).

### Key to West Palaearctic *Heterarthrus* species (imagines)

- 1      **a** Fore wing costa entirely whitish, much paler than black or dark brown pterostigma (Figs 4, 5, 7, 9) ..... **2**
- **aa** Fore wing costa entirely translucent grey to almost black [or mainly dark with base and apex pale], and pterostigma similarly dark (Figs 29, 32, 37, 38) ..... **5**
- 2(1)   **a** ♀♀ ..... **3**
- **aa** ♂♂. [Antenna: 10–11 antennomeres; completely pale (Figs 5, 56). Upper mesepisternum extensively pale; abdomen laterally and ventrally completely pale (Figs 58, 61, 62)] ..... *Heterarthrus vikbergi* Liston, Mutanen & Viitasari, sp. nov. ♂
- 3(2)   **a** 10–11 antennomeres (Figs 9, 55); **b** Lateral mesoscutal lobe entirely black (Figs 4, 8); **c** Abdomen laterally with at most a series of posterior white flecks on terga (Figs 9, 51); **d** Mesepisternum mostly black, except at most for a small posterior whitish fleck (Figs 9, 51) ..... **4**
- **aa** 14–17 antennomeres (Fig. 7); **bb** Triangular white marking on interior of lateral mesoscutal lobe (Fig. 6); **cc** Abdomen laterally with contiguous broad white band (Fig. 7); **dd** Upper mesepisternum extensively pale (Fig. 7). [Male unknown. Femora entirely pale (Fig. 7). Body length 4.5–6.8 mm. Hosts: *Populus* spp.] ..... *Heterarthrus fasciatus* (Malaise, 1931) ♀
- 4(3)   **a** Femora basally black; basal halves of coxae black (Fig. 9); **b** Scape and pedicel mostly black (Fig. 9); **c** In dorsal view setae on valvulae 3 longer than combined width of valvulae, and very strongly curved (Fig. 13); **d** Upper outer orbits completely black (Fig. 8). [Male unknown. Body length 4.0–6.0 mm. Hosts: *Betula* species] ..... *Heterarthrus nemoratus* (Fallén, 1808) ♀
- **aa** Femora entirely pale; coxae nearly entirely pale except for extreme base (Fig. 51); **bb** Scape and pedicel whitish (Fig. 55); **cc** In dorsal view setae on valvulae 3 shorter than combined width of valvulae, and not especially curved (Fig. 14); **dd** Upper outer orbits partly pale (orange-brown) (Fig. 53). [Body

- length 3.0–4.0 mm. Host: *Populus balsamifera* L.] .....  
 ..... ***Heterarthrus vikbergi* Liston, Mutanen & Viitasaari, sp. nov.** ♀
- 5(1) **a** Basal abdominal terga dull, with dense sculpture (Fig. 15); **b** Median mesoscutal lobes with sculpture at least on anterior (Fig. 17); **c** Median mesoscutal lobes with clear transverse depressions on anterior (Fig. 17); **d** Abdomen mainly black, sometimes with margins of terga and / or sterna finely white **6**
- **aa** Basal abdominal terga shiny, more or less setose, but without sculpture (Fig. 16); **bb** Median mesoscutal lobes either with sculpture throughout, or entirely without sculpture (Fig. 18); **cc** Median mesoscutal lobes without, or with weak, transverse depressions on anterior (Fig. 18); **dd** Abdomen mainly black, sometimes with margins of terga and / or sterna finely white, or extensively yellow-red ..... **10**
- 6(5) **a** Lower face entirely pale, except for anterior tentorial pits (Fig. 10); **b** Pale parts of head and thorax bright yellow to reddish-yellow (Figs 11, 12); **c** Scape and pedicel sometimes entirely pale or extensively pale (Figs 11, 12) ..... **7**
- **aa** Lower face with at least some larger dark areas (Fig. 40); **bb** Pale parts of head and thorax whitish (Figs 39–41); **cc** Scape and pedicel mostly or entirely black (Fig. 41) ..... **8**
- 7(6) **a** Outer orbits black (Fig. 12); **b** Female: 11 antennomeres (Fig. 12). [Male: 11 antennomeres] [Host: *Acer platanoides* L.] .....  
 ..... ***Heterarthrus flavicollis* (Gussakovskij, 1947)** ♀♂
- **aa** Outer orbits yellow-orange (Fig. 11); **bb** Female: 12 antennomeres (Fig. 11). [Male: 11–13 antennomeres] [Host: *Acer obtusifolium* Sm.] .....  
 ..... ***Heterarthrus cypricus* Schedl, 2005** ♀♂
- 8(6) **a** ♀♀ ..... **9**
- **aa** ♂♂. [see taxon accounts] ..... ***Heterarthrus wuestneii* (Konow, 1905), *H. cuneifrons* Altenhofer & Zombori, 1987** ♂
- 9(8) **a** Serrulae of lancet longer, not so especially protruding (Figs 19, 20). [Tegula from completely white, to completely dark] ..... ***Heterarthrus wuestneii* (Konow, 1905), *H. cuneifrons* Altenhofer & Zombori, 1987** ♀
- **aa** Serrulae of lancet shorter, more protruding (Fig. 21). [Tegula interior dark, margin pale (Fig. 17)] [Host: *Acer pseudoplatanus* L. Male unknown] .....  
 ..... ***Heterarthrus flora* Liston, sp. nov.** ♀
- 10(5) **a** ♀♀ ..... **11**
- **aa** ♂♂ ..... **14**
- 11(10) **a** Tegula nearly entirely dark; **b** Abdominal terga and sterna partly yellow, or entirely black ..... **12**
- **aa** Tegula entirely pale; **bb** At least abdominal sterna mainly yellow; terga usually also extensively yellow. [Valvulae 3 in dorsal view wide relative to length; longest setae longer than combined width of valvulae, and very strongly curved (Fig. 25). Metafemur entirely yellow, except at most for extreme base. Metatibia mostly yellow. Body length 5.0–6.0 mm]. [Hosts: *Salix* species] ...  
 ..... ***Heterarthrus microcephalus* (Klug, 1818)** ♀

- 12(11)** **a** At most basal half of metafemur darkened (Fig. 30); **b** Metatrochanter and metatrochantellus mainly pale (Fig. 30); **c** Abdomen completely black (Figs 30, 31) to extensively pale (yellow) (Fig. 32)..... **13**
- **aa** Metafemur black except for extreme apex (whitish) (Fig. 29); **bb** Metatrochanter and metatrochantellus mainly black (Fig. 29); **cc** Abdomen completely black (Fig. 29). [Valvulae 3 in dorsal view rather narrow compared to length, subparallel-sided, with longest setae about as long as combined width of valvulae (Fig. 26). Body length 5.5–7.5 mm] [Hosts: *Acer pseudoplatanus* L. and *campestre* L.] ..... *Heterarthrus leucomela* (Klug, 1818) ♀
- 13(12)** **a** Valvulae 3 in dorsal view about as long as broad, more or less dilated apically; longest apical setae longer than combined width of valvulae and strongly curved (Fig. 27); **b** Fore wing membrane basally dark up to about pterostigma, and apically subhyaline (Fig. 31); **c** Median mesoscutellar lobes medioanteriorly finely and densely punctured (Fig. 33); **d** Abdomen black except for whitish hypopygium and sometimes posterior margins of sterna (Figs 30, 31). [Body length 5.0–6.5 mm] [Hosts: *Populus* species]..... *Heterarthrus ochropoda* (Klug, 1818) ♀
- **aa** Valvulae 3 in dorsal view much longer than broad, subparallel-sided; longest apical setae shorter than combined width of valvulae and only slightly curved (Fig. 28); **bb** Fore wing membrane more or less uniformly dark (Fig. 32); **cc** Median mesoscutellar lobes nearly entirely smooth (Fig. 18); **dd** Abdomen *usually* with at least sterna extensively yellow-orange. [Body length 3.0–6.0 mm] [Hosts: *Alnus* species] ..... *Heterarthrus vagans* (Fallén, 1808) ♀
- 14(10)** **a** Mesepisternum entirely black; **b** Pedicel mainly black, and *usually* also scape..... **15**
- **aa** Upper mesepisternum largely pale; **bb** Pedicel and scape pale..... **16**
- 15(14)** **a** Malar space shorter than diameter of median ocellus (Fig. 35); **b** Median mesoscutellar lobes without sculpture; **c** Abdomen often with extensively pale (yellow-orange) sterna, sometimes also terga. [Body length 2.5–4.5 mm. 11–12 antennomeres. Tegula *usually* dark, and metafemur yellow-red, at most darkened on basal half: except for 1♂ from Corsica]..... *Heterarthrus vagans* (Fallén, 1808) ♂
- **aa** Malar space about 3 × as long as diameter of median ocellus (Fig. 36); **bb** Median mesoscutellar lobes medioanteriorly finely sculptured. **cc** Abdomen mainly black, with narrow margins of terga and sterna white. [Body length 3.5–6.5 mm. 11–13 antennomeres. Tegula white. Metafemur nearly entirely black]..... *Heterarthrus leucomela* (Klug, 1818) ♂
- 16(14)** **a** Fore wing costa mainly dark with base and apex contrastingly pale (Fig. 37); **b** Median mesoscutellar lobes medioanteriorly finely sculptured; **c** Metafemur basally black. [Body length 4.0–5.0 mm. 12–14 antennomeres]..... *Heterarthrus ochropoda* (Klug, 1818) ♂
- **aa** Fore wing costa entirely dark (Fig. 38); **bb** Median mesoscutellar lobes without sculpture; **cc** Metafemur entirely pale. [Body length 3.5–4.5 mm. 14–15 antennomeres] ..... *Heterarthrus microcephalus* (Klug, 1818) ♂



## Taxon accounts and descriptions of new *Heterarthrus* species

### *Heterarthrus cuneifrons* Altenhofer & Zombori, 1987

*Heterarthrus cuneifrons* Altenhofer & Zombori, 1987: 193–195. Holotype ♀, in HNHM (examined). Type locality: Austria, Lower Austria, Neulengbach.

**Material examined.** AUSTRIA: Lower Austria: 3♀, 2♂ (holotype ♀ and paratypes of *cuneifrons*), Neulengbach, ex larvae *Acer pseudoplatanus*, 05.06.1985 (em. 1986), leg. E. Altenhofer (HNHM).

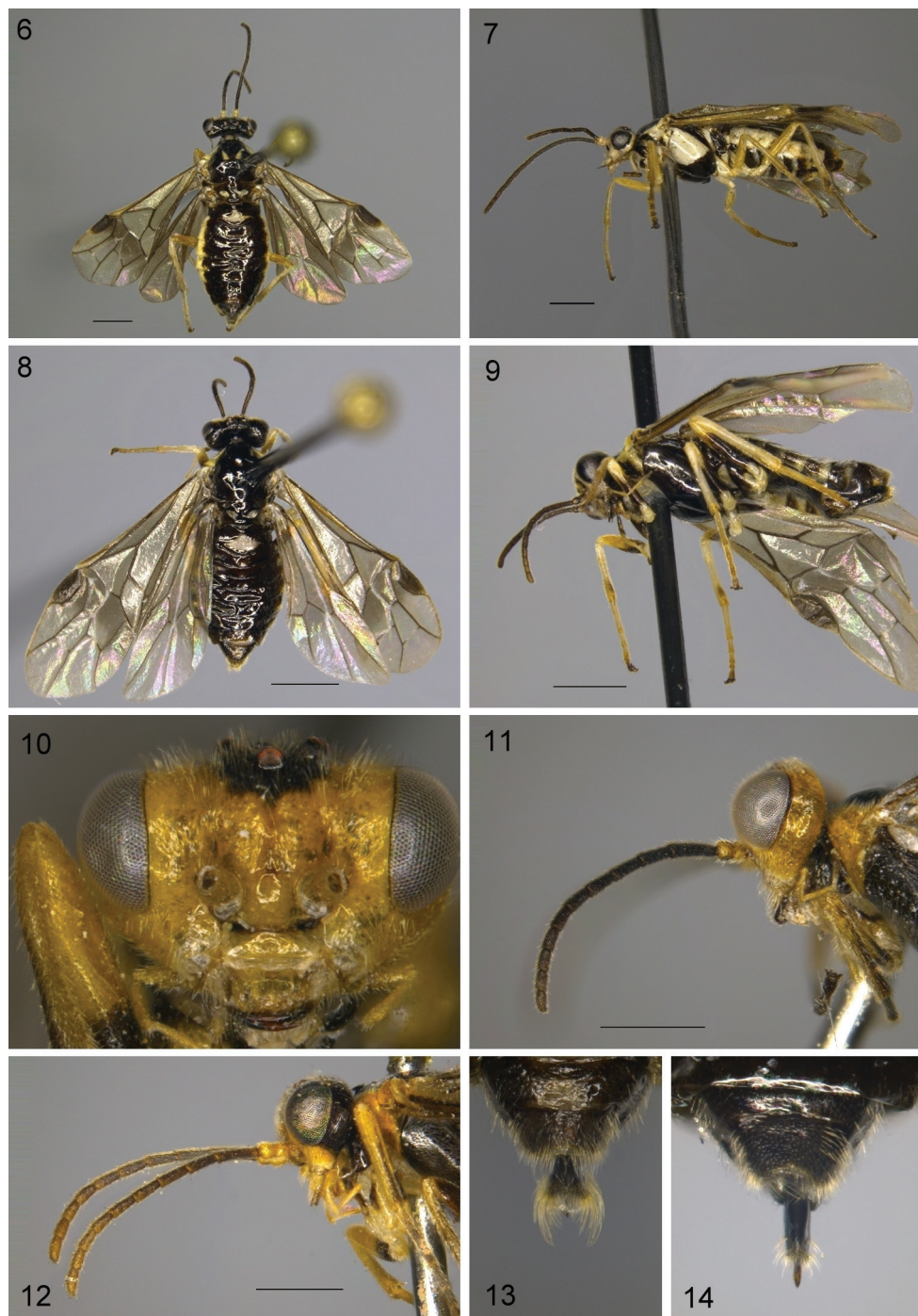
ITALY: South Tyrol: 2♀ (DEI-GISHym31979, 31984) 3♂ (DEI-GISHym31988), Salurn, reared *Acer pseudoplatanus*, 07.2000 (em. 04.2001), leg. K. Hellrigl (SDEI).

**Remarks.** Biologically, *H. cuneifrons* differs from the closely similar *H. wuestneii* and *fiora*, in that it oviposits into the interior of the leaf-blade, whereas the latter oviposit into the margin of the leaf. Furthermore, males of *H. cuneifrons* and *wuestneii* are frequent, but not known in *H. flora*. *Heterarthrus cuneifrons* and *fiora* have the same host plant species, *Acer pseudoplatanus*, whereas *H. wuestneii* uses different species of *Acer*.

Altenhofer and Zombori (1987) described several morphological characters which they considered to be useful for separating these three species:

- Shape of the sawteeth of the lancet (♀)
- Shape of the hypopygium (♀)
- Shape of the head behind the eyes, in dorsal view (♀)
- Colour of the malar space and tegula (♀)
- Penis valve morphology (♂)

We have already commented (under Character states) on the difficulty of comparing the shape of the head behind the eyes, and on not being able to find the differences in the hypopygium described by Altenhofer and Zombori (1987). In comparing characters between these three nominal species, we relied on reared material from named hosts. Although the sawteeth of *H. flora* are clearly more prominent than the flatter teeth of *H. cuneifrons* and *wuestneii* (Figs 19–21), we did not find any way of distinguishing the lancets of the latter two from each other. Nor is the colour of the malar space and tegula useful for separating *H. cuneifrons* and *wuestneii*, because of wide variability in *H. wuestneii*. The structure of the lower frons and interantennal area of *H. cuneifrons*, which according to Altenhofer and Zombori (1987) differs greatly from the other two species, appeared to us to be indistinguishable. Perhaps even more so than with head shape, slight changes in viewing angle and illumination have a major effect on the perception of the shape of the raised and depressed parts of the face. Initially, we thought that some correlation might exist between the proportions of the penis valve parts, and the segregates which Altenhofer and Zombori (1987) called *H. cuneifrons* and *healyi* (= *H. wuestneii*). An attempt to quantify this was made by measuring the distance (1) from the tip of the valvura to the highest point on the pseudoceps, and the distance (2) from the highest point on the pseudoceps to the tip of the pseudoceps



**Figures 6–14.6** *Heterarthrus fasciatus* ♀, DEI-GISHym19669 dorsal **7** *H. fasciatus* ♀, DEI-GISHym83889 lateral **8, 9** *H. nemoratus* ♀ DEI-GISHym83888; dorsal, lateral **10, 11** *H. cypricus* ♀ DEI-GISHym83890; head frontal, head and thorax lateral **12** *H. flavicollis* lectotype ♀, head and thorax lateral **13, 14** valvulae 3 dorsal: **13** *H. nemoratus* DEI-GISHym83888 **14** *H. vikbergi* sp. nov. DEI-GISHym83892. Scale bar: 1mm.

(see Fig. 69). The ratios of (1) divided by (2) were 1.32–1.87 in *H. cuneifrons* and 1.37–2.42 in *H. wuestneii* (Table 1).

For the moment, we conclude that *H. cuneifrons* is not distinguishable from *H. wuestneii* using morphological characters or COI barcodes. Nevertheless, the apparent biological differences make us reluctant to synonymise them. Further examination of their status should be made, including analyses of nuclear DNA.

**Host plants and biology.** *Acer pseudoplatanus* L. is the only recorded host. Oviposition in the middle of the leaf blade, not in the edge. Cocoon falls from leaf before the leaf falls. Univoltine.

**Distribution.** Central Europe, south to northern Italy, and in southern England (Taeger et al. 2006).

### *Heterarthrus cypricus* Schedl, 2005

*Heterarthrus cypricus* Schedl, 2005: 137–139. Holotype ♂, in Zoological Museum, University of Amsterdam (not examined). Type locality: Cyprus, Troodos Mountains. Liston and Späth (2008): description of female.

**Material examined.** CYPRUS: 11♀ (including DEI-GISHym83890), 30♂ (SDEI: see Liston and Späth 2008).

**Host plants and biology.** *Acer obtusifolium* Sm. (Schedl 2005, Liston and Späth 2008). Oviposition in the leaf-edge. Cocoon falls from leaf before the leaf falls. Univoltine.

**Distribution.** Cyprus (Schedl 2005, Liston and Späth 2008).

**Table 1.** Proportions of penis valves (see Fig. 69) of the lectotype (male) of *Heterarthrus wuestneii*, reared males of *cuneifrons* and *wuestneii*, and non-reared Greek males of *wuestneii* (1) distance from the tip of the valvura to the highest point on the pseudoceps, and (2) distance from the highest point on the pseudoceps to the distal tip of the pseudoceps (3) ratio of 1 divided by 2. Measured from paper prints of photographic images. Measurements at different scales between specimens.

Species name	Specimen identifier / source of image	Country	Host (reared specimens)	1	2	3 (ratio)
<i>H. wuestneii</i>	DEI-GISHym 3798 Lectotype	Denmark	–	70	51	1.37
	DEI-GISHym 31987	Austria	<i>Acer campestre</i>	92	40	2.30
	DEI-GISHym 31987	Austria	<i>Acer campestre</i>	92	38	2.42
	DEI-GISHym 31992	Austria	<i>Acer campestre</i>	84	45	1.86
	DEI-GISHym 31992	Austria	<i>Acer campestre</i>	82	45	1.82
	DEI-GISHym 31993	Austria	<i>Acer campestre</i>	99	58	1.71
	DEI-GISHym 31993	Austria	<i>Acer campestre</i>	76	49	1.55
	DEI-GISHym 31994	Greece, Peloponnese	–	93	53	1.75
	DEI-GISHym 31994	Greece, Peloponnese	–	87	58	1.50
	Schedl 1981, fig. 3a	Greece, Crete	–	48	29	1.66
	Schedl 1981, fig. 3b	Greece, Crete	–	46	31	1.48
	Liston 2007, fig. 4	Germany	<i>Acer monspessulanum</i>	58	30	1.93
	Altenhofer and Zombori 1987, fig. 11	?	<i>Acer campestre</i>	48	35	1.37
<i>H. cuneifrons</i>	DEI-GISHym 31988	Italy	<i>Acer pseudoplatanus</i>	86	65	1.32
	DEI-GISHym 31988	Italy	<i>Acer pseudoplatanus</i>	87	61	1.43
	Altenhofer and Zombori 1987, fig. 12	–	<i>Acer pseudoplatanus</i>	71	38	1.87

***Heterarthrus fasciatus* (Malaise, 1931)**

*Phyllotoma fasciata* Malaise, 1931: 28–29. Holotype ♀, in NHRS (not examined).

Type locality: Russia, Kamtchatka, Elisowo.

*Heterarthrus fasciatus*. Hara (2012): holotype of *Phyllotoma fasciata* examined, redescription, hosts, biology, first records from Japan.

**Material examined.** JAPAN: Hokkaido: 1 ♀ (DEI-GISHym19669), Bibai, Koshunai, 43.29950N, 141.84940E, reared *Populus suaveolens*, 16.08.2010 (emergence date), leg. H. Hara (SDEI).

RUSSIA: Tuva Republic: 1 ♀ (DEI-GISHym83889), East Sayan Mountains, Black Irkut, river shingle and rocks, 1691m, 30.06.2012, leg. W.-H. Liebig (SDEI).

**Host plants and biology.** Published host plant records are *Populus suaveolens* Fisch. ex Poiteau & A. Vilm. (Hara 2012, Kirichenko et al. 2018) and *P. nigra* L. (Hara 2012). According to the images associated with the reared specimen from the Moscow Region (see below), *Populus balsamifera* L. is also a host. No males have yet been found. The cocoon remains within the leaf. Possibly multivoltine (Hara 2012).

**Distribution.** The previously known distribution comprises Japan (Hokkaido: Hara 2012), Kamtchatka (Malaise 1931), and East Siberia (Buryat Republic: Sundukov 2017; Novosibirsk and Irkutsk Oblasts: Kirichenko et al. 2018). *Heterarthrus fasciatus* also occurs in European Russia, based on images by Andrej Ponomarev of a reared female. The specimen, misidentified as *H. ochropoda*, is illustrated on the website insecta.pro (insecta.pro/), accessed on 27.03.2019: photos [adult] #68936–68938, [leaf-mines] #68930–68935. The photos are labelled [transliterated]: Moskovskaja obl., Orehovo-Zuevskij r-n, pos. Topolinyj, na topole, with date for one image of leaf-mine 04.07.2014.

***Heterarthrus flora* Liston, sp. nov.**

<http://zoobank.org/9468A718-FEED-4DD8-AD6E-DE0F7BC6F359>

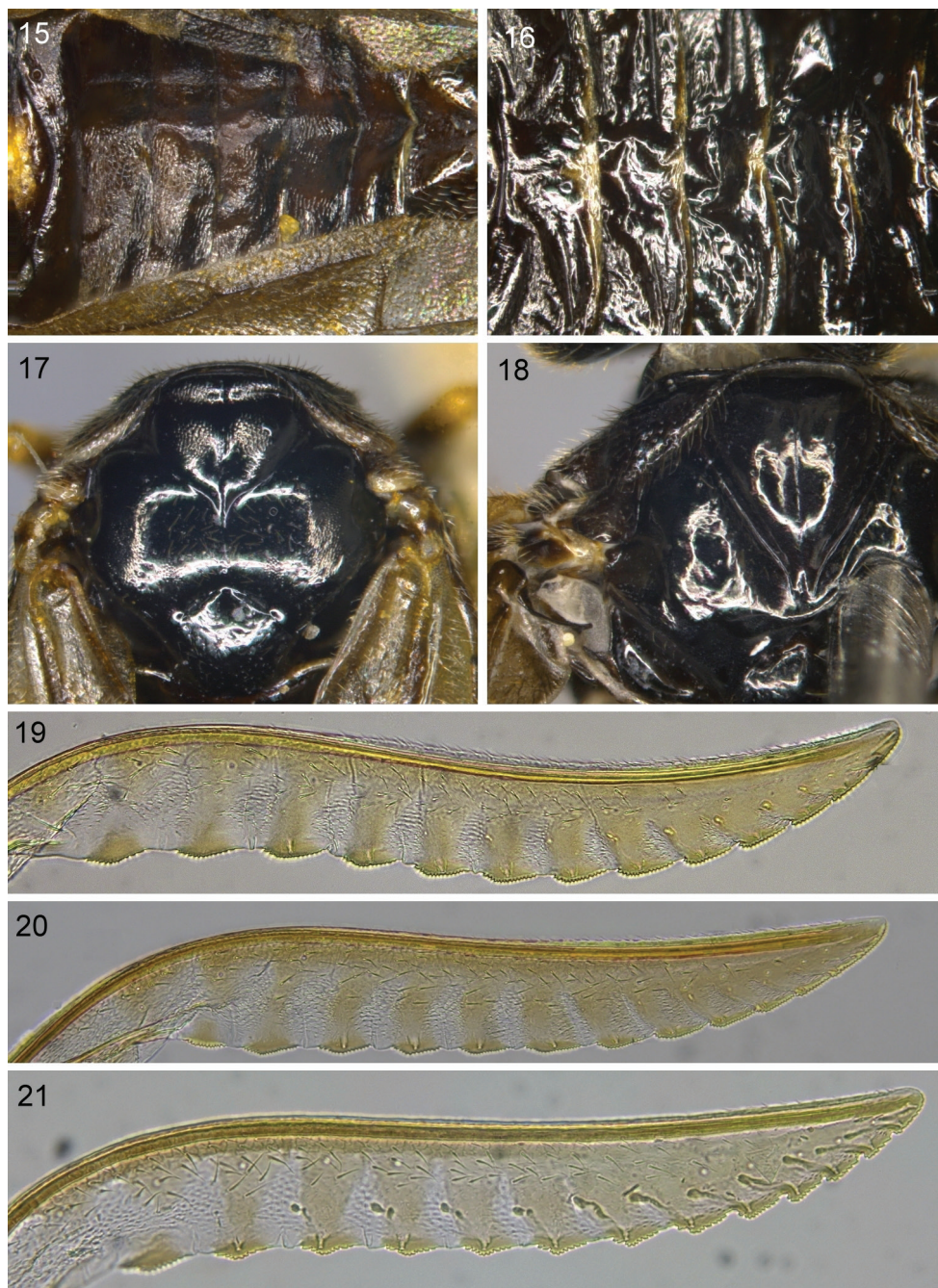
*Heterarthrus aceris*: misidentification. Altenhofer and Zombori 1987: 188–189, figs 2, 5, 6, 14, 15.

**Description. Female** (Figs 15, 17, 21, 24, 39–46).

**Body length.** 3.5–4.5 mm.

**Colour.** Shiny black and dirty white (Figs 39, 43). Head: black with the following parts pale: labrum, anterior and lateral parts of clypeus, malar space partly, a band along inner orbit about half way up the eye, a U-shaped fleck on supraclypeal area, labial palpomeres 2 and 3, maxillary palpomeres 3 and 4, base of mandible (Fig. 40). Antenna black with 2–3 apical flagellomeres more or less red-brown (Fig. 46). Thorax: black with the following parts white: very narrow lateral and hind margin of pronotum.





**Figures 15–21.** *Heterarthrus* ♀ **15, 16** basal abdominal terga: **15** *H. flora* sp. nov. holotype **16** *H. leucomela* DEI-GISHym31980 **17, 18** median mesoscutal lobes: **17** *H. flora* sp. nov. DEI-GISHym31976 **18** *H. vagans* DEI-GISHym83893 **19–21** lancets: **19** *H. wuestneii* DEI-GISHym31983 **20** *H. cuneifrons* DEI-GISHym31979 **21** *H. flora* sp. nov. DEI-GISHym31976.

tum, margins of tegula (Fig. 17). Legs black; pale are apices of coxae, femora, more or less anterior surfaces of all tibiae. Wings light brownish infusate, veins and pterostigma dark brown. Abdomen: black. Very narrow posterior edges of terga more or less white. Sterna entirely dark.

**Structure.** Head: with sparse, silvery pubescence. Frons divided in the middle by a longitudinal depression that is rather broad just below the median ocellus, becoming very narrow ventrally, and ending well before an imaginary line connecting the upper margins of the toruli (Fig. 40). Postocellar area short, medially 1.5 times as long as diameter of an ocellus (Figs 41, 42). Malar space  $0.29\text{--}0.33 \times$  as long as height of eye. Head in dorsal view strongly contracted behind eyes. Usually 12 antennomeres, rarely 11 (Fig. 46). Ratio of lengths of flagellomeres 1–8 approximately as: 100, 75, 71, 62, 51, 46, 42, 40. Thorax: Median mesoscutal lobes with straight transverse grooves at about 0.25 from anterior; coriaceous sculpture on anterior two-thirds (Fig. 17). Lateral lobes with lateral longitudinal coriaceous band. Mesoscutellum shiny with sparse, weak punctures, mesoscutellar appendage highly polished. Metascutellum transversally wrinkled. Mesopleuron covered with short pubescence and finely punctate, but pectus bare and shiny. Abdomen: Tergum 1 less densely sculptured than 2, and more distinctly shiny. Terga 2–7 with dense sculpture, but slightly shiny (Fig. 15). Apical terga with very weak sculpture basally, otherwise unsculptured. Hypopygium deeply emarginate medially (Fig. 24). Sawsheath in dorsal view subparallel-sided, with apex blunt (Fig. 44). Setae curved and directed backwards. Lancet with 13 teeth. 8–11 denticles per tooth (Fig. 21). Apical teeth, apart from last two, clearly separated from each other.

**Male.** Unknown: the species is exclusively parthenogenetic (Altenhofer and Zombori 1987). Mentions of males under the name *H. aceris* by, for example, Benson (1952) are based on misidentifications of other *Acer*-feeding *Heterarthrus* species (particularly *H. wuestneii* and *H. cuneifrons*) which resemble *H. flora*.

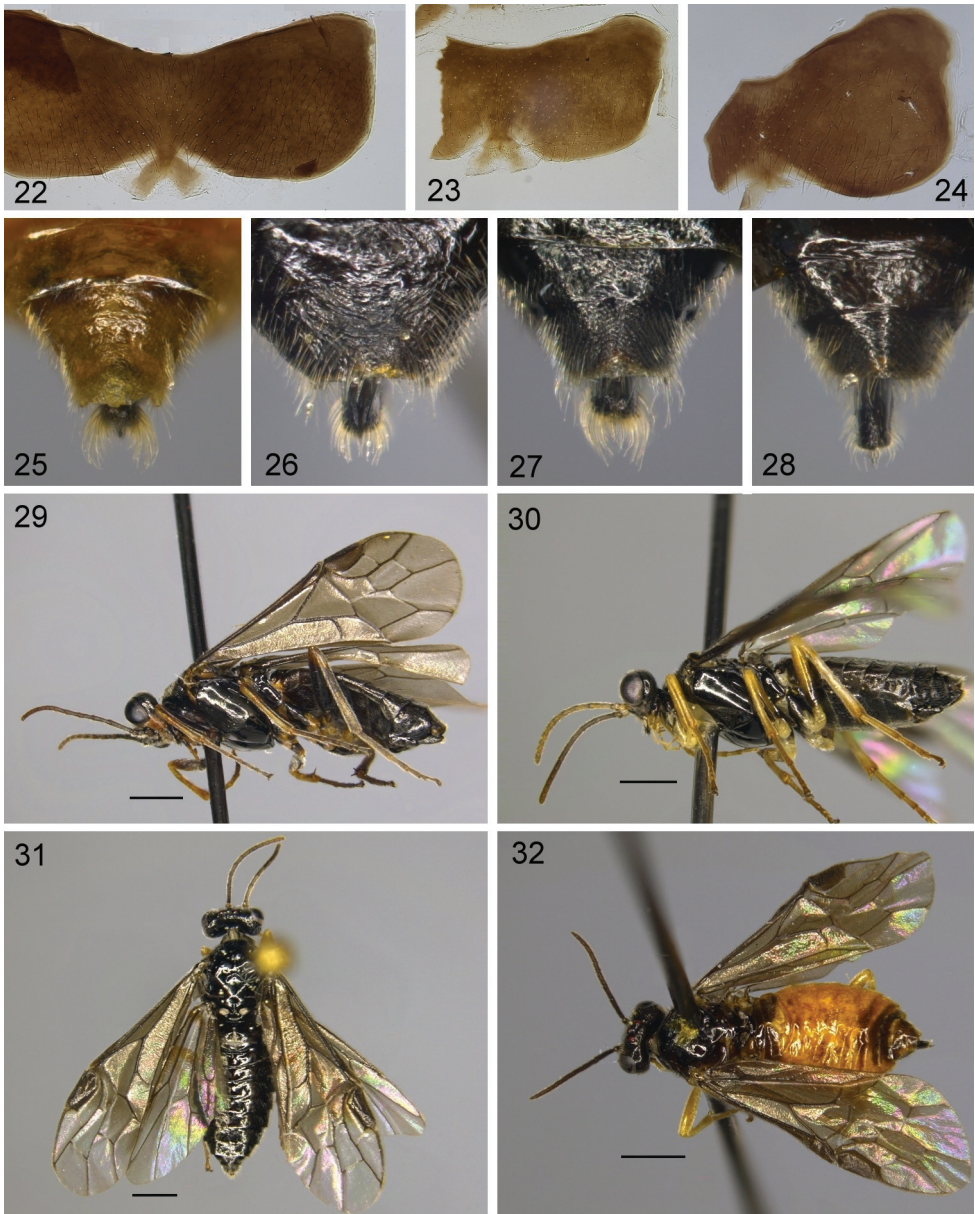
**Variability.** Examined specimens are all highly similar, with only very slight differences in the extent of the pale pattern on the head.

**Holotype:** Female. [Four printed labels:] Austria, Kammern, 12.v.1977, leg. Altenhofer. Larva ex *Acer pseudoplatanus* 8.vii.1976. *Heterarthrus aceris* Kalt. det. Zombori 1977. DEI-GISHym31975. Deposited in HNHM.

**Paratypes:** Austria: 7♀ (including DEI-GISHym31976, 31977, 83900) same collection data as holotype, but only one specimen with label indicating that it was determined as *H. aceris* by L. Zombori. Deposited in HNHM, except for one specimen, without head, in SDEI. Ireland: 1♀, Tyrone, Pomeroy, 27.5.1987, leg. A. Liston (NMS). Scotland: 1♀, Edinburgh, Corstorphine Hill, ovipositing in leaf edge of *Acer pseudoplatanus*, 1.6.1979, leg. A. Liston (NMS).

**Diagnosis.** Very similar to *Heterarthrus wuestneii* and *cuneifrons* in size, colour, and external morphology. The lancet teeth of *H. flora* are somewhat angular, each with 8–11 denticles, and the apical teeth, apart from last two, are clearly separated from each other (Fig. 21). The teeth of *H. wuestneii* and *H. cuneifrons* are more rounded, lower, with 12–15 smaller denticles, and the apical teeth are not clearly separated from each other (Figs 19, 20).





**Figures 22–32.** *Heterarthrus* **22–24** hypopygia: **22** *H. wuestneii* DEI-GISHym20656 **23** *H. cuneifrons* DEI-GISHym31984 **24** *H. flora* sp. nov. DEI-GISHym31976 **25–28** valvulae 3 dorsal: **25** *H. microcephalus* DEI-GISHym11397 **26** *H. leucomela* DEI-GISHym83894 **27** *H. ochropoda* DEI-GISHym83895 **28** *H. vagans* DEI-GISHym83896 **29** *H. leucomela* ♀ DEI-GISHym83894 lateral **30, 31** *H. ochropoda* ♀ DEI-GISHym83895 lateral, dorsal **32** *H. vagans* ♀ DEI-GISHym83897 dorsal. Scale bar: 1mm.

**Note.** the key by Altenhofer and Zombori (1987) states that *H. aceris* (= *flora*) has malar space and entire tegula dirty white, whereas in *H. cuneifrons* the malar space and basal half of tegula black. These characters are in our opinion not reliable: the tegula of

*H. flora* is normally dark on the interior and margined with white (as is in fact written in the description of *H. aceris* by Altenhofer and Zombori, 1987), and *H. cuneifrons* may also have a nearly completely pale malar space. According to Altenhofer and Zombori (1987) the head of *H. aceris* auct. is relatively narrowed behind the eyes, like *H. cuneifrons*, but we are not convinced that any interspecific differences in head shape exist.

**Etymology.** The name, to be treated as a noun, is derived from the Scottish Gaelic *fior-chrainn* (sycamore tree, *Acer pseudoplatanus* L.).

**Host plants and biology.** *Acer pseudoplatanus* L.: as recorded by Altenhofer and Zombori (1987), and Späth and Liston (2003). The leaf-mine develops from the edge of the leaf. The circular cocoon, constructed in part from the upper leaf epidermis, separates from the leaf and falls to the ground before the leaf falls from the tree. Univoltine.

**Distribution.** Probably widespread in Europe, but many records under the name *aceris* are unreliable because of nomenclatural and taxonomic confusion.

### *Heterarthrus flavicollis* (Gussakovskij, 1947)

*Phyllotoma flavicollis* Gussakovskij, 1947: 179–181. Syntypes 10♀, 9♂, in ZISP (Lectotype designated below). Type locality: Georgia, Tbilisi.

**Type material examined.** **Lectotype** *Phyllotoma flavicollis*, here designated: ♀ “DEI-GISHym4753”, “Tbilisi, 1946, iz min na klena, T. Zhizhilashvili”, “*Phyllotoma flavicollis*, sp. nov. ♀ (typus) Gussakovski det. 1947”, “Lectotype *Phyllotoma flavicollis* Gussakovskij, 1947 designated A. Liston 2010” (ZISP). Paralectotype ♂: “DEI-GISHym4754”, same data as lectotype (ZISP). Further paralectotypes in ZISP were not examined.

**Other material examined.** SWEDEN: 6♂, Skåne (see Liston 1993).

**Remarks.** Apart from its darker head, *H. flavicollis* is very similar to *H. cypricus*. The slightly different number of antennomeres given in the key as distinguishing these species needs to be checked in a greater number of specimens.

**Host plants and biology.** *Acer platanoides* L. (Altenhofer and Zombori 1987). Mine starts near leaf centre (Liston 1995). Cocoon falls from leaf before the leaf falls from tree. Univoltine.

**Distribution.** Central Europe, north to southern Sweden (Taeger et al. 2006), but rarely recorded, and occurrence apparently very local; Georgia (Gussakovskij 1947).

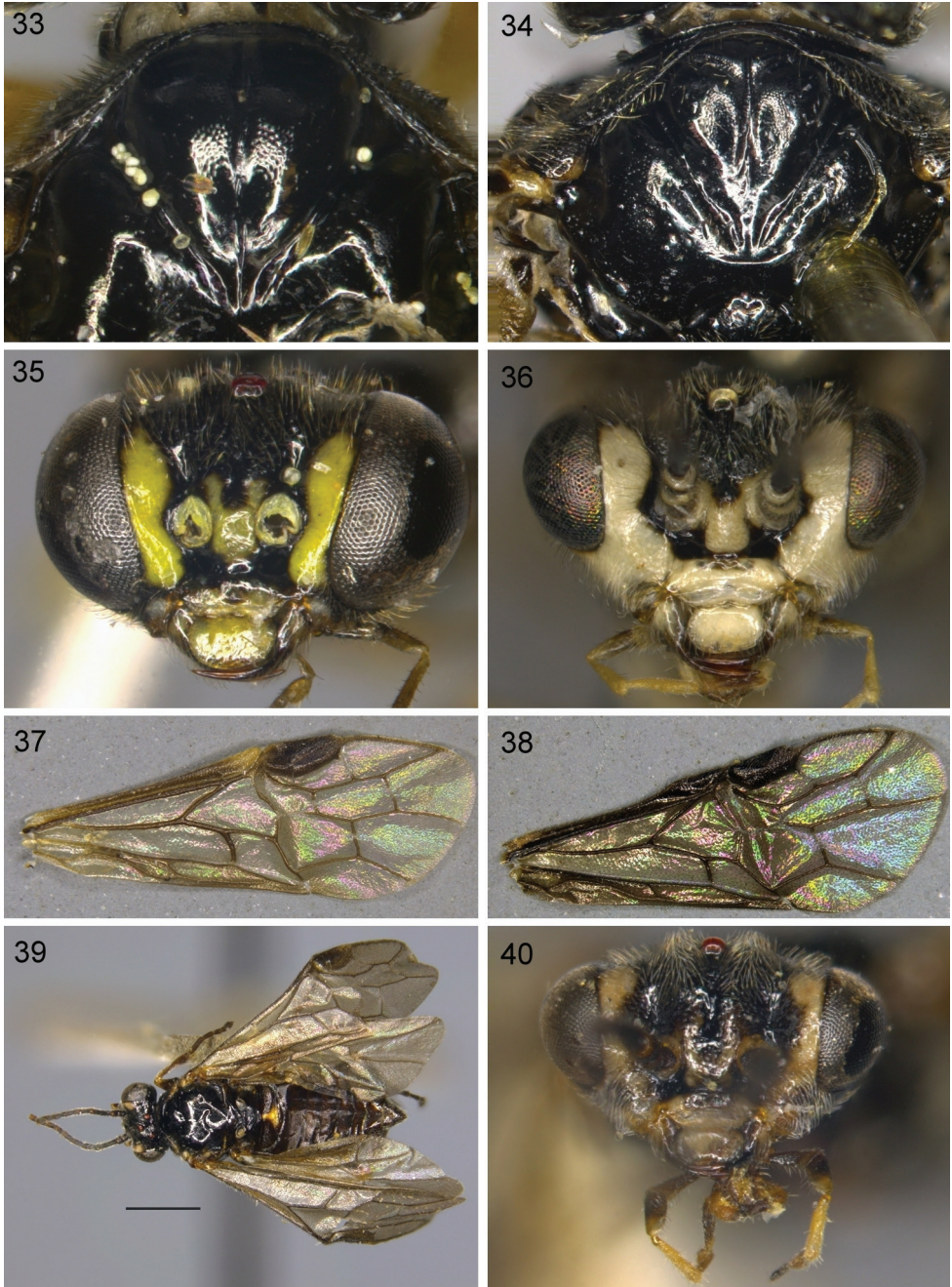
### *Heterarthrus fruticolum* Ermolenko, 1960

*Phyllotoma fruticolum* Ermolenko, 1957: 6–7, 9. Not available. Nomen nudum.

*Phyllotoma fruticolum* Ermolenko, 1959: 122, 128. Not available. Nomen nudum.

*Heterarthrus fruticolum* Ermolenko, 1960: 207–208. Holotype ♀, Schmalhausen Institute, Kiev (not examined). Type locality: Ukraine, Slavsky District, Khol'sk Pass.





**Figures 33–40.** *Heterarthrus* **33, 34** median mesoscutal lobes ♀: **33** *H. ochropoda* DEI-GISHym83895 **34** *H. leucomela* DEI-GISHym31980 **35, 36** head frontal ♂: **35** *H. vagans* DEI-GISHym11095 **36** *H. leucomela* DEI-GISHym31981 **37, 38** fore wing ♂: **37** *H. ochropoda* DEI-GISHym83898 **38** *H. microcephalus* DEI-GISHym83899 **39, 40** *H. fiona* sp. nov. ♀ holotype: **39** dorsal **40** head frontal. Scale bar: 1mm.

**Remarks.** The holotype was collected from *Alnus alnobetula* ssp. *alnobetula* (Ehrh.) K. Koch at subalpine levels in the Carpathians. Apart from the single type specimen, only Beneš (2013) has published a record of this taxon: also a single female, from the Giant Mountains (Czech Republic). Although compared in the original description only with *H. ochropoda*, the characters described for *H. fruticicolum* by Ermolenko much more closely resemble *H. vagans*. In fact, in the original description, the only difference seems to be the entirely black body of *H. fruticicolum*. Karel Beneš (personal communication to Liston by electronic mail, 2006) commented on the Czech specimen: “From Ermolenko’s description it is difficult to separate [*H. fruticicolum*] from dark forms of *H. vagans*. However, in *H. fruticicolum* the sheath viewed from above seems to be somewhat broader, slightly wider than hind metatarsus. Antennae are more slender and longer (in my specimen only 9 segments left), scape and pedicel black, apex ventrally piceous. Head width as antennomeres 3 to 8 combined. Segment 8 more than  $2 \times$  as long as wide, segment 6 more than  $3 \times$  as long as wide. Head pattern as in *H. vagans*, basal segments of maxillar palpi black, thorax including regulae, and abdomen completely black, only hypopygium brownish. Legs with coxae, trochanters and femora black, only very narrow posterior margins paler; tibiae blackish dorsally, brownish ventrally, tarsi brown. Pterostigma narrower, nearly  $3 \times$  as long as wide. Saw seems to have more flat teeth (I saw only several apical teeth protruding from the sheath). This female is very similar to *H. vagans*, [and] maybe only a subalpine race”. Two female specimens (SDEI) of *H. vagans* reared by E. Altenhofer from *Alnus alnobetula* ssp. *alnobetula* in subalpine Austria have an extensively pale abdomen, and do not otherwise differ from lowland *H. vagans* specimens reared from other *Alnus* species. The status of *H. fruticicolum* is in need of further study.

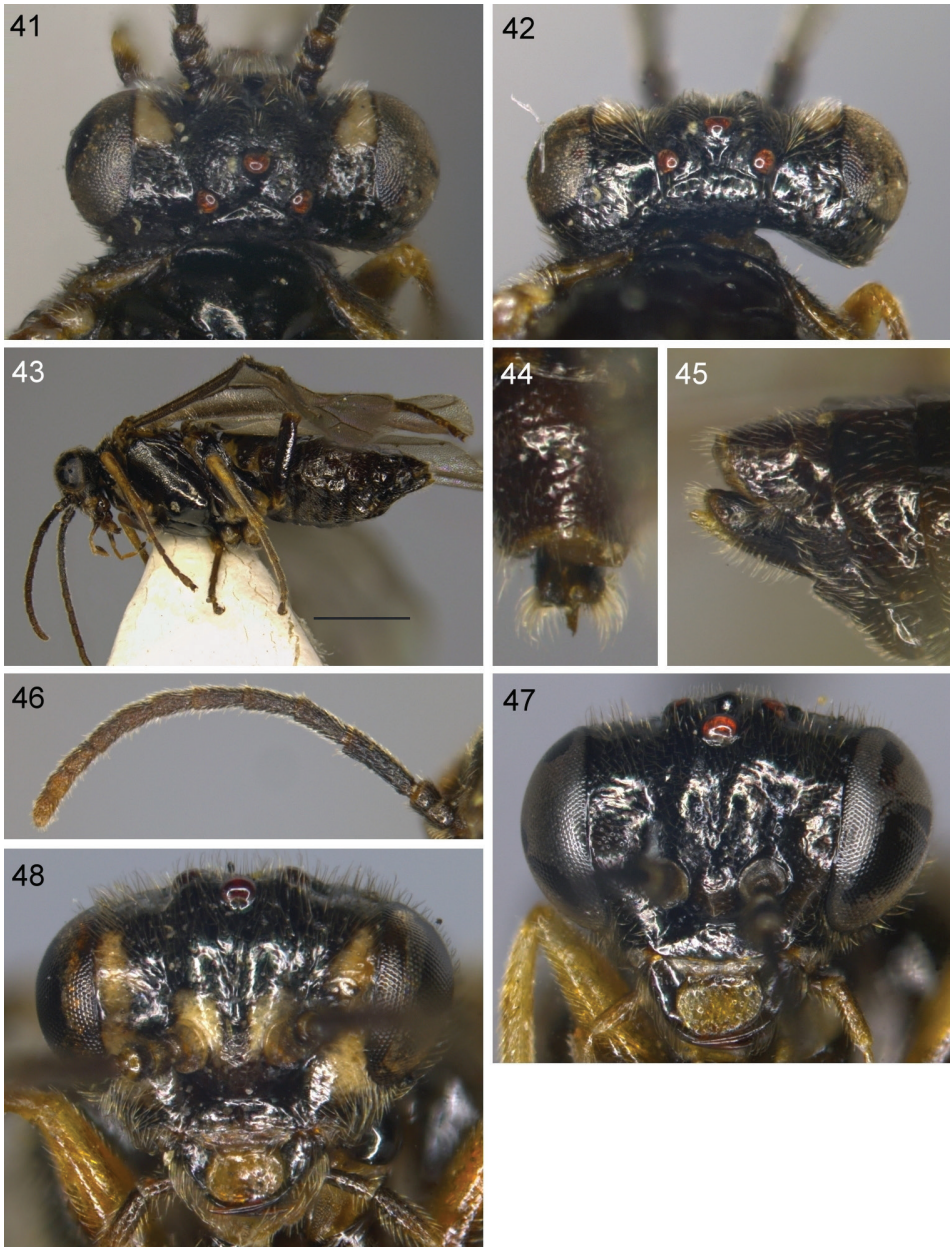
### ***Heterarthrus fumipennis* (Cameron, 1888), species inquirenda**

*Phyllotoma fumipennis* Cameron, 1888: 218. Syntypes assumed, sex not stated. Type locality: England, Norwich [“taken on alder by Mr. J. B. Bridgman”].

**Remarks.** It was thought possible that type material might be deposited in the Natural History Museum, London (BMNH), as are most other of Cameron’s sawfly types. Gavin Broad and Sue Ryder kindly looked there for possible type material in the Cameron Collection, but found no specimen or record of such which indicated that syntypes of *P. fumipennis* were ever deposited there. Tony Irwin informed Liston (electronic mail of 21.04.2008) that no specimen which can be regarded as a type is amongst the sawflies in the Bridgman Collection housed in the Castle Museum, Norwich, and a search by Darren Mann at the Oxford University Museum of Natural History, where a collection of sawflies bought from Cameron in 1884 is deposited, was also fruitless.

*Heterarthrus fumipennis* has often been treated as the valid name for a species attached to *Acer campestre*, with *Phyllotoma wuestneii* as a junior synonym (e.g. Enslin 1914, Berland 1947, Zirngiebl 1954, Dadurian 1962, Zombori 1982, Zhelochovtsev 1988), but also as a synonym of *Heterarthrus aceris* (McLachlan, 1867) (Konow 1905b)





**Figures 41–48.** *Heterarthrus* 41–46 *H. flora* ♀: 41, 42 head dorsal at different viewing angles, holotype 43 DEI-GISHym83900 lateral 44, 45 DEI-GISHym83900 sawsheath dorsal, lateral 46 DEI-GISHym31977 antenna 47, 48 head frontal ♀: 47 *H. vagans* DEI-GISHym11091 48 *H. kamtschaticus* (*H. aihinoensis* holotype). Scale bar: 1mm.

or *H. aceris* (Kaltenbach, 1856) (e.g. Lacourt 1999, Taeger et al. 2010). However, as far as we know, none of these authors examined type material of *P. fumipennis*, and the original description does not include any characters which will unequivocally identify

it. As occurs repeatedly in descriptions of “new” sawfly species by Cameron, his failure to indicate the sex of his type specimen(s) makes interpretation very difficult. The comment that the specimen (or specimens) was collected from alder [*Alnus*] initially tempts one to think that he could have had before him a specimen of *H. vagans*, but his description of the tegulae as white, and the femora and tibiae extensively dark, contradict this interpretation. The wing colour mentioned by Cameron (1888) was considered by Konow (1905a) and Enslin (1914) to be of value in separating what at that time were presumed to be two European species with similar morphology feeding on maples, but according to present knowledge (Altenhofer and Zombori 1987), wing colour cannot be used to separate any of the now three species of this group known in the British Isles (*H. cuneifrons*, *H. flora*, and *H. wuestneii*). The apparently completely white tegulae described for *H. fumipennis* would fit either *H. wuestneii* or *cuneifrons*, but not *flora*. Accordingly, it seems best at present to treat *Phyllotoma fumipennis* as a species inquirenda.

### ***Heterarthrus kamtschaticus* (Malaise, 1931), species revocata**

*Phyllotoma kamtschatica* Malaise, 1931: 29. Syntypes ♀, in NHRS (lectotype designated below). Type locality: Russia, Kamtschatka, Elisowo.

*Heterarthrus kamtschaticus*. Lindqvist (1969): synonymised with *H. vagans* (Fallén, 1808). Ermolenko (1981): treated as valid species, recorded from Kuriles, associated with *Alnus*. Taeger et al. (2010): Listed as synonym of *H. vagans* (Fallén, 1808)

*Heterarthrus aihinoensis* Haris, 2006: 193. Holotype ♀, in HNHM (examined). Type locality: Russia, Kuriles, Aihino. Syn. nov.

**Type material examined.** *Lectotype* *Phyllotoma kamtschatica*, here designated: ♀ “Kamtschatka Malaise”, “E”, “Typus”, “NHRS-HEVA000001264”, “Syntype *Phyllotoma kamtschatica* Malaise, 1931 teste Taeger & Vardal 2011” (NHRS). Paralectotype: ♀, labels as for lectotype, but: “Paratypus”, “NHRS-HEVA000001265” (NHRS).

**Holotype** *Heterarthrus aihinoensis*: ♀ “Szovjetunió, Kuril-szigetek, Kunasir-sziget, Aihino”, 30.vii.1973. leg. Ermolenko”, “Holotypus *Heterarthrus aihinoensis* sp. nov. Haris 2006”, “Hungarian Natural History Museum Hymenoptera Coll. Budapest”, “DEI-GISHym31973” (HNHM).

**Remarks.** The coloration of female *Heterarthrus vagans* is highly variable (see under that name). Lindqvist (1969) examined the syntypes of *P. kamtschatica* and concluded that these are indistinguishable from very dark-coloured females of *H. vagans*. He also observed that nearly completely dark-bodied female *H. vagans* occur in Finland, and wrote that [translated from German] “While the abdomen of the nominate form of *H. vagans* is completely or mostly reddish-yellow, in *H. kamtschaticus* this is so extensively black, that at most the base of the venter is slightly pale. All other body parts as well as the wings are similarly darker than in the nominate form”. He also examined the lancets of the *P. kamtschatica* types, and found no differences to *H. vagans*. We disagree with parts of his statement: The *P. kamtschatica* types show no trace of pale colour on



the basal abdominal sterna, the head has a pale pattern which is as extensive as any examined *H. vagans* females, but slightly differently distributed (Fig. 48), the fore wing is basally smoky up to about the level of the pterostigma and less so at the apex (whereas the fore wing of *vagans* is uniformly smoky), and the tegulae are paler than the rest of thorax (always black in examined *H. vagans*, apart from a specimen from Corsica). Perhaps more significantly, female *H. kamtchaticus* have smaller eyes than *H. vagans*: malar space of *H. kamtchaticus*  $0.27\text{--}0.33 \times$  height of eye, in *vagans*  $0.18\text{--}0.22 \times$  height of eye. Furthermore, unlike Lindqvist, we did observe differences between the shape of the lancet sawteeth: in *H. kamtchaticus* they are longer in proportion to their height, the denticles more numerous, with basal denticle smaller and more acute, and the basal and median teeth are less widely separated from each other (compare Fig. 50 with Fig. 49). These differences are significantly greater than the range of infraspecific variability normally encountered in *Heterarthrus*. Probably, these two taxa are indeed closely related. Genetic data, currently lacking for *H. kamtchaticus*, should help to clarify their relationship, but for the present, it seems preferable to treat them as separate species.

Perhaps because its coloration is somewhat similar to female *H. ochropoda*, Haris (2006) compared *H. aihinoensis* to that species, rather than *H. vagans*, although the sawsheath shape of the *H. aihinoensis* holotype strongly resembles the latter. We found only one difference between the *H. aihinoensis* holotype and the *P. kamtchatica* types: the tegulae of the former are slightly paler. This single difference does not seem likely to be significant. Even the colour pattern of their faces is very similar. Accordingly, we propose the synonymy of *H. aihinoensis* and *H. kamtchaticus*.

**Host plants and biology.** Associated by Ermolenko (1981) with an *Alnus* species, because adults were collected from this.

**Distribution.** Kamtchatka (Malaise 1931), Kuriles (Ermolenko 1981), and possibly north-east China (Wei 1998).

### *Heterarthrus leucomela* (Klug, 1818)

*Tenthredo* (*Emphytus*) *leucomela* Klug, 1818: 274. Holotype ♀, in ZMHUB (examined). Type locality: Silesia (now Poland). Note: the name is a noun and therefore not declinable.

*Heterarthrus leucomelus* (Klug, 1814), misspelling. Altenhofer and Zombori (1987: 186–188): description of adult, larva and biology.

*Phyllotoma aceris* Kaltenbach, 1856: 257–258. Syntypes (sex not stated), larva, host *Acer pseudoplatanus*. Type material apparently lost. Type locality not stated (but presumably Germany, according to title of the work). New synonym.

**Type material examined.** Holotype *Tenthredo* (*Emphytus*) *leucomela*: ♀ “Silesia m. Kl.”, “Leucomela Kl”, “14138”, “GBIF-GISHym2425” (ZMHUB).

**Other material examined.** AUSTRIA: Upper Austria: 8♀ 3♂, Linz, larva ex *Acer pseudoplatanus*, 08.1976 (em. 13.5.1977), leg. E. Altenhofer (HNHM). 4♀ 5♂, Linz, larva ex *Acer campestre*, 12.09.1976 (em. 7.5.1977), leg. E. Altenhofer (HNHM). Salz-



**Figures 49–54.** *Heterarthrus* **49, 50** lancets: **49** *H. vagans* DEI-GISHym31974 **50** *H. kamtschaticus* HEVA-1264 **51–54** *H. vikbergi* sp. nov. ♀ DEI-GISHym83572: **51** lateral **52** head frontal **53** head dorsal **54** abdomen apex ventral. Scale bar: 1mm.

burg: 2♀, Straßwalchen, larva ex *Acer campestre*, 25.08.1977 (em. 3.05.1978), leg. E. Altenhofer (HNHM). 1♂ (DEI-GISHym31981), Puch bei Hallein, reared *Acer pseudoplatanus*, 02.08.1975, leg. E. Altenhofer (SDEI). Lower Austria: 1♀, Riedenberg, reared ex *Acer campestre*, 08.08.1975 (em. 24.5.1976), leg. E. Altenhofer (private collection M. Viitasaari). 1♀ (DEI-GISHym31980), Etzen, reared ex *Acer pseudoplatanus*, 02.09.1988 (em. 25.04.1989), leg. E. Altenhofer (SDEI).

GERMANY: Bavaria: 1♀ (DEI-GISHym19032), Dingolfing, Alm, ovipositing in *A. pseudoplatanus* leaf, 15.05.2004, leg. A. Liston (SDEI). Thuringia: 1♀ (DEI-GISHym83894), Luisenthal, 24.05.1986, leg. L. Behne (SDEI).

**Remarks.** The fate of the type material of *Phyllotoma aceris* Kaltenbach, 1856 is not known. According to Horn et al. (1990), the Kaltenbach Collection was auctioned in London in 1880. The description by Kaltenbach (1856) has in the past been misinterpreted, or overlooked, partly because it appeared in a rare journal which is not available in most libraries. By contrast, the book with the same title, by Kaltenbach (1874), was a widely available and popular work of reference. In Kaltenbach (1874), *P. aceris* is still referred to as a new species. As a result of this, subsequent taxonomists who were unaware of Kaltenbach's 1856 description regarded *Phyllotoma aceris* Kaltenbach, 1874 as a junior homonym (and usually also a synonym) of *Phyllotoma aceris* McLachlan, 1867. All authors of this period assumed that only a single species of *Heterarthrus* occurred on maples. It is important to note that whilst the description of the adult is exactly the same in both Kaltenbach publications, the description of the early stages is more extensive and the biology is described significantly differently in the work of 1874. Either Kaltenbach (1874) had found more material during the intervening years, but failed to recognize that this new material belonged to a species of *Acer*-feeding *Heterarthrus* different to the one which he originally described, or perhaps he revised his text in the light of the observations published by Healy (1867) on the biology of *P. aceris* McLachlan. Altenhofer and Zombori (1987) were sure that the latter explanation is correct. Whatever the reason for the differences between the two Kaltenbach descriptions, only the first description published in 1856 is relevant when considering the identity of *P. aceris* Kaltenbach. The text in Kaltenbach (1856) reads (translated from German):

"*Phyllotoma* (*Emphytus* not *Ericampa* as on p. 176) *Aceris* m. The yellowish larva lives in July and August as a mini-caterpillar in the leaves of sycamore (*Acer pseudoplatanus* [sic!]). It eats out large areas between the two skins of the leaf, which become noticeable as wan [falbe (sic!), probably typographical error for "fahle"], sickly patches on the leaf upperside. To metamorphose, it spins within the mine a circular, flattened cocoon (similar to that of *Tischeria complanella* in oak leaves, and exactly as in *Phyllotoma melanopygus* Klg. and *Phyl. salicis* m. living respectively in the leaves of alder and willow), overwinters as a larva therein and first pupates in the following spring. I obtained the wasp as early as the beginning of May by rearing indoors.

Wasp: black, smooth; antennae 12-membered, towards the apex ringed with brownish; palps whitish, apical member of labial palps black, the thicker basal mem-



bers of the maxillary palps ringed with black; area of mouth, the inner edge of the green-violet eyes and the tegulae bone-white. Legs black; all knees and the inner sides of the four front legs dirty yellow-white; tarsi brownish to brown. Wings uniformly dark smoky. Length 1.5–2” [approx. 3.4–4.5 mm. 1 line = approx. 2.25 mm]”.

Most significantly, the cocoon of *P. aceris* is stated by Kaltenbach (1856) to remain within the leaf, as is indeed the case with *H. vagans* (Fallén) (= *P. melanopygus* (Klug, 1818)) and *H. microcephalus* (Klug) (= *P. salicis* Kaltenbach, 1856). In the European *Acer*-feeding *Heterarthrus*, cocoons of all species except *H. leucomela* separate from the leaf and fall to the ground soon after they are formed (Altenhofer and Zombori 1987). Healy (1867) describes the latter behaviour for *P. aceris* McLachlan. The relatively late date of collection of Kaltenbach’s larvae only fits the slow larval development recorded for *H. leucomela* by Altenhofer and Zombori (1987) and Späth and Liston (2003). All other maple-feeding *Heterarthrus* species finish feeding earlier in the year. Furthermore, only the male of *H. leucomela* has the pattern of black and white colour on the palps (see Altenhofer and Zombori 1987) which Kaltenbach describes for *P. aceris*. The relatively small body size given by Kaltenbach (females of *H. leucomela* are conspicuously larger than other species of *aceris* group) also indicates that the syntypes of *P. aceris* were males: Altenhofer and Zombori (1987: 187) give a body length of 3.5–5.5 mm for male *H. leucomela* and 5.5–7.0 mm for females.

**Host plants and biology.** *Acer campestre* L. and *A. pseudoplatanus* L. (Altenhofer and Zombori 1987). Oviposition in the leaf edge. The cocoon remains within the leaf. Univoltine.

**Distribution.** Central and south-east Europe (Taeger et al. 2006).

### *Heterarthrus microcephalus* (Klug, 1818)

*Tenthredo* (*Emphytus*) *microcephala* Klug, 1818: 274–275. Holotype ♀, in ZMHUB (examined). Type locality: Berlin area [“in hiesiger Gegend”].

*Phyllotoma salicis* Kaltenbach, 1856: 257. Syntypes, cocoons. Type locality not stated (but presumably Germany, according to title of the work). This name is available according to the International Code of Zoological Nomenclature, Article 12 (Names published before 1931): Kaltenbach’s short description of the cocoon constitutes an indication (Article 12.2.8.). New synonym.

**Type material examined.** Holotype *Tenthredo* (*Emphytus*) *microcephala*: ♀ “Microcephala Kl.”, “M. Kl.”, “14139”, GBIF-GISHym2426” (ZMHUB).

**Other material examined.** FINLAND: 1♀, Kiiminki, 65.10980N, 25.84960E, 7.8.2016, leg. M. Mutanen (ZMUO.029395). 1♀, Linnanmaa, 65.06390N, 25.48070E, 08.08.2016, leg. M. Mutanen (ZMUO.029396).

FRANCE: Ariège: 1♀ (DEI-GISHym11397), Aulus-les-Bains, 08.07.2009, leg. H. Savina (private coll. Savina).

GERMANY: Berlin: 1♂, Berlin, April 1920, leg. M. Hering, (ZMHUB). Brandenburg: 1♂, Königs Wusterhausen, leg. Bischoff (ZMHUB). 1♀, Prötzel, 10.06.2006, leg. Liston



(SDEI). 1♀, Waldsiedersdorf, 25.05.2006, leg. Liston (SDEI). Thuringia: 1♀, Apfelstädt, NSG Kleiner See, 27.05.1999, leg. M. Hartmann (Naturkundemuseum Erfurt).

NORWAY: 1♂, Finnmark, Varanger Peninsula, Båtsfjord, 70.631N, 29.696E, 27.06.2019, leg. Liston & Prous (SDEI).

SWEDEN: Öland: 1♀, Ölandsleden, 56.523N, 16.571E, 28.05.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Västergötland: 1♂, Sörhamn, 19.06.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Dalarna: 1♀ 1♂ (DEI-GISHym83899), Öje, 11.06.2013, leg. Liston, M. Prous & A. Taeger (SDEI). Jämtland: 1♂, Sveg 24 km E, 18.06.2014, leg. Liston & Prous (SDEI). Torne Lappmark: 1♀, Torneträsk Station, 68.215N, 19.740E, 21.06.2012, leg. Liston & A. Taeger (SDEI).

**Remarks.** Kaltenbach's (1856) new name, *Phyllotoma salicis*, has apparently been overlooked until now, and was not mentioned in Taeger et al. (2010), or earlier catalogues. The name appears only once in Kaltenbach's series of papers which catalogued the host associations of phytophagous insects in Germany, in the context of the description of *Phyllotoma aceris* Kaltenbach, 1856 (see under *Heterarthrus leucomela*). Later, Kaltenbach apparently realised that his *P. salicis* had already been described, because he refers to the taxon as *Phyllotoma microcephala* Klug (Kaltenbach 1869: 129).

**Host plants and biology.** numerous *Salix* species (e.g. Buhr 1941). Oviposition in the tip of the leaf. Bivoltine; the second generation more abundant (Altenhofer 2003).

**Distribution.** Widely distributed in Europe (Taeger et al. 2006), to north of the Arctic circle, the British Isles, and Iberian Peninsula; Transpalaearctic through Armenia, Kyrgystan, Kasachstan, West and East Siberia to the Russian Far East (Sundukov 2017).

### *Heterarthrus nemoratus* (Fallén, 1808)

*Hylotoma nemorata* Fallén, 1808: 47. Syntypes ♀, possibly in MZLU. Type locality: Västergötland [Sweden, Västergötland].

*Heterarthrus nemoratus*. Taeger et al. (2010: 373): complete synonymy listed.

**Material examined.** ESTONIA: 1♀, Vasavere 1.5km E, 04.06.2015, leg. Liston, Prous & Taeger (SDEI).

FINLAND: 1♀, Liminka 2 km NE, 31.05.2018, leg. Liston & Prous (SDEI).

GERMANY: Berlin: 1♀, Treptow, 31.05.1906 (ZMHUB). Brandenburg: 1♀, Müncheberg, Gumnitz, 20.05.2011, leg. Liston (SDEI).

SWEDEN: Dalarna: 1♀ (DEI-GISHym83888), Mora 17km SW, 13.06.2013, leg. Liston, Prous & Taeger (SDEI).

**Remarks.** The type locality of *Hylotoma nemorata* is not mentioned explicitly by Fallén (1808) on page 47, but the opening sentences of his paper (page 39) state that material collected during a journey to Västergötland [sic!] comprised the basis of his publication.

**Host plants and biology.** *Betula* species. In semi-natural habitats in Europe recorded on *Betula pubescens* Ehrh. and *B. pendula* Roth (Pschorn-Walcher and Altenhofer 2000). Many additional species of *Betula* are hosts in European amenity plantings and botanic gardens (Pieronek and Soltyk 1993), and within the non-native range

of *H. nemoratus* in North America (Digweed et al. 2009). Oviposition into leaf edge. Cocoon remains in leaf. Entirely parthenogenetic; male unknown. Adults appear late, and larvae develop rather slowly; univoltine (Drouin and Wong 1984).

**Distribution.** Widespread in northern and central Europe, including the British Isles, but absent in the Iberian Peninsula (Taeger et al. 2006); Armenia, West and East Siberia (Sundukov 2017); introduced to North America where it is present across Canada and adjacent parts of the USA (Digweed et al. 2009).

### *Heterarthrus ochropoda* (Klug, 1818)

*Tenthredo* (*Emphytus*) *ochropoda* Klug, 1818: 273–274. Syntypes ♀, in ZMHUB (lectotype designated below). Type locality: Germany.

*Heterarthrus ochropoda*. Taeger et al. (2010: 373): complete synonymy listed.

**Type material examined.** **Lectotype** *Tenthredo* (*Emphytus*) *ochropoda*, here designated: ♀ “Ochropoda Kl.”, “M. Kl.”, “14137”, “GBIF-GISHym2427” (ZMHUB). Paralectotype: same labels as lectotype except “GBIF-GISHym2428” (ZMHUB).

**Other material examined.** AUSTRIA: 1♂ (DEI-GISHym83898), Etzen, 08.1990, em. 18.06.1991, reared *Populus tremula*, leg. E. Altenhofer (SDEI).

ESTONIA: 3♀ (including DEI-GISHym83589, DEI-GISHym83895), Paadrema 2km NE, 06.06.2015, leg. Liston, Prous & Taeger (SDEI).

FRANCE: Ariège: 1♂, Prades, col de Marmore, 9.6.2018, leg. H. Savina (SDEI).

GERMANY: Bavaria: 1♂, Fürth, leg. E. Enslin (SDEI). Brandenburg: 1♀, Rüdersdorf, 11.05.1919, leg. M. Hering (ZMHUB).

RUSSIA: Khabarovskiy Kray: 1♀, Bikin N 20 km, Boitsovo, Bolshoi Sontsepyok Hill, 26.05.1993, leg. A. Taeger (SDEI).

SWEDEN: Västmanland: Lindesberg 13km W, 01.06.2013, leg. Liston, Prous & Taeger (SDEI). Dalarna: Lima 33km NW, 10.06.2013, leg. Liston, Prous & Taeger (SDEI).

**Host plants and biology.** *Populus* species, including *P. tremula* L., *P. alba* L. (Pschorn-Walcher and Altenhofer 2000), *P. × canadensis* Moench, *P. deltoides* W. Bartram ex Marshall (Arru 1967), and *P. nigra* L. (Buhr 1941). Has sometimes been stated to cause significant damage to planted poplars (e.g. Arru 1967, Çalmasur and Özbek 2004).

**Distribution.** Through much of Europe, including the British mainland, but not recorded in the Iberian Peninsula (Taeger et al. 2006); Turkey, Kyrgyzstan, West and East Siberia, Russian Far East (Sundukov 2017).

### *Heterarthrus smithi* Ermolenko, 1994

*Heterarthrus smithi* Ermolenko, 1994: 17–22. Holotype ♀, in Schmalhausen Institute, Kiev (not examined). Type locality: Azerbaidjan, Talysh, near Lerik village.

**Remarks.** The type series was collected from *Acer ibericum* M. Bieb., now usually treated as a subspecies of *A. monspessulanum* L. From the original description, *H. smithi* resembles *H. leucomela* in its large size (compared to other *H. aceris* group species), with the body length given as 5.5 mm (♀) and 4.5 mm (♂), and the shape of the serrulae of the lancet illustrated by Ermolenko for *H. smithi* fits well with the illustration for *H. leucomela* by Altenhofer and Zombori (1987). The extensively pale malar space and lower gena, which distinguish female *H. leucomela* from some other *H. aceris* group females, are also shared by *H. smithi*, as are its conspicuously darkened wings. Most of the other characters given by Ermolenko for *H. smithi* do not differ from *H. leucomela*, but are also found in most of the other *Acer*-feeding *Heterarthrus* species. However, the penis valve figure of *H. smithi* by Ermolenko differs considerably from that of *H. leucomela* figured by Altenhofer and Zombori (1987), e. g. the valvura is much more slender in *smithi*. However, we have already expressed our strong doubts on the significance of penis valve characters in *Heterarthrus* (see under Character states, and discussion of *H. cuneifrons*).

### *Heterarthrus vagans* (Fallén, 1808)

*Hylotoma vagans* Fallén, 1808: 47. Syntypes ♀♂, possibly in MZLU. Type locality: Västergötland [Sweden, Västergötland].

*Heterarthrus vagans*. Taeger et al. (2010: 373): complete synonymy listed; but note that *Phyllotoma kamtschatica* is no longer considered to be conspecific.

**Material examined.** AUSTRIA: Lower Austria: 1 ♀ (DEI-GISHym31974), no locality, 10.1988, reared *Alnus glutinosa*, em. August 1989, leg. E. Altenhofer (SDEI).

CORSICA: 1 ♂ (DEI-GISHym21130), Haut Ascu, 1493m, 13.06.2013, leg. E. Heibo (private collection E. Heibo).

CYPRUS: Paphos District: 1 ♀ (DEI-GISHym11091), Kidasi, 16.04.2011, leg. Liston (SDEI). 3 ♂ (DEI-GISHym11184, 11189, 11095), Kidasi, 17.04.2011, leg. Liston (SDEI).

ESTONIA: Saaremaa: 1 ♀ (TUZ109299), Abruksa, gravel pit, 26.07.2017, leg. V. Soon (Univ. Tartu, Nat. Hist. Mus.).

GERMANY: Brandenburg: 2 ♀, Langer Berg im Grumsiner Forst, 3–10.8.1994, leg. DEI Projekt (SDEI). 1 ♀, Langer Berg im Grumsiner Forst, 26.07–02.08.1995, leg. DEI Projekt (SDEI). 1 ♂, Langer Berg im Grumsiner Forst, 09.08–16.08.1995, leg. DEI Projekt (SDEI). 1 ♀, Langer Berg im Grumsiner Forst, 5–12.6.1996, leg. DEI Projekt (SDEI). 1 ♀ (DEI-GISHym11000), Müncheberg, Gumnitz, 29.05.2010, leg. Liston (SDEI). 1 ♀ (DEI-GISHym83893), Müncheberg, Gumnitz, 25.05.2008, leg. Liston (SDEI). Thuringia: 2 ♀, Brandesbachtal bei Netzkater, 27.07–31.05.1996, Malaise trap, leg. A. & M. Taeger (SDEI). 1 ♀, Brandesbachtal bei Netzkater, 22.07–1.08.1996, Malaise trap, leg. A. & M. Taeger (SDEI).

ITALY: Sicily: 1 ♀ (DEI-GISHym11097), Portella Zilla, ca 9km E Floresta, 18.05.2010, leg. Liston (SDEI).

PORTUGAL: Guarda: 1♂, Seia 9 km W, 400 m, 40.42638N, 7.80716W, 4.5.2012, leg. Blank, Jacobs, Liston & Taeger (SDEI) [first record from Portugal].

SWEDEN: Torne Lappmark: Abisko National Park, tributary Abisko River, 68.357N, 18.762E, larva in *Alnus incana kolaensis* (Orlova) Å. Löve & D. Löve, 27.08.2018, leg. Liston (SDEI). Abisko National Park, mouth of Abisko River, 68.323N, 18.745E, 5 larvae in *Alnus incana kolaensis*, 28.08.2018, leg. Liston (SDEI).

**Remarks.** As already noted above, under Character states, the head and abdomen colour of this species is highly variable. In females the abdomen may be almost completely yellow-red, with only tergum 1 and the apical 2–3 terga and sterna more or less dark (Fig. 32). Equally frequent are however females with nearly the entire dorsum of the abdomen dark. According to Lindqvist (1969), the abdomen may sometimes be nearly completely black, with only the basal sterna obscurely paler. We have not, however, ourselves examined such dark females. Male *H. vagans* are generally darker than females, with the dorsum of abdomen usually completely dark, and frequently the whole abdomen dark. In females, the face is usually extensively pale on the inner orbits and interantennal area as in Fig. 35, but sometimes completely black (Fig. 47). The pale colour varies from white, to bright yellow. In both sexes, the coxae and femora are usually completely pale, but occasionally the coxae may be nearly completely black except apically, and up to the basal half of the femora is more or less dark. The thorax is usually entirely black, except for the more or less yellow posteroventral edge of the pronotum, but a male from Corsica (DEIGISHym21130) has entirely yellow tegulae and the downturned lateral edges of terga 2–6 yellow, with the rest of the abdomen black. This specimen is genetically the most distant from central and northern European, and Canadian *H. vagans*, which have a quite uniform barcode. Only *Alnus alnobetula* subsp. *suaveolens* (Req.) Lambinon & Kerguelen occurs at the Corsican collection locality, so that this can be assumed to be the host. Less distant from the other European and Canadian specimens are specimens from Cyprus and Sicily. See also notes under *H. fruticicolum*, which may only be a dark specimen of *H. vagans*.

**Host plants and biology.** *Alnus* species, including all the native West European taxa: *A. glutinosa* (L.) Gaertn., *A. incana* (L.) Moench., *A. cordata* (Loisel.) Duby, and *A. alnobetula* ssp. *alnobetula* (Ehrh.) K. Koch (Buhr 1941, Pschorn-Walcher and Altenhofer 2000); also *A. orientalis* Decne. (Liston and Jacobs 2012), *A. rubra* Bong. (Humble 2010), and *A. subcordata* C. A. Mey. (Liston 2011). The cocoon remains in the leaf. Bivoltine; the second generation more abundant (Altenhofer 2003).

**Distribution.** Widespread in Europe, including the British Isles and Iberian Peninsula (Taeger et al. 2006), from north of the Arctic circle to some of the larger Mediterranean islands; Turkey (Muche 1983); introduced to western North America (British Columbia and Washington; Humble 2010, Looney et al. 2016). According to Sundukov (2017), *H. vagans* has a wide distribution through the East Palaearctic, to the Russian Far East. However, records from at least some of these territories might refer to *H. kamtchaticus*, and voucher specimens therefore require checking.



***Heterarthrus vikbergi* Liston, Mutanen & Viitasaari, sp. nov.**

<http://zoobank.org/F7AD9636-DD88-4062-9CF9-6254E68E39C5>

**Description. Female** (Figs 4, 14, 51–55, 57).

**Body length.** 3.0–4.0 mm.

**Colour** (Figs 4, 51–55). Head (Figs 52–53): mostly pale, shading from yellow-brown dorsally to whitish ventrally. Contiguously dark (black) are occiput, a patch covering postocellar area and frontal field, extending laterally over vertex, and frontally narrowly more or less along antennal furrows to dorsal tentorial maculae. Frontal groove black. Apex of mandible more or less darkened. Apical maxillary and labial palpomeres slightly dark. Antenna (Fig. 55): scape and pedicel whitish; flagellomeres yellowish, 1 and 2 more or less darkened.

**Thorax** (Figs 4, 51, 53): black. Whitish are postspiracular sclerite, tegula, broad posterodorsal margins of pronotum, metascutum at least laterally, a fleck on medio-posterior of mesepisternum, margins of metepimeron. Legs entirely pale (yellowish), except for very narrowly darkened bases of coxae, and more or less darkened tarsomeres 4 and 5. Wings (Fig. 4): fore wing membrane darkened broadly below pterostigma, and within anal cell, but hyaline distal of apex of pterostigma. Hind wing membrane extensively darkened, but hyaline are apical ca. 0.3, extreme base, and jugal lobe. Venation largely dark. Pale are: C, Sc, small anterior part of fore wing pterostigma basally and apically, all veins in approx. basal 0.25 of fore wing (but R completely dark) and basal 0.2 of hind wing (but 3A completely dark).

**Abdomen** (Figs 4, 51, 54): black. Obscurely pale are more or less hypopygium (Fig. 54), and margins of downturned parts of terga (Fig. 51).

**Structure.** Postocellar area about  $4 \times$  as broad as long (Fig. 53). Inner margins of eyes in frontal view subparallel (Fig. 52). Antenna: 11–12 antennomeres; about  $1.5 \times$  as long as greatest width of head (Fig. 4); pedicel slightly broader than scape. Ratio of lengths of flagellomeres 1–7 approximately as: 100, 62, 58, 58, 51, 44, 42 (Fig. 55). Frontal groove broad, shallow, poorly defined (Fig. 52). Malar space 0.30–0.35 as long as height of compound eye.

Body shiny, without surface sculpture except for sculpture on narrow median part of median mesoscutal lobe. Pubescence pale: length varying from about  $0.3 \times$  diameter of median ocellus on upper head, to almost as long as median ocellus on inner orbits, lower head, and mesepisternum. Anterior of median mesoscutal lobe without transverse depressions (Fig. 53). Dorsum of thorax almost entirely glabrous, with only a few minute setae on mesoscutum and posterior of mesoscutellum. Upper ca. 0.6 of mesepisternum densely and evenly setose, lower 0.4 entirely glabrous.

Metatarsomere 1 about as long as combined lengths of following tarsomeres. Inner tooth of tarsal claw about as high as basal lobe and 0.6–0.7 as long as outer; teeth very close together; basal lobe well-developed, acute. Metatibial spurs slightly shorter than apical width of metatibia.



**Figures 55–63.** *Heterarthrus vikbergi* sp. nov. **55** ♀ DEI-GISHym83572 antenna **56** ♂ DEI-GISHym83573 antenna **57** DEI-GISHym31972 lancet **58–63** ♂ DEI-GISHym83573: **58** lateral **59** head frontal **60** head dorsal **61** abdomen apex dorsal **62** abdomen apex ventral **63** penis valve. Scale bar: 1mm.

Terga 1–8 unsculptured, with sparse, extremely short setae. Terga 9–10 dull, with distally increasingly dense sculpture, and longer setae. Valvulae 3 (Fig. 14) in dorsal view parallel-sided, at least 3 × as long as basal width, apically densely setose; all setae shorter than width of sheath. Lancet (Fig. 57) with 13–14 sawteeth. Each tooth with 6–10 small denticles. Compact groups of ctenidia on venter of lancet above saw teeth 9–10, occupying more than half the length of the basal 2 annular sutures, but proximally the groups become progressively smaller.

**Male** (Figs 5, 56, 58–63).

**Body length.** 3.0–3.5 mm.

**Colour** (Figs 5, 58–62). Head and ventro-lateral parts of body markedly paler than female.

**Head** (Figs 59, 60): dark dorsal patch extends only slightly anterior of median ocellus; lower head entirely pale. Antenna (Fig. 56): scape and pedicel white, flagellum yellowish.

**Thorax** (Figs 5, 58): dorsum black, except for tegula, upper edge of pronotum, lateral part of metascutum. Underside of thorax predominantly pale (whitish) except for extreme anterior of pronotum, more or less edges of propleuron, mesepimeron, flecks on the metapleuron, and underside of mesepisternum. Metascutum entirely dark. Legs entirely pale, except for more or less darkened apical tarsomere of mid and hind leg.

**Abdomen** (Figs 5, 58, 61, 62): pale, except for a broad, black median stripe on terga 1–8.

**Structure.** As female except for: Antenna ca. 1.8–1.9 as long as widest width of head (Fig. 5). Terga 1–5 largely unsculptured, with sparse, extremely short setae. Terga 6–8 dull, with distally increasingly dense sculpture. Penis valve: Fig. 63.

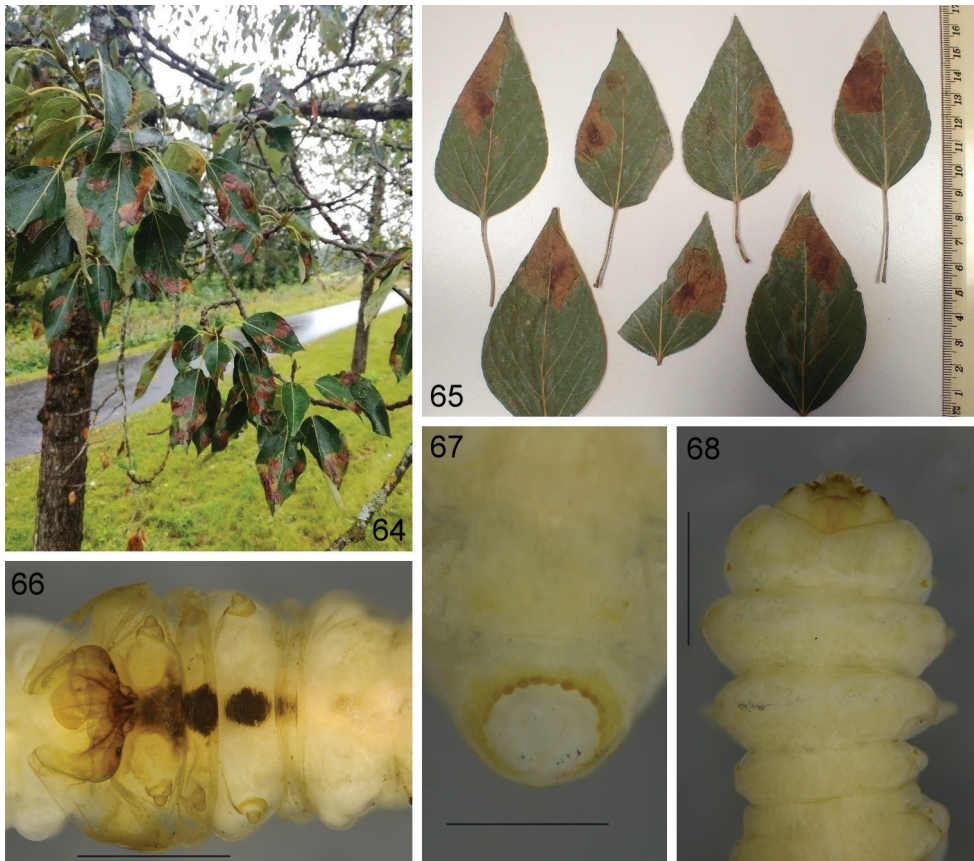
**Variability.** Female and male. Approximately equal numbers of specimens with 10 or 11 antennomeres: sometimes each antenna of the same specimen appears to have a different number of antennomeres. Relative length proportions of the apical 3 antennomeres highly variable. Fore wing vein 3r-m present or absent, or partly obsolete: frequently unequally developed in each wing of the same specimen. Mesoscutellar appendage black or slightly brown. Female: fleck on medioposterior of mesepisternum variable in size, and sometimes nearly invisible. Lateral part of metascutum always more or less white, but interior from pale brown to black.

Male: usually but not always present is a small pale fleck on anterior of each median mesoscutal lobe, and a pale streak on postero-lateral edge of lateral lobe.

Larva, full-grown. Length 8–10 mm. Pro-, meso- and metathorax ventrally each with dark median fleck, decreasing in size towards posterior; abdominal sterna one and two also with faint dark markings (Fig. 66). Teeth on sclerotised ring around anal prolegs mostly not clearly separated from each other (Fig. 67).

**Holotype:** ♀. Finland: Karelia borealis, Tohmajärvi 6906:3673 [Finnish grid: = 62.299N, 30.374E], larva 24.08.2017 on *Populus balsamifera* L., M. Mutanen leg. Deposited in the ZMUO.





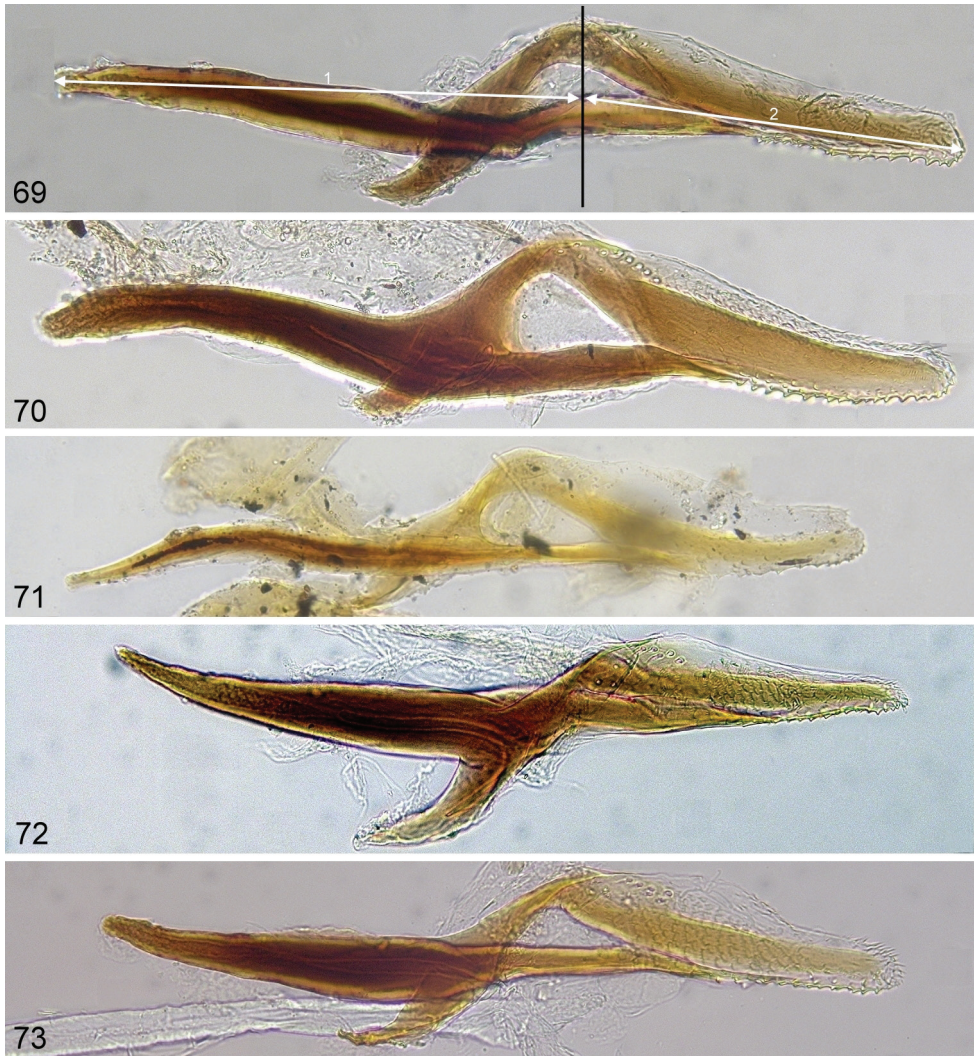
**Figures 64–68.** *Heterarthrus vikbergi* sp. nov. **64** young *Populus balsamifera* at type locality, with numerous leaf-mines (sawfly mines mixed with mines of *Isochnus sequensi* (Stierlin, 1894): Coleoptera, Curculionidae) **65** pressed *P. balsamifera* leaves containing mines **66** mature larva preserved during moult, ventral **67** mature larva posterior ventral **68** mature larva anterior dorsal. Scale bar: 1mm.

**Paratypes:** Total: 41♂, 35♀. All same collection data as holotype, except for dates. 5♂, 6♀, larvae collected 26.07.2016. 36♂, 29♀, larvae collected 24.08.2017. Deposited in the Finnish Museum of Natural History, Helsinki, Finland; HNHM; National Museum of Nature and Science, Tsukuba, Japan; NHRS; Private Collection Matti Viitasaari, Helsinki, Finland; Private Collection Veli Vikberg, Janakala, Finland; SDEI; Tartu University Zoological Museum, Tartu, Estonia; United States National Museum, Washington DC, USA; ZMUO.

**Other material (immature stages).** Two mature larvae (or pronymphs?), collection data as for holotype: DEI-GISHym31985 preserved during ecdysis, with more darkly pigmented cuticle attached (Fig. 66); and DEI-GISHym31986, moulted [weakly pigmented] (Figs 67, 68).

**Diagnosis.** The female of *H. vikbergi* differs from all other described *Heterarthrus* species in its combination of narrow and proportionately long valvulae 3 in





**Figures 69–73.** *Heterarthrus* penis valves **69, 70** *H. cuneifrons* DEI-GISHym31988, see *H. cuneifrons* taxon account and Table 1 for details of measurements **71** *H. wuestneii* lectotype **72** *H. wuestneii* DEI-GISHym31987 **73** *H. wuestneii* DEI-GISHym31993.

dorsal view (Fig. 14), the nearly entirely pale fore wing veins C and Sc (which contrast with the otherwise mostly dark venation), and the only partly strongly darkened fore wing membrane (Fig. 4). All other described *Heterarthrus* species have at least the antennal flagellum largely black, whereas male *H. vikbergi* have completely pale antennae (Fig. 56), and females only flagellomeres 1 and 2 more or less dark (Fig. 55). Furthermore, the extensively pale and tricoloured head of *H. vikbergi* is highly distinctive (Figs 52, 59): only the Mediterranean *H. cypricus* Schedl, 2005 has a similarly extensively pale head (but bicoloured: orange and black). For further

diagnostic characters of adults, see key to species. Compared to the description of the larva of *H. ochropoda* by Lorenz & Kraus (1957), *H. vikbergi* differs in having a dark marking on venter of abdominal segment 1 (Fig. 66), and the teeth on anal leg ring closer to each other (Fig. 67).

**Etymology.** The new species is named in honour of Veli Vikberg, whose life-long work on the taxonomy, biology and distribution of sawflies has greatly advanced our understanding of the group.

**Host plants and biology.** All specimens were reared from leaf-mines on *Populus balsamifera*. Mines were rather abundant on less than ten approximately 20-year old trees, planted in three short rows along the roadside in Tohmajärvi village (Fig. 64). The positions of mines in pressed leaves (Fig. 65) indicate that oviposition is normally in the leaf edge. In this sample, only one mine / larva is present in each leaf. During rearing, many cocoons detached from the leaves, but it is not clear if under natural conditions this takes place before or after leaf-fall. Diameter of 14 cocoons recovered from the rearing pots was 5–7 mm.

**Distribution.** Only known so far from the type locality, in eastern Finland. The species is unlikely to be indigenous there (see Discussion).

### *Heterarthrus wuestneii* (Konow, 1905)

*Phyllotoma aceris* McLachlan, 1867: 104. Syntypes ♀ (probably lost). Type locality: not specified [but probably England: see Healy 1867]. Primary homonym of *Phyllotoma aceris* Kaltenbach, 1856 [= *Heterarthrus leucomela* (Klug, 1818)].

*Phyllotoma Wüstneii* Konow, 1905a: 156. Syntypes ♀, ♂. Lectotype ♂, in SDEI (examined) designated by Muche (1977). Type locality: Denmark, Sonderburg, Insel Alsen.

*Heterarthrus imbrosensis* W. Schedl, 1981: 151–152. Holotype ♀, in Collection W. Schedl, Innsbruck (examined). Type locality: Greece, Crete, Imbros. **Syn. nov.**

*Heterarthrus tauricus* Ermolenko, 1984: 53–56. Holotype ♀, in Schmalhausen Institute, Kiev (not examined). Type locality: Ukraine, Crimea, southern slopes of Al-Petri. Synonymy with *wuestneii* suggested by Liston (2007) and adopted by Taeger et al. (2010).

*Heterarthrus healyi* Altenhofer & Zombori, 1987: 191–193. Replacement name for *Phyllotoma aceris* McLachlan.

**Type material examined.** *Lectotype* *Phyllotoma Wüstneii*: ♂ “Sonderburg. 12.V.04.”, “Coll. Konow”, “Eberswalde coll. DEI”, “*Heterarthrus wüstnei* Konow determ. Muche 1976. Mikrosk. Präp. Ty.”, “Type”, “GBIF-GISHym3798”, “*Paralectotypus* *Phyllotoma Wüstneii* Konow, 1905 des. Zombori 1980”, “*Paralectotypus* ♂ *Phyllotoma wuestneii* Konow, 1905 des. S. M. Blank 2001”, with separate penis valve preparation on glass slide (Symphyta Coll. Nr: 444, SDEI), SDEI. *Paralectotypes*: 3♀, 1♂ “Sonderburg. 12.V.04.”, and a variety of subsequent labels (SDEI).

**Holotype** *Heterarthrus imbrosensis*: ♀ “Kreta: Imbros, Nomos Chania, 6.5.1980, leg. W. Schedl”, “Holotypus *Heterarthrus imbrosensis* Schedl, det. W. Schedl” (Collection W. Schedl, Innsbruck).

**Other material examined.** AUSTRIA: Upper Austria: 3♂ (DEI-GISHym31987, 31992), Linz, larva ex *Acer campestre*, 3.6.1977 (em. 4.5.1978), leg. E. Altenhofer (HNHM). Lower Austria: 1♂ (DEI-GISHym31993), St Pölten, Mine ex *Acer campestre*, 16.6.1976 (em. 20.4.1977), leg. E. Altenhofer (HNHM). 2♀ (DEI-GISHym31983), St Pölten, Mine ex *Acer campestre*, 16.6.1976 (em. 20.4.1977), leg. E. Altenhofer (HNHM). 1♀ (DEI-GISHym31978), St Pölten, *Acer campestre*, 16.6.1976 (em. 28.4.1977), leg. E. Altenhofer (HNHM). 1♀, St Pölten, *Acer campestre*, 16.6.1976 (em. 27.4.1977), leg. E. Altenhofer (HNHM). 1♀ (DEI-GISHym31982), St Pölten, *Acer campestre*, 5.6.1976 (em. 30.4.1977), leg. E. Altenhofer (HNHM).

GERMANY: Bavaria: 1♀ (DEI-GISHym19407) 3♂ (DEI-GISHym19408), Franconia, Trimberg, reared ex *Acer monspessulanum*, 25.05.2003, leg. Liston (SDEI).

GREECE: Peleponnese: 7♀ (DEI-GISHym11102) 2♂, Sparti W 6km, Mistrás, 700 m, 13.04.2008, leg. Liston (SDEI). 1♀, Kalámata SE 15km, Vorio, 650m, 13.04.2008, leg. Liston (SDEI). 4♀ 1♂ (DEI-GISHym31994), Kastanitsa, 25.04.2015, leg. E. Altenhofer (SDEI). 3♀ 2♂, Agios Panteleimonas, 23.04.2015, leg. E. Altenhofer (SDEI). Crete: 5♀ (including DEI-GISHym20656) 7♂ (Liston et al. 2015).

**Remarks.** Liston et al. (2015) discussed the taxonomy of *H. imbrosensis* and *wuestneii*, pointing out that there is no clear way of separating them morphologically, especially when intermediate specimens from the Peleponnese are taken into account. In any case, the only apparent differences are details of coloration. Greek specimens, especially those from Crete, are usually darker than Central European ones. Neither is the divergence in CO1 barcodes strongly suggestive of the existence of more than one species. Accordingly, we propose the synonymy of *H. imbrosensis* with *H. wuestneii*.

The coloration of *H. wuestneii* varies significantly, even between central European specimens. In females, the malar space can vary from extensively whitish to entirely black, and the supraclypeal area and lower frons may be partly white, or entirely black. The tegula may be entirely white, or only with posterior third whitish.

We have not found any morphological characters which will distinguish *H. wuestneii* from *H. cuneifrons*. According to Altenhofer and Zombori (1987), the structure of the frons should be different, but this was not evident in the specimens which we examined. Variability in penis valve morphology is considerable: see also discussion under *H. cuneifrons*. The form of the penis valve is somewhat different for these species as illustrated by Altenhofer and Zombori (1987, figs 11 and 12). However, the penis valve of the *H. wuestneii* lectotype (Fig. 71) does not fit very well with either of their drawings, and the penis valve of the reared *H. wuestneii* specimen illustrated by Liston (2007, fig. 4) looks different from any of these. The drawing of a penis valve of *H. wuestneii* by Muche (1977), presumably representing the lectotype, which was dissected by Muche and permanently mounted on a glass slide, is very misleading. Only the sclerotised part of the valviceps is outlined; the membranous dorsal part is omitted. We suggest that because of variability, *H. cuneifrons* and *wuestneii* males cannot be distinguished by penis valve morphology.

**Host plants and biology.** As a result of the synonymy proposed above, *H. wuestneii* is known to use two different host species: *Acer campestre* L. (Altenhofer and Zombori 1987), and *A. sempervirens* (Liston et al. 2015). The records from *A. monspessula-*



*num* L. (Liston 2007) require confirmation, because the specimens could either belong to *H. wuestneii* or *H. cuneifrons*.

**Distribution.** Central and southern Europe (Taeger et al. 2006), including some of the larger Mediterranean Islands (Corsica, Sicily, Crete).

## Discussion

Four West Palaearctic *Heterarthrus* species are associated with Salicaceae (*H. microcephalus* on *Salix*; *H. fasciatus*, *ochropoda* and *vikbergi* on *Populus*), and two with Betulaceae (*H. nemoratus* on *Betula*; *H. vagans* on *Alnus*). The status of each of these as separate species is supported by clear differences in morphology, DNA barcodes, and for *H. nemoratus* and *vagans* also by host association. Further studies on the morphologically and genetically highly variable *H. vagans* would however be desirable, particularly to include West Palaearctic samples from *Alnus alnobetula*, and forms in the East Palaearctic which are morphologically similar. Species limits of the morphologically and genetically distinctive *Acer*-feeding *Heterarthrus leucomela* also seem unambiguous. Less clear is the taxonomy of the other five West Palaearctic *Acer*-feeding species *H. cuneifrons*, *cypricus*, *fiora*, *flavicollis*, and *wuestneii*, which we here for the meantime treat as valid. Leppänen et al. (2012, fig. 1) indicated that *H. wuestneii* (under the names *healyi* and *imbrosensis*), *fiora* (as *aceris*) and *cuneifrons* are very closely related. However, currently available genetic data for this species complex does not include *H. flavicollis*, and interpretation of data for the other species is difficult because of misidentifications and nomenclatural inconsistency. On the other hand, as summarised in the identification key, morphological differentiation of these taxa is in most cases possible, except for *H. cuneifrons* and *wuestneii*. Unclear is how strongly host plant specificity is correlated with these characters. Previous studies have postulated strict monophagy of most *Acer*-mining *Heterarthrus* species on single *Acer* species (e.g. Altenhofer 1980a, Altenhofer and Zombori 1987), but we suspect that host associations in this group of species are sometimes less strict. A misleading impression has possibly arisen, because older data on host plant associations are nearly all from central Europe, where only three native species of *Acer* are widely available as potential hosts. Our now widened species limits for *H. wuestneii* entail the recognition of two different *Acer* species as its hosts: one in Central Europe, the other in the southern Balkans and Crete. Also, *Heterarthrus leucomela* has long been known to have two host species in Central Europe, so far without any evidence of genetic or morphological differences between the sawflies on the different host species. We conclude that the majority of West Palaearctic *Heterarthrus* species are oligophagous on several species within a single host plant genus, as has for example been recorded for *H. microcephalus* (Buhr 1941), *H. nemoratus* (Digweed et al. 2009, table 1), *H. ochropoda* (Arru 1967, Pschorn-Walcher and Altenhofer 2000), and *H. vagans* (Humble 2010).

The discovery of a previously undescribed but distinctive *Heterarthrus* species in Europe is a surprise. Because the only known place of occurrence of *vikbergi* is located in eastern Finland, close to the Russian border, it is tempting to speculate that it may also occur further east. The host plant species, *Populus balsamifera*, is native to North



America, with a transcontinental range from the northern limit of tree growth at about 68°N, southwards in the western mountains to about 42°N in Colorado (Zasada and Phipps 1990). In Europe, *P. balsamifera* is widely planted, mostly for amenity, and less so for timber. It is unlikely that *Heterarthrus vikbergi* originated in North America, because no natural occurrence of *Heterarthrus* is known from there. On the other hand, the appearance of *H. vikbergi* in large numbers on a species of plant growing outside its native range, suggests that the sawfly may have been introduced, or recently spread naturally from elsewhere. There seems little point in speculating further on this before we know more about the distribution and host associations of *H. vikbergi*.

Previous investigations suggest that DNA barcodes discriminate species of sawflies less effectively than in most other insect groups (Schmidt et al. 2017, Liston et al. 2017, Prous et al. 2016, 2017). This is especially true in Tenthredinidae, and particularly in its subfamily Nematinae, within which DNA barcode sharing between closely related species has been detected in many groups (Liston et al. 2017). Such problems may be attributable to increased levels of mitochondrial introgression in haplodiploid organisms (Patten et al. 2015, Sloan et al. 2017). Based on our data, species of *Heterarthrus* show a mean divergence between species of 4.47% and can mostly be reliably identified by their DNA barcodes (Fig. 1). Exceptions are the closely related species *H. cuneifrons*, *H. flora* and *H. wuestneii*. Of these, *H. flora* and *H. cuneifrons* show not even a single diagnostic nucleotide substitution in the DNA barcode region. On the contrary, it seems possible that *H. wuestneii* can be distinguished from these two species by its DNA barcode, although we have not been able to verify the identity of two analysed specimens (DEIGISHym19407 and DEIGISHym19408), which may belong to *H. cuneifrons* or *H. wuestneii*. A future effort to obtain sequences for some nuclear genes should be made to clarify the taxonomy of this species complex. The newly described *H. vikbergi* is well-characterized by its DNA barcode as showing a minimum of 6.07% divergence to its nearest neighbour *H. ochropoda*.

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# The Eumeninae (Hymenoptera, Vespidae) of Hong Kong (China), with description of two new species, two new synonymies and a key to the known taxa

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## Abstract

A total of 38 species belonging to 26 genera of Eumeninae are recorded from Hong Kong, among which two new species, namely *Allorhynchium radiatum* **sp. nov.** and *Orientalicesa nigra* **sp. nov.** are described and illustrated. *Symmorphus tsushimanus* Yamane, 1990 is newly recorded from China and its female is firstly described. Eighteen species are newly recorded for Hong Kong. *Antepipona ferruginea* Kim & Yamane, 2003 is synonymized with *Antepipona rufescens* (Smith, 1857) (**syn. nov.**) and *Eumenes quadratus obsoletus* Dover, 1926 is synonymised with *Eumenes quadratus quadratus* Smith, 1852 (**syn. nov.**). A checklist, a key and illustrations to Hong Kong Eumeninae are also provided.

## Keywords

Hymenoptera, Vespidae, Eumeninae, new species, Hong Kong, China

## Introduction

The Hong Kong Special Administrative Region of the People's Republic of China (HK-SAR), covers an area of 1076 km<sup>2</sup>, of which about 40% is urbanized (430 km<sup>2</sup>), while the rest (645 km<sup>2</sup>) comprises undeveloped land. The topography of the HKSAR is extremely rugged and consists essentially of a series of hills and ridges of igneous or vol-

canic origin, the highest point culminating at ca 950m asl. Historically the landscape of Hong Kong has been greatly modified by human activity and in the late 1940's hardly any forest cover remained. Today the North facing slopes are forested while the south facing ones are generally covered in grasses, shrubs and low bushes. The low lying areas were historically farmland, now abandoned, and those areas not occupied by human activities are now composed of seasonal or perennial wetlands/marshes and/or covered in dense and mature secondary forests. The climate is tropical with clear summer (wet) and winter (dry) monsoons, the latter can bring short-lived surges of cold Siberian air. Zero or sub-zero Celsius temperatures are regularly recorded (Dudgeon and Corelett 1994).

The Eumeninae are all solitary wasps, although some species display behaviours that are considered precursors of eusociality in Vespidae, such as communal nesting and progressive provisioning of food for the brood. The subfamily contains about 3800 valid species worldwide, in 204 extant genera (Carpenter 1986; Yamane 1990; Zhou et al. 2011; Tan et al. 2018; Pannure et al. 2016; Ferreira et al. 2018; Li and Carpenter 2018; Selis 2018; Carpenter unpubl.). They are usually predators of Lepidoptera or Coleoptera larvae, although predation on larvae of sawflies is also recorded. The preys are fed to the wasp brood, the adults feeding on body fluids of the prey and plant nectar only. The eumenine wasps are difficult taxonomically, partially because no recent global revision of the subfamily exists although recent regional revisions are clarifying the picture, partially because of the past creation of many new names; a consequence of the extreme colour variability intraspecifically in many taxa (e.g. *Delta*, *Phimenes*, *Pseumenes*, *Anterhynchium*) and a wealth of synonyms that has confused nomenclature.

Asian species have been partially reviewed in the last decade or so and we will refer the reader to the works of Yamane 1990, Nugroho et al. 2013, Nguyen et al. 2014, Girish Kumar and Sharma 2014, 2015, Pannure et al. 2016, Tan et al. 2018b, and Li and Carpenter 2018, 2019 for additional and comparative information. Prior to this study, 22 species in 15 genera of the subfamily Eumeninae were fragmentarily reported in the literature from Hong Kong. Dover (1926) described 14 species from the HKSAR, *Labus exiguus* Sauss., [misidentification, = *Labus edenticulus* Li & Carpenter, 2018], *Eumenes petiolata* Fabr. [= *Delta pyriforme pyriforme* Fabricius, 1781], *Eumenes gracilis* var. *esuriens* Fabr. [misidentification, = *Delta campaniforme campaniforme* (Fabricius, 1775)], *Eumenes arcuata* Fabr. [= *Phimenes flavopictus flavopictus* (Blanchard, 1849)], *Eumenes architectus* Sm. [misidentification], *Eumenes coarctata* var. *punctata* Sauss. [= *Eumenes punctatus* de Saussure, 1852], *Eumenes quadrata* var. *obsoleta* Dover, 1926 [= *Eumenes quadratus quadratus* Smith, 1852, Syn. nov.], *Pareumenes quadrispinosa* Sauss. [= *Pareumenes quadrispinosus acutus* Liu, 1941 (?)], *Pareumenes depressa* Sauss. [= *Pseumenes depressus depressus* (de Saussure, 1855)], *Odynerus* (*Rygchium*) *flavomarginatum* Sauss. [= *Anterhynchium flavomarginatum flavomarginatum* (Smith, 1852)], *Odynerus* (*R.*) *haemorrhoidalis* var. *quinquecincta* Fabr. [= *Rhynchium quinquecinctum quinquecinctum* (Fabricius, 1787)], *Odynerus* (*R.*) *flavopunctatum* Smith [= *Rhynchium flavopunctatum flavopunctatum* (Smith, 1852)], *Odynerus bipustulatus* Sauss. [probable misidentification (see below), = *Antepipona bipustulata* (de Saussure, 1855)], *Odynerus trilobus* Fabr. [= *Euodynerus trilobus* (Fabricius, 1787)]. Of these 14 species three are misidentifications



and therefore Dover's list only contains 10 traceable species for Hong Kong. Later in 1941 Giordani Soika recorded *Eumenes citreolineatus* Giordani Soika, 1941 [= *Eumenes atrophicus* (Fabricius, 1798)] and in 1986 *Antepipona menkei* Giordani Soika, 1986, and Gusenleitner in 2002 described *Parancistrocerus hongkongensis* Gusenleitner, 2002. In 2012 Barthélémy recorded an additional six species, *Allorhynchium* sp.1 [= *Allorhynchium chinense* (Saussure, 1862)], *Anterhynchium* sp.1 [= *Anterhynchium* (*Dirhynchium*) *flavolineatum* (Smith, 1857)], *Xenorhynchium* sp.1 [misidentification, = *Anterhynchium flavomarginatum flavomarginatum* (Smith, 1852)], *Apodynerus* sp.1 [= *Apodynerus troglodytes troglodytes* (de Saussure, 1855)], *Pararrhynchium* sp.1 [misidentification, = *Orancistrocerus aterrimus erythropus* (Bingham, 1897)] and *Zethus* sp.1 [= *Zethus dolosus* Bingham, 1897]. Li and Carpenter described *Labus edenticulus* Li & Carpenter, 2018. Dover, by all accounts was the most prolific author in terms of describing local species, however his material from Hong Kong is most likely lost: no specimens are deposited; as he suggests in his paper (Dover 1926), in the NHMUK under his name and those allegedly deposited at HK University have indeed been lost, as checked by CB. In addition, it seems that Dover's species concepts may have been at times rather broad as is suggested by dubious local records of taxa such as *Labus exiguus* or *Eumenes architectus*.

From the study of material collected by Barthélémy in Hong Kong (over 300 specimens) and the historical literature of the subfamily we can confirm that the local fauna comprises at least 38 species in 26 genera, of which two species are new to science; *Allorhynchium radiatum* sp. nov. and *Orientalicesa nigra* sp. nov., which we describe and illustrate in detail. The genus *Allorhynchium* van der Vecht, 1963 contains 19 species worldwide; it was revised by Tan et al. (2018a). The genus *Orientalicesa* Koçak & Kemal, 2010 has all six known species occurring only in the Oriental Region; it was revised by Giordani Soika (1994). Eighteen species recorded here are new to the territory, nearly doubling the known number of species and two are new records for China. We propose to synonymise *Antepipona ferruginea* Kim & Yamane, 2003 with *Antepipona rufescens* (Smith, 1857) and *Eumenes quadratus obsoletus* Dover, 1926, with *E. quadratus quadratus* Smith, 1852. We also provide the first description of the female of *Symmorphus tsushimanus* Yamane, 1990, a new record for China. Six species only were recorded in Hong Kong from the literature which are not in our collected material: *Eumenes atrophicus* (Fabricius, 1798), *Antepipona menkei* Giordani Soika, 1986, *Eumenes architectus* Smith, 1859, *Labus exiguus* (de Saussure, 1855), *Antepipona bipustulata* de Saussure, 1855 and *Anterhynchium flavopunctatum flavopunctatum* (Smith, 1852), the last four recorded by Dover (1926) are unlikely occurrences in Hong Kong and we recognise only two species recorded in the literature but not collected by us. *Paraleptomenes miniatus miniatus* (de Saussure, 1855) is recorded on i-Naturalist but we have not examined specimens. It can be expected that additional species either new to science or Hong Kong and China will be described in the future.

In addition, both a checklist and a key to the 38 species are given along with plates illustrating the 36 collected species. We also give locally occurring colour variants of *Eumenes quadratus quadratus* Smith, 1852, *E. punctatus* de Saussure, 1852 and *Anterhynchium flavomarginatum flavomarginatum* (Smith, 1852).

## Materials and methods

Specimens were obtained from Hong Kong mainly by C. Barthélémy but also from C. Taylor (Hong Kong University) and John X. Q. Lee, as noted. The chief mode of acquisition was through active hand netting (sampling around 200 specimens), Malaise traps where also extensively used, and set in various locations for varying periods of time depending on the location (1 month to 10 years) and the collecting bottle changed on average every two weeks; the more common species were sampled through nest trapping and rearing, with results published by Barthélémy (2012).

Identifications were made using a stereomicroscope (Nikon SMZ1500), according to the descriptions or keys of Schulthess (1934), Yamane (1990), Giordani Soika (1994), Girish Kumar et al. (2013), Girish Kumar and Sharma (2013), Nguyen (2015), Nguyen and Carpenter (2016), Girish Kumar et al. (2016), Girish Kumar et al. 2017, Li and Chen (2014a, b, 2016a, b), Nugroho et al. (2016), Li and Carpenter (2018), Ma et al. (2017), Tan et al. (2018a), Tan et al. 2018b and Li and Carpenter 2019 and comparing the Hong Kong material with specimens deposited in the American Museum of Natural History (USA).

The specimens examined are deposited in the American Museum of Natural History, and in the second author's collection in Hong Kong, the holotypes of the two new species are kept at the American Museum of Natural History. Descriptions and measurements of the two new species were made under a stereomicroscope (Nikon SMZ1500), and the corresponding figures were taken with Microptics-USA/Visionary Digital photomicrographic system developed by Roy Larimer and multiple layers stacked using Helicon Focus. All other habitus illustrations were made with a Leica M205 C stereomicroscope and stacking software LAS v.4. at increments of 20–50 steps. For the larger specimens and those live, images were taken using a Nikon D200 camera equipped with a Nikkor 60 mm macro-lens and Sunpak D12 ring flash. The ratios used throughout the descriptions were measured in the same magnification of the stereomicroscope. All measurements were taken as the maximal length of body parts measured. Body length was measured from the anterior margin of the head to the posterior margin of metasomal tergum 2. For the density description of punctures, “sparsely” means that interspaces are larger than punctures diameter, “moderately” means equal to the diameter, and “densely” means less than the diameter.

The abbreviations used in the text are shown as follows:

<b>A1</b>	for antennal segment 1,	<b>T2</b>	for metasomal tergum 2,
<b>A2</b>	for antennal segment 2,	<b>S1</b>	for metasomal sternum 1,
<b>T1</b>	for metasomal tergum 1,	<b>S2</b>	for metasomal sternum 2, and so on.

<b>AMNH</b>	American Museum of Natural History, New York, USA
<b>CBC</b>	Christophe Barthélémy's collection, Hong Kong
<b>CQNU</b>	Chongqing Normal University, Chongqing

<b>HUM</b>	Hokkaido University, Matsumura, Japan
<b>LACM</b>	Los Angeles County Museum, Los Angeles, USA
<b>MHNG</b>	Museum d'Histoire Naturelle, Genève, Switzerland
<b>MNHN</b>	Museum National d'Histoire Naturelle, Paris, France
<b>MRSN</b>	Museo Regionale di Scienze Naturali, Torino, Italy
<b>MSNV</b>	Museo di Storia Naturale di Venezia, Venice, Italy
<b>NMW</b>	Naturhistorisches Museum Wien, Vienna, Austria
<b>NHMUK</b>	The Natural History Museum, London, UK
<b>OCMNH</b>	Osaka City Museum of Natural History, Osaka, Japan
<b>OUM</b>	Oxford University Museum, Hope Entomological Collections, Oxford, UK
<b>RMNH</b>	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherland
<b>USNM</b>	National Museum of Natural History, Washington, D.C., USA
<b>UZH</b>	Zoological Museum, University of Zurich, Switzerland
<b>ZMUC</b>	Universitets København, Zoologisk Museum, København, Denmark

In the list below we do not show the complete synonymy of each taxon as this information is readily available and we follow here the format proposed by Tan et al. 2018, however we give details of the type species at generic and specific levels.

The UTM references on labels of material examined refer to grid reference WGS 84/HK 1980 datum and new records are asterisked (\*).

## Species list

### Tribe EUMENINI

#### 1. Genus *Delta* de Saussure, 1855

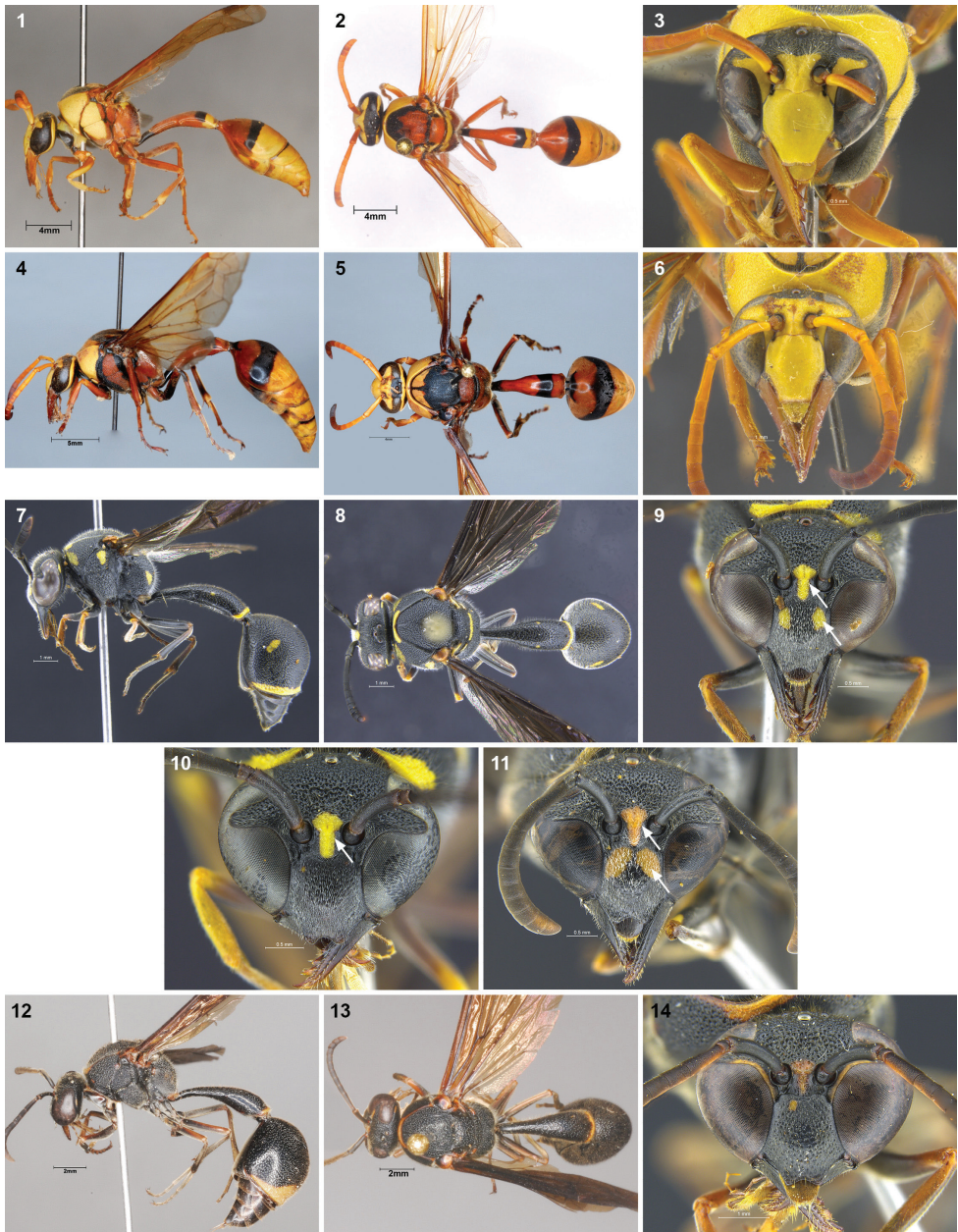
*Delta* de Saussure, 1855: 130, 132, 143. Type species: *Vespa maxillosa* DeGeer, 1773, by subsequent designation of Bequaert, 1925: 137.

#### (1) *Delta campaniforme campaniforme* (Fabricius, 1775)

Figs 1–3

*Vespa campaniformis* Fabricius, 1775: 371, “Nova Hollandia”, NHMUK. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Lantau Isl., Tai O, hand net, 25.xi.2008, UTM: 49Q GE 949 638, 4m, ref.: 0306.S.Hy.1 [CBC]; 1♀, Ping Shan Chai, 140m, Malaise trap, 22.xi–20.xii. 2014, UTM: 50Q KK 106 893, 140m, ref.: M186.D.Hy.6 [CBC].



**Figures 1–14.** *Delta campaniforme campaniforme*, female **1** habitus (lateral view) **2** habitus (dorsal view) **3** head (frontal view) **4–6** *Delta pyriforme*, female **4** habitus (lateral view) **5** habitus (dorsal view) **6** head (frontal view) **7–11** *Eumenes punctatus*, female **7** habitus (lateral view) **8** habitus (dorsal view) **9** head (frontal view) **10–11** variation of face markings **12–14** *Eumenes quadratus quadratus*, female **12** habitus (lateral view) **13** habitus (dorsal view) **14** head (frontal view).



**Distribution.** China (Fujian, Guangdong, Guangxi, Hainan, Hong Kong, Jiangxi, Sichuan, Yunnan, Zhejiang); Nepal; Thailand; Cambodia; Vietnam; India; Indonesia; Papua New Guinea; Australia; Philippines; adventive in U. S. A.: Hawaii.

**Remarks.** A common wasp in Hong Kong. First recorded from Hong Kong by Dover (1926) as *Eumenes gracilis* var. *esuriens* Dover, 1926.

## (2) *Delta pyriforme pyriforme* (Fabricius, 1775)

Figs 4–6, 130–131

*Vespa pyriformis* Fabricius, 1775: 371, “in China”, type repository unknown. Type: Sex not stated.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, hand net, 02.x.2012, UTM: 50Q KK 242 849, 70m, ref.: 0489.A.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, Lantau isl., Tai O, hand net, 25.xi.2008, UTM: 49Q GE 949 638, 4m, ref: 0306.S.Hy.2 [CBC]; 2♂, Pak Sha O, hand net, 24. ix.2012 & 25.xi.2012, UTM: 50Q KK 242 849, 70m, refs.: 0487.A.Hy.1 & 0493.A.Hy.1 [CBC].

**Distribution.** China (Fujian, Guangdong, Guangxi, Hainan, Yunnan, Hong Kong); Pakistan; India; Sri Lanka; Bhutan; Nepal; Myanmar; Thailand; Laos; Vietnam.

**Remarks.** A common wasp in Hong Kong. First recorded from Hong Kong by Dover (1926) as *Eumenes petiolata* Latreille, 1802.

## 2. Genus *Eumenes* Latreille, 1802

*Eumenes* Latreille, 1802: 360. Type species: “*Eumenes coarctata* Fab.” [= *Vespa coarctata* Linnaeus, 1758], by subsequent designation of Latreille, 1810: 438.

## (3) *Eumenes (Eumenes) atrophicus* (Fabricius, 1798)

*Vespa atrophica* Fabricius, 1798: 264, “In India orientali”, ZMUC. Type: female.

**Material examined.** No specimens, known from the literature only.

**Distribution.** China (Hong Kong); India; Nepal; Myanmar; Thailand; Laos.

**Remarks.** Described previously by Giordani Soika from Hong Kong as *Eumenes citreolineatus* Giordani Soika, 1941. Not observed by the authors, probably scarce in Hong Kong.

**(4) *Eumenes (Eumenes) punctatus* de Saussure, 1852**

Figs 7–11, 132–133

*Eumenes punctata* de Saussure, 1852: 37, “La Chine”, NHMUK. Type species: female, male.

**Material examined.** CHINA: Hong Kong: 6♀, Ping Shan Chai, Malaise trap, 26.iv.–05.v.2006, 10–25.x.2015, 12–26.v.2018 & 26.v.–14.vii.2018, UTM: 50Q KK 106 893, 140m, refs: M038.A.Hy.9, M223.D.Hy.1, M348.C.Hy.4 & M351.D.Hy.5 [CBC], same location 21–26.vi.2006 & 30.vii.–03.ix.2016, refs.: M044.A.Hy.11, M258.D.Hy.2, leg. C. Barthélémy [AMNH], 1♀, same location, hand net, 04.vi.2016, ref.: 0592.B.Hy.8 [CBC]; 2♀, Pak Sha O, 20.vi.2009 hand net & 05.iv.2010 reared, UTM: 50Q KK 242 849, 70m, ref.: 0347.A.Hy.1 & 0391.A.Hy.1 [CBC], 1♂ same location, 01.vii.2011 reared, ref.: 0443.A.Hy.1 [CBC]; 2♂, Mang Kung Wo, Malaise trap, 07–21.vii.2018 & 21.vii.–04.viii.2018, UTM: 50Q KK 174 760, 60m, refs.: M353.C.Hy.1 & M356.C.Hy.2 [CBC].

**Distribution.** China (Hebei, Hong Kong, Inner Mongolia, Kiangsu, Sichuan); India; Sri Lanka; Korea; Japan; Russia.

**Remarks.** An abundant wasp in Hong Kong with Palearctic affinities. First recorded by Dover (1926) as *Eumenes coarctatus punctatus* Sauss. In our collected material we have at least three colour variants of this species, which are illustrated in figures 10–14.

**(5) *Eumenes (Eumenes) quadratus quadratus* Smith, 1852**

Figs 12–20, 134

*Eumenes quadratus* Smith, 1852: 37, “near Ning-po-foo” (China), NHMUK. Lectotype: female.

*Eumenes quadratus obsoletus* Dover, 1926: 233, female, “Hong Kong”, Type depositary unknown, specimen lost. Syn. nov.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, hand net, 20.vi.2006, 50Q KK 242 849, 70m, ref.: 0199.A.Hy.1, leg. C. Barthélémy [AMNH]; 3♀, Mang Kung Wo, hand net, 17.vii.2012, 22.v.2016 & 28.iv.2018, UTM: 50Q KK 174 760, 60m, refs.: 0477.A.Hy.1, 0597.A.Hy.1 & 0650.A.Hy.1 [CBC]; 1♂, Mang Kung Wo, hand net, 23.iv.2016, same UTM references, refs.: 0597.A.Hy.1 [CBC]; 1♀, Ping Shan Chai, Malaise trap, 30.vii.–03.ix.2015, UTM: 50Q KK 106 893, 140m, ref.: M258.D.Hy.2 [AMNH].

**Distribution.** China (Beijing, Hong Kong, Shanghai); Laos; Vietnam.

**Remarks.** Dover (1926) listed *Eumens quadratus* var. *obsoletus* from Hong Kong, however, as he recognized himself the justification for this new subspecies lied in the distinct color difference albeit identical structural features between his subspecies and the nominate type species deposited in NHMUK. In our collected material we can recognize at least three color forms of the same species (figs 14–20), these variations are particularly notable on the face, pronotum and T1–T2; the darker form; basis of



**Figures 15–29.** *Eumenes quadratus quadratus*, female **15–17** variations of face markings **18–20** variations of T1 & T2 markings **21–23** *Eumenes rubronatus*, female **21** habitus (lateral view) **22** habitus (dorsal view) **23** head (frontal view) **24–26** *Oreumenes decoratus*, female **24** habitus (lateral view) **25** habitus (dorsal view) **26** head (frontal view) **27–29** *Phimenes flavopictus flavopictus*, female **27** habitus (lateral view) **28** habitus (dorsal view) **29** head (frontal view).

Dover's new subspecies, is less common locally than the distinctly marked one. Given the identical structural characters of the various colors forms and the evidence presented by Dover, we propose to synonymise *Eumenes quadratus obsoletus* Dover, 1926

with *E. quadratus quadratus* Smith, 1852. It is a common wasp in Hong Kong and has Palearctic affinities. Dissected cells were mass-provisioned with caterpillars in the family Erebidæ (CB pers. obs., det. Dr. Roger Kendrick, Hong Kong)

**(6) *Eumenes (Eumenes) rubronotatus* Pérez, 1905**

Figs 21–23

*Eumenes rubronotatus* Pérez, 1905: 25, 85, “Yokohama, Japon” (Japan), MNHN. Type species: male.

**Material examined.** CHINA: Hong Kong: 1 ♀, Sai Kung Town, hand net, 26.xi.2008, 3m, ref.: 0307.M.Hy.1 [CBC].

**Distribution.** China (Beijing, Fujian, Guangxi, Guangdong, \*Hong Kong, Jiangsu, Zhejiang); Russia; Vietnam; Korea; Japan.

**Remarks.** Known from a single record. Scarce in Hong Kong.

**3. Genus *Oreumenes* Bequaert, 1926**

*Oreumenes* Bequaert, 1926: 488. Type species: *Eumenes harmandi* Perez, 1905 [= *Eumenes decoratus* Smith, 1852], by original designation and monotypy.

**(7) *Oreumenes decoratus* (Smith, 1852)**

Figs 24–26

*Eumenes decoratus* Smith, 1852: 36, “Tein-tung” (China), NHMUK. Type species: female.

**Material examined.** CHINA, 1 ♀, Hong Kong: Ping Shan Chai, hand net, 21.x.2017, UTM: 50Q KK 104891, 140m, ref.: 0641.B.Hy.1 [CBC].

**Distribution.** China (Chongqing, Guangxi, Guizhou, Hebei, \*Hong Kong, Hunan, Jiangsu, Jiangxi, Jilin, Liaoning, Shaanxi, Shanxi, Shandong, Sichuan, Taiwan, Yunnan, Zhejiang); Japan; Korea.

**Remarks.** Known from a single specimen. This is a species with Palearctic affinities.

**4. Genus *Phimenes* Giordani Soika, 1992**

*Phimenes* Giordani Soika, 1992: 41, 66, replacement name for *Phi* de Saussure, 1855, non de Saussure, 1854. Type species *Vespa arcuata* Fabricius, 1775, by subsequent designation of Bequaert, 1926: 487, as type species of *Phi* de Saussure, 1855.



**(8) *Phimenes flavopictus flavopictus* (Blanchard, 1849)**

Figs 27–29

*Eumenes flavopictus* Blanchard, 1849: 8, pl. 2 figs. 2, 6, type locality unknown, MNHN.  
Type species.

**Material examined.** CHINA: Hong Kong: 1♀, Sha Lo Tong, hand net, 26.vii.2014, UTM: 50Q KK 101886, 160m, ref.: 0531.B.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, Pak Sha O, hand net, 14.v.2009, UTM: 50Q KK 242 849, 70m, ref.: 0335.C.Hy.2 [CBC].

**Distribution.** China (Fujian, Guangdong, Guangxi, Hong Kong, Shichuan, Yunnan, Zhejiang); India; Sri Lanka; Nepal; Myanmar; Thailand; Laos; Vietnam; Malaysia; Singapore; Indonesia.

**Remarks.** An abundant wasp in Hong Kong. First recorded from Hong Kong by Dover (1926) as *Eumenes arcuata* Fabr.

**Tribe ODYNERINI****5. Genus *Allorhynchium* van der Vecht, 1963**

*Allorhynchium* van der Vecht, 1963: 57, 58. Type species: *Vespa argentata* Fabricius, 1804, by original designation.

**(9) *Allorhynchium chinense* (Saussure, 1862)**

Figs 30–32, 135–138

*Rhynchium chinense* de Saussure, 1862: 186, “La Chine”, MHNG. Type.

**Material examined.** CHINA: Hong Kong: 1♂, Pak Sha O, Malaise trap, 03–14.v.2011, UTM: 50Q KK 242 852, 70m, ref.: M091.C.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, same locality, reared, 09.vii.2010, UTM: 50Q KK 242 852, 70m, ref.: 0420.A.Hy.1, leg. C. Barthélémy [AMNH]; 2♀, Pak Sha O, reared, 07.xii.2010 & 04.viii.2018, UTM: 50Q KK 242 849, 70m, refs.: 0380.A.Hy.2 & 0656.C.Hy.1 [CBC]; 2♂, same locality, 13.iv.2010 & 14.viii.20014, refs.: 0393.A.Hy.1 & 0530.A.Hy.1 [CBC]; 1♀, same locality, Malaise trap, 01–10.vi.2010, ref.: M077.C.Hy.1 [CBC]; 3♂, same locality, Malaise trap, 16.vi–03.vii.2010, 10–24.viii.2013 & 19.v–08.vii.2018, refs.: M078.C.Hy.1, M137.C.Hy.2 & M350.C.Hy.1 [CBC]; 2♀, Ping Shan Chai, Malaise trap, 26.v–14.vii.2018, UTM: 50Q KK 106 893, 140m, ref: M351.D.Hy.6 [CBC].

**Distribution.** China (Fujian, Guangdong, Guangzhou, Guangxi, Henan, Hong Kong, Jiangxi, Macao, Sichuan, Shanghai, Taiwan, Yunnan); Vietnam; Philippines.

**Remarks.** Displays elaborate nesting biology, particularly progressive provisioning. Construct cell partitions and entrance collar with resinous material (likely as an ant



**Figures 30–42.** *Allorhynchium chinense*, female **30** habitus (lateral view) **31** habitus (dorsal view) **32** head (frontal view) **33–39** *Allorhynchium radiatus* sp. nov., female **33** habitus (lateral view) **34** habitus (dorsal view) **35** face (frontal view) **36** metasoma (dorsal view) **37** propodeum (dorsal view) **38** vertex (dorsal view) **39** part of fore wing **40–42** *Antepipona rufescens*, female **40** habitus (lateral view) **41** habitus (dorsal view) **42** head (frontal view).

repellent). Recorded by Barthélémy (2012) as *Allorhynchium* sp.1. Cells are progressively-provisioned with caterpillars belonging to the family Tortricidae (Barthélémy, 2012). An abundant wasp in Hong Kong.

**(10) \**Allorhynchium radiatum* sp. nov.**

<http://zoobank.org/A2171C9D-0B32-4AF1-86A3-F4EB581F3B64>

Figs 33–39

**Material examined.** CHINA: Hong Kong: HOLOTYPE, ♀, Mang Kung Wo, Malaise trap, 11.viii.2015, UTM: 50Q KK 174 760, 60m, M060, C.Hy.2, leg. C. Barthélémy [AMNH].

**Description.** Female (Figs 33–34): body length 13.0 mm; fore wing length 13.5 mm. Black, with the following parts yellow: two separated spots of clypeus basally (Fig. 35), a band of ocular sinus lower, inter-antennal spot, and border between posterior and dorsa-lateral surfaces of propodeum (Fig. 37); mandible mostly, A3–A12, tegula exclude inner side, apex of parategula, and terminal tarsi dark ferruginous. Wings darkly infuscated.

Head. Head in frontal view wider than long. In frontal view, clypeus (Fig. 35) coarsely punctate, interspaces carinate and irregularly reticulate, swollen in the middle, clypeal maximum width  $1.19\times$  its length, apical width  $1.30\times$  distance between antennal sockets (Fig. 35), width of clypeus  $2.82\times$  apical width, apex deeply emarginated medially and forming acute tooth on each lateral side; frons coarsely punctuate, interspaces carinate and reticulate; vertex punctate, punctures a little sparser than frons and clypeus, with two small separated cephalic foveae somewhat bigger than surrounding punctures, depression for cephalic foveae absent, area behind posterior ocelli depression (Fig. 38); occipital carina complete; interocular distance on vertex  $1.06\times$  that at clypeus in frontal view.

Mesosoma. Mesosoma much longer than wide in dorsal view. Pronotal carina complete; pronotum, mesoscutum, scutellum and metanotum coarsely punctate, these punctures very similar to those on frons; mesoscutum slightly convex, about as long as wide between tegulae; scutellum almost flat; metanotum convex and sloping down to apical margin; mesopleuron coarsely punctate, punctures denser than mesoscutum except large area of epicnemium coriaceous; epicnemial carina present and strong; metapleuron coriaceous and with few minute punctures; propodeum (Fig. 37) without lateral carina, dorsal face coarsely punctate, interspaces between punctures carinate and reticulate, lateral face coarsely and irregularly striate and with a few sparse and shallow punctures, posterior face deeply excavated, basal triangular area with a deep fovea, about  $1/3$  of length of medio-longitudinal carina, with strong median carina connecting a few oblique striae; border between posterior and dorsa-lateral surfaces round (Fig. 37). Parastigma of fore wing much more than half as long as stigma (Fig. 39); tegula not reaching parategula.

Metasoma. T1 in dorsal view slightly more than twice as wide as ( $2.12\times$ ) long (Fig. 37), and slightly narrower than T2 (Fig. 36), basally with transverse carina interrupted mesally; anterior vertical surface of T1 convex, coriaceous, with a few sparse shallow punctures, and obviously separating from dorsal horizontal part; dorso-lateral area behind transverse carina with a few coarse punctures similar to those of mesoscutum, interspaces between punctures slightly carinate; dorsal surface except apex densely punctate, interspaces between punctures not reticulate, and punctures much smaller and sparser than those of head and mesosoma; T2 slightly wider than ( $1.08\times$ ) long, densely punctate, punctures at the base relatively bigger and sparser than those

in other part of T2; S2 coarsely punctate and slightly lowered basally; visible parts of T3–T5 minutely punctate, punctures much smaller than those of T2 (Fig. 36).

Male. Unknown.

**Distribution.** \*China (\*Hong Kong).

**Remarks.** This species is related to *A. diffinis* (Giordani Soika, 1986) by T1 with distinct transverse carina (Fig. 37), a yellow band at lower part of ocular sinus, and a yellow inter-antennal spot. It can be distinguished from the related species and other members of the genus by following combination of characters: punctures of T1 basally sparser than *A. diffinis*, clypeus basally with two separated yellow spots (Fig. 35), and pronotum, mesepisternum, metanotum and metasoma wholly black (Figs 33–34).

**Etymology.** The specific name *radiatum* is Latin for radiation, referring to the notable marking on the face of the holotype resembling that of the infamous Nuclear Radiation pictogram.

## 6. Genus *Antepipona* de Saussure, 1855

*Antepipona* de Saussure, 1855: 244. Type species: *Odynerus silaos* de Saussure, 1853, by subsequent designation of van der Vecht, 1967: 30.

### (11) *Antepipona menkei* Giordani Soika, 1986

*Antepipona menkei* Giordani Soika, 1986: 130–131, “Cina: Hong Kong, Is. Lantau”, USNM. Type: female.

**Material examined.** No specimens.

**Distribution.** China (Hong Kong).

**Remarks.** Described from Hong Kong by Giordani Soika, 1986.

### (12) *Antepipona rufescens* (Smith, 1857)

Figs 40–42

*Odynerus rufescens* Smith, 1857: 61, “Ceram”, NHMUK. Type: female.

*Antepipona ferruginea* Kim & Yamane, 2003: 287, 291, figs 9–16, “Jansui, Formosa”, HUM. Syn. nov.

**Material examined.** CHINA: Hong Kong: 1♀, Kam Tin, hand net, 25.viii.2006, UTM: 50Q JK 975 843, 10m, ref.: 0227.G.Hy.2 [CBC].

**Distribution.** China (Hong Kong, Shanghai, Sichuan, Taiwan); India; Thailand; Myanmar; Laos; Malaysia; Indonesia.



**Remarks.** First recorded from Hong Kong by Giordani Soika 1986. Comparing the specimen from Hong Kong and other specimens of *A. rufescens* in the AMNH with the description of *A. ferruginea* shows that they are identical in the features cited as diagnostic by Kim and Yamane (2003). Accordingly, the species *A. ferruginea* Kim & Yamane, 2003 from Taiwan is synonymized with *A. rufescens* (Smith, 1857).

## 7. Genus *Anterhynchium* de Saussure, 1863

*Anterhynchium* de Saussure, 1863: 205. Type species: *Rygius synagroides* de Saussure, 1852, by subsequent designation of van der Vecht, 1963: 73.

### (13) *Anterhynchium* (*Anterhynchium*) *mellyi* (Saussure, 1852)

Figs 43–45

*Rygius mellyi* de Saussure, 1852: 116, “Les Indes, La Chine”, MHNG. Type: female.

**Material examined.** CHINA: Hong Kong: 3♀, Sha Lo Tong, hand net, 29.vi.2014, 18.vi.2016, UTM: 50Q KK101886, 160m, 50Q KK 100 883180m & 50Q KK 101 887, ref. 0526.E.Hy.1, leg. C. Barthélémy [AMNH], 0524.N.Hy.2 [CBC] & 0598.B.Hy.10 [CBC]; 1♀, Pak Sha O, hand net, 10.vi.2005, UTM: 50Q KK 242 849, 70m, ref.: 0134.A.Hy.1.

**Distribution.** China (Fujian, \*Hong Kong, Yunnan); India; Myanmar; Thailand; Vietnam.

**Remarks.** An occasional wasp in Hong Kong.

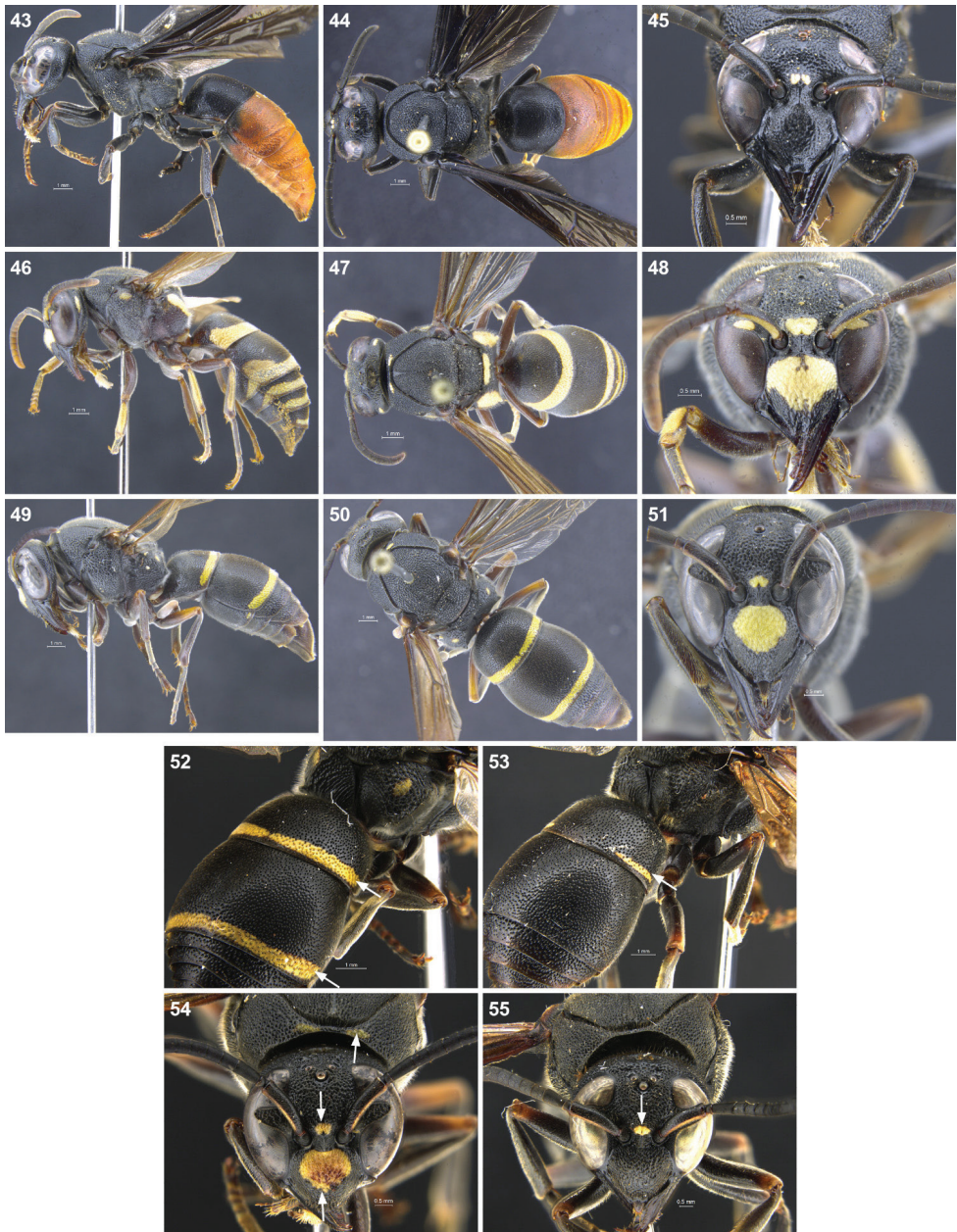
### (14) *Anterhynchium* (*Dirhynchium*) *flavolineatum flavolineatum* (Smith, 1857)

Figs 46–48, 139–142

*Odynerus flavo-lineatus* Smith, 1857: 60, “Java”, NHMUK. Type: female.

**Material examined.** CHINA: Hong Kong: 1♂, Pak Sha O, hand net, 21.iv.2009, UTM: 50Q KK 242 849, 70m, ref.: 0323.E.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, Pak Sha O, reared, 12.vi.2010, UTM: 50Q KK 242 849 70m, ref.: 0413.A.Hy.1, leg. C. Barthélémy [AMNH]; 4♀, same location, 09.v.2006, 06.vi.2010, 28.vi.2010 & 08.vii.2010; refs.: 0183.C.Hy.1 hand net, 0409.A.Hy.2 reared, 0418.A.Hy.1 reared & 0419.A.Hy.1 reared, [CBC]; 1♀, Ping Shan Chai, Malaise trap, 08–21.v.2016, UTM: 50Q KK 106 893, 140m, ref.: M245.D.Hy.1 [CBC].

**Distribution.** China (Hong Kong, Yunnan); India; Myanmar; Vietnam; Malaysia; Indonesia.



**Figures 43–55.** *Anterhynchium mellyi*, female **43** habitus (lateral view) **44** habitus (dorsal view) **45** head (frontal view) **46–48** *Anterhynchium flavolineatum*, female **46** habitus (lateral view) **47** habitus (dorsal view) **48** head (frontal view) **49–55** *Anterhynchium flavomarginatum flavomarginatum*, female **49** habitus (lateral view) **50** habitus (dorsal view) **51** head (frontal view) **52–53** variation of markings on propodeum, T1 & T2 **54–55** variation of face markings.

**Remarks.** A frequent wasp in Hong Kong. Its nesting biology was described by Barthélémy (2012) as *Antherychium* sp.1. Cells are mass-provisioned with caterpillars belonging to the family Crambidae (Barthélémy, 2012).

**(15) *Anterhynchium* (*Dirhynchium*) *flavomarginatum flavomarginatum* (Smith, 1852)**

Figs 49–55, 143–146

*Rhynchium flavo-marginatum* Smith, 1852: 35, type locality: not indicated although probably North China, NHMUK. Type: female.

**Material examined.** CHINA: Hong Kong: 4♀4♂, Pak Sha O, reared, 20.iv.2010, 01.v.2010, 19.v.2010, 19.v.2013 & 11.vi.2016, UTM: 50Q KK 242 852, 70m, refs.: 0395.A.Hy.1, 0403.A.Hy.1, 0502.A.Hy.1 & 0596.G.Hy.1 [CBC]; 1♀, High Island Reservoir, Sai Kung, hand net, 28.viii.2012, UTM: 50Q KK 269 786, 150m, ref.: 0482.B.Hy.6 [CBC]; 1♀, Ping Shan Chai, hand net, 04.vi.2016, UTM: 50Q KK 106 893, 140m, ref.: 0592.B.Hy.7 [CBC]; 13♂, Pak Sha O, reared, 22.vi.2009, 11.viii.2009, 25.iv.2010, 22.vii.2010, 24.vii.2010, 29.vii.2010, 28.iv.2011, 15.vi.2011, 12.v.2013, 17.v.2013 & 24.iv.2016, UTM: 50Q KK 242 849, 70m, refs.: 0349.A.Hy.2 [CBC], 0369.A.Hy.1 [CBC], 0398.A.Hy.1 [CBC], 0422.A.Hy.1, leg. C. Barthélémy [AMNH], 0424.A.Hy.1 & 2 [CBC], 0425.A.Hy.1 & 2 [CBC], 0438.A.Hy.1 [CBC], 0441.A.Hy.1 [CBC], 0498.A.Hy.1 [CBC], 0501.A.Hy.1 [CBC] & 0583.C.Hy.1, leg. C. Barthélémy [AMNH]; 6♀, same location, Malaise Trap, 14–31.v.2009, 31.v.–23.vi.2009, 21.xi.–26.xii.2010, 03–24.vii.2011 & 29.ix.–14.x.2012, refs.: M062.C.Hy.10 [CBC], M063.C.Hy.1 [CBC], M085.C.Hy.1 & 2, leg. C. Barthélémy [AMNH], M095.C.Hy.2, leg. C. Barthélémy [AMNH] & M116.C.Hy.1 [CBC].

**Distribution.** China (Chongqing, Fujian, Guangxi, Hong Kong, Jiangxi, Shanghai, Sichuan, Zhejiang); Pakistan; India; Nepal; Laos; Vietnam, Mongolia; Korea; Japan.

**Remarks.** An abundant wasp in Hong Kong. Dover (1926) first recorded this species from Hong Kong as *Odynerus* (*Rygius*) *flavomarginatus* Sauss. Its nesting biology was described by Barthélémy (2012) and erroneously identified as *Xenorhynchium* sp.1. Cells are mass-provisioned with caterpillars belonging to the family Crambidae (Barthélémy, 2012). There are two colour forms locally (see Figs 52–55). In fact this taxon is known for its colour variability and the nominotypical species has no less than 11 recognised subspecies, which is far from being satisfactory, further elucidation of this taxon is needed.

## 8. Genus *Apodynerus* Giordani Soika, 1993

*Apodynerus* Giordani Soika, 1993: 155. Type species: *Odynerus troglodytes* de Saussure, 1855, by original designation and monotypy.

**(16) *Apodynerus formosensis formosensis* (von Schulthess, 1934)**

Figs 56–58

*Odynerus formosensis* von Schulthess, 1934: 101, “Formosa, Kankau, Kosempo, Taihorin, Taihorinsho”, UZH. Type: Female & Male.

**Material examined.** CHINA: Hong Kong: 3♀, Ping Shan Chai, hand net, 04.v.2006, 08.vii.2006 & 12.v.2018, UTM: 50Q KK 104 891, 50Q KK 104 889 & 50Q KK 103 890, 180m, refs.: 0182.B.Hy.2 [CBC], 0210.B.Hy.2, leg. C. Barthélémy [AMNH] & 0651.B.Hy.7 [CBC]; 1♀, Kam Tin (Wetland), hand net, 25.viii.2006, UTM: 50Q JK 975 843, 10m, ref.: 0227.G.Hy.3 [CBC]; 1♀, Yuen Long, hand net, 28.viii.2007, UTM: 50Q JK 975 843, 20m, ref.: 0280.N.Hy.2 [CBC]; 1♀, Lamma Island, Hung Shing Ye, 03.v.2008, UTM: 50Q KK 031 600, 15m, ref.: 0288.N.Hy.6 [CBC]; 1♀, Ha Tin Liu Ha, hand net, 01.v.2009, UTM: 50Q KK 058 849, 60m, ref.: 0328.J.Hy.3 [CBC]; 1♀, Mai Po Nature Reserve, hand net, 02.viii.2014, UTM: 50Q JK 959 903, 1m, ref.: 0528.G.Hy.2 [CBC]; 1♀, Sha Lo Tong, hand net, 18.vi.2016, UTM: 50Q KK 101 887, 160m, ref.: 0598.B.Hy.11 [CBC]; 4♀, Pak Sha O, Malaise trap, 31.v.–06.vi.2004, 04–11.x.2004, 26.iv.–02.v.2005 & 15–31.v.2010, UTM: 50Q KK 242 849, 70m, refs.: M017.C.Hy.24, M025.C.Hy.2, M028.C.Hy.1 & M076.C.Hy.1 all [CBC]; 1♂, same location, Malaise trap, 19.vi.–03.vii.2011, ref.: M094.C.Hy.2, leg. C. Barthélémy [AMNH].

**Distribution.** China (\*Hong Kong, Taiwan).

**Remarks.** An abundant wasp in Hong Kong.

**(17) *Apodynerus troglodytes troglodytes* (de Saussure, 1855)**

Figs 59–61, 147–149

*Odynerus troglodytes* de Saussure, 1855: 249, “le Sénégal” (likely an error), MRSN. Type: male.

**Material examined.** CHINA: Hong Kong: 5♀, Pak Sha O, Malaise trap, 27.ix.–04.x.2004, 26.ix.–18.x.2009, 30.iv.–15.v.2010, 15–31.v.2010 & 05–18.v.2018, UTM: 50Q KK 242849, 70m, refs.: M024.C.Hy.3 [CBC], M067.C.Hy.13 [CBC], M075.C.Hy.7, leg. C. Barthélémy [AMNH], M076.C.Hy.2 [CBC] & M346.C.Hy.2 [CBC]; 3♀, Mang Kung Wo, Malaise trap, 14–28.iv.2018, 12–26.v.2018 & 21.vii.–04.viii.2018, UTM: 50Q KK 174 760, 60m, refs.: M342.C.Hy.2, M348.C.Hy.6 & M356.C.Hy.1 all [CBC]; 1♀, Ping Shan Chai, Malaise trap, 14–28.vii.2018, UTM: 50Q KK 106 893, 140m, ref.: M354.D.Hy.1 [CBC].

**Distribution.** China (Guangdong, Guangxi, Hainan, Hong Kong, Yunnan); India; Myanmar; Thailand; Laos; Vietnam; Malaysia; Singapore; Indonesia; Philippines.

**Remarks.** A frequent wasp in Hong Kong. It is a tube renter; Barthélémy (2012) reported on its nesting biology as *Apodynerus* sp.1.





**Figures 56–70.** *Apodynerus formosensis formosensis*, female **56** habitus (lateral view) **57** habitus (dorsal view) **58** head (frontal view) **59–61** *Apodynerus troglodytes troglodytes*, female **59** habitus (lateral view) **60** habitus (dorsal view) **61** head (frontal view) **62–64** *Coleuemenes burmanicus*, female **62** habitus (lateral view) **63** habitus (dorsal view) **64** head (frontal view) **65–67** *Ectopioglossa ovalis*, female **65** habitus (lateral view) **66** habitus (dorsal view) **67** head (frontal view) **68–70** *Epsilon dyscherum*, female **68** habitus (lateral view) **69** habitus (dorsal view) **70** head (frontal view).

## 9. Genus *Coeleumenes* van der Vecht, 1963

*Coeleumenes* van der Vecht, 1963: 45. Type species: *Montezumia impavida* Bingham, 1897: 351, by original designation.

### (18) *Coeleumenes burmanicus* (Bingham, 1897)

Figs 62–64

*Montezumia burmanica* Bingham, 1897: 350, fig. 101, “Tenasserim” (Myanmar), NHMUK. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Sha Lo Tong, hand net, 11.vii.2015, UTM: 50Q KK 100 886, 160m, Ref.: 0553 C.Hy.6, leg. C. Barthélémy [AMNH]; 1♀, Ping Shan Chai, hand net, 28.vii.2018, UTM: 50Q KK 102 895, 180m, ref.: 0654.B.Hy.1 [CBC]; 3♀, Ping Shan Chai, Malaise trap, 21.v.–04.vi.2016, 16–30.vii.2016 & 21.x.–18.xi.2017, UTM: 50Q KK 106 893, 140m, refs. M247.D.Hy.1, M255.D.Hy.2 & M319.D.Hy.1 all [CBC].

**Distribution.** China (Guangxi, \*Hong Kong, Zhejiang); India; Myanmar; Thailand; Laos; Vietnam; Malaysia.

**Remarks.** An occasional wasp in Hong Kong.

## 10. Genus *Ectopioglossa* Perkins, 1912

*Ectopioglossa* Perkins, 1912:118. Type species: *Ectopioglossa australensis* Perkins, 1912 by monotypy.

### (19) *Ectopioglossa ovalis* Giordani Soika, 1993

Figs 65–67

*Ectopioglossa ovalis* Giordani Soika, 1993: 160, “Cina: IS. Hainan, Ta Hian”, RMNH. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, Malaise trap, 03–24.vii.2011, UTM: 50Q KK 242 849, 70m, ref.: M095.C.Hy.3 [CBC].

**Distribution.** China (Guangdong, Hainan, \*Hong Kong).

**Remarks.** Known from a single specimen, scarce in Hong Kong.

## 11. Genus *Epsilon* de Saussure, 1855

*Epsilon* de Saussure, 1855: 229, 252. Type species: *Odynerus dyscherus* de Saussure, 1852, by subsequent designation of van der Vecht, 1967: 31.

### (20) *Epsilon dyscherum* (Saussure, 1852)

Figs 68–70

*Odynerus dyscherus* de Saussure, 1852: 175, “La Chine. Manilla?”, MNHN. Type: male.

**Material examined.** CHINA: Hong Kong: 1♀, Ping Shan Chai, hand net, 30.v.2015, UTM: 50Q KK 106883, 140m, ref.: 0546.B.Hy.2 [CBC].

**Distribution.** \*China (\*Hong Kong); Philippines.

**Remarks.** Known from a single specimen.

## 12. Genus *Euodynerus* Dalla Torre, 1904

*Euodynerus* Dalla Torre, 1904: 38. Type species: *Vespa dantici* Rossi, 1790: 89, by subsequent designation of Blüthgen, 1938 (1937): 277.

### (21) *Euodynerus (Euodynerus) dantici violaceipennis* Giordani Soika, 1973

Figs 71–73

*Euodynerus dantici violaceipennis* Giordani Soika, 1973: 124, “China: Canton”, MSNV. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Sha Lo Tong, hand net, 16.vii.2016, UTM: 50Q KK101 887, 160m, ref.: 0606.B.Hy.2 [CBC].

**Distribution.** China (Guangdong, \*Hong Kong, Jiangsu, Taiwan); Vietnam; Korea; Japan.

**Remarks.** Known from a single specimen; it has Palearctic affinities.

### (22) *Euodynerus (Pareuodynerus) trilobus* (Fabricius, 1787)

Figs 74–76

*Vespa triloba* Fabricius, 1787: 290, “China”, ZMUC. Type: sex unknown.

**Material examined.** CHINA: Hong Kong: 1♀, Wang Tong, Lantau Isl., hand net, 05.vii.2016 UTM: 49Q HE 087 660, 10m, leg. Paul Aston [CBC].





**Figures 71–85.** *Euodynerus dantici violaceipennis*, female **71** habitus (lateral view) **72** habitus (dorsal view) **73** head (frontal view) **74–76** *Euodynerus trilobus*, female **74** habitus (lateral view) **75** habitus (dorsal view) **76** head (frontal view) **77–79** *Labus edenticulus*, female **77** habitus (lateral view) **78** habitus (dorsal view) **79** head (frontal view) **80–82** *Lissodynerus septemfasciatus feanus*, female **80** habitus (lateral view) **81** habitus (dorsal view) **82** head (frontal view) **83–85** *Orancistrocerus aterrimus erythropus*, female **83** habitus (lateral view) **84** habitus (dorsal view) **85** head (frontal view).



**Distribution.** China (Anhui, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Jiangsu, Jiangxi, Shanghai, Sichuan, Taiwan, Zhejiang); British Indian Ocean Territories; Mauritius; Réunion; Vietnam; Malaysia; Indonesia; Japan.

**Remarks.** Known from a single specimen. Firstly recorded from Hong Kong by Dover (1926) as *Odynerus trilobus* Fabr. This species has Palearctic affinities.

### 13. Genus *Labus* de Saussure, 1867

*Labus* de Saussure, 1867: 3. Type species: Male, *Labus spiniger* de Saussure, 1867, by subsequent designation of Bingham, 1897: 348.

#### (23) *Labus edenticulus* Li & Carpenter, 2018

Figs 77–79

*Labus edenticulus* Li & Carpenter, 2018, Hong Kong, AMNH. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Hung Fa Leng, Malaise trap, 16.iv.–16.v.2014, UTM: 50Q KK 108 854, 435m, Yiu Vor, Ref.: HFL-M001.FHy.9, leg. C. Barthélémy [AMNH]; 1♂, Yung Shue O, hand net, 18.x.2012, ref.: JXQL001-Hy.1, leg. John X.Q.Lee [CBC].

**Distribution.** China (Hong Kong).

**Remarks.** A scarce species in HK. Described from Hong Kong by Li and Carpenter (2018).

### 14. Genus *Lissodynerus* Giordani Soika, 1993

#### (24) *Lissodynerus septemfasciatus feanus* (Giordani Soika, 1941)

Figs 80–82, 150–154

*Ancistrocerus septemfasciatus* var. *feanus* Giordani Soika, 1941: 239, “Carin Cheba, Burma” (Myanmar), MHNG. Lectotype: female.

**Material examined.** CHINA: Hong Kong: 4♀, Pak Sha O, reared, 23.v.2013, 28.v.2013 & 08.viii.2014, UTM: 50Q KK 242 849 70m, refs.: 0519.A.Hy.1 [CBC], 0521.A.Hy.2 [CBC], 0521.A.Hy.3 [CBC] & 0529.A.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, Sha Lo Tong, hand net, 16.vii.2016, UTM: 50Q KK 101 887, 160m, ref.: 0606.B.Hy.1 [CBC]; 1♀3♂♂, Guangdong Prov., Shaoguan City, Shixing County, Chebaling National Nature Reserve, V. 6. 2017, leg. Fei-Yue Dou (CQNU).

**Distribution.** China (Guangxi, \*Guangdong, \*Hong Kong); India; Myanmar; Vietnam; Malaysia.

**Remarks.** An occasional wasp in Hong Kong. Nests are constructed inside cavities and the species readily accepts bamboo segments as nesting site. Cell partitions are constructed with a resinous material (Figs 150–154). Dissected cells were mass-provisioned with caterpillars in the family Geometridae and probably also Erebidae (CB pers. obs., det. Dr. Roger Kendrick, Hong Kong).

## 15. Genus *Orancistrocerus* van der Vecht, 1963

*Orancistrocerus* van der Vecht, 1963: 58. Type species: *Odynerus drewseni* de Saussure, 1857: 318, by original designation.

### (25) *Orancistrocerus aterrimus erythropus* (Bingham, 1897)

Figs 83–85, 155–158

*Rhynchium erythropus* Bingham, 1897: 352, 353, “Tenasserim” (Myanmar), NHMUK. Type: male.

**Material examined.** CHINA: HONG KONG: 3♀, Pak Sha O, reared, 04.v.2009, 05.v.2009 & 28.v.2013, UTM: 50Q KK 242 849, 70m, refs.: 0331.A.Hy.1 [CBC], 0332.A.Hy.1, leg. C. Barthélémy [AMNH], 0521.A.Hy.1 [CBC]; 2♂, same location, reared, 17.iv.2009 & 19.iv.2009, refs.: 0319.A.Hy.1, leg. C. Barthélémy [AMNH] & 0321.A.Hy.2 [CBC]; 2♀, same location, hand net, 01.xi.2003 & 19.v.2018, refs.: 0101.C.Hy.1 & 0652.C.Hy.1 both [CBC].

**Distribution.** China (Guangdong, Guangxi, Hong Kong, Sichuan, Yunnan, Zhejiang); Myanmar; Laos; Thailand.

**Remarks.** Barthélémy (2012) reported on the nesting biology of this species under the erroneous name *Pararrhynchium* sp.1. Dissected cells were mass-provisioned with caterpillars in the subfamily Spilomelinae (Crambidae) (Barthélémy 2012).

## 16. Genus *Orientalicesa* Koçak & Kemal, 2010

*Kennethia* Giordani Soika, 1994: 4, 289.

*Kennetia* Giordani Soika, 1994: 289. Incorrect original spelling of *Kennethia* Giordani Soika.

*Orientalicesa* Koçak & Kemal, 2010: 4, replacement name for *Kennethia* Giordani Soika, 1994, non De Dekker, 1979.

**Type species.** *Odynerus unifasciatus* von Schulthess, 1934, by original designation.

**(26) \**Orientalicesa nigra* sp. nov.**

<http://zoobank.org/F1D39412-263A-466D-9390-601FADE7E897>

Figs 86–91

**Material examined.** CHINA: Hong Kong, HOLOTYPE, ♀, Park Sha O, hand net, 15–27.iv.2008, UTM: 50Q KK 242 849, 70m, 0554.C.Hy.1, leg. C. Barthélémy [AMNH].

**Description.** Female (Figs 86–91): body length 9.0 mm; fore wing length 10.5 mm. Black, with the following parts yellow: two small interantennal spots (Fig. 88), scape ventrally, a small spot on base of mandible, and a small band of fore tibia inside; antenna except scape, mandible except a spot, all legs except the band of fore tibia, tegula, and apex of parategula dark ferruginous. Wings brown, infusate, veins dark brown.

Head. Clypeus (Fig. 88) 1.02× as wide as long, medially convex, coarsely punctate, interspaces between punctures more or less reticulate; apex slightly emarginated medially and forming blunt tooth on each lateral side, total width 3.29× apical width, apical width 7× emargination depth and as wide as interantennal space; interantennal carina prominent; frons slightly convex and coarsely punctate, distinctly carinate and reticulate between punctures; vertex (Fig. 89) with two large cephalic foveae, brown pubescence inserted mesally, depression for cephalic foveae distinctly concave, and with a medio-longitudinal carina from anterior ocellus to occipital carina and connecting occipital carina, punctures on other parts of vertex and gena relatively sparser; occipital carina complete.

Mesosoma. Mesosoma not visibly depressed; pronotal carina complete and strong, anterior sloping face of pronotum obviously polished; pronotum, mesoscutum, mesepisternum, scutellum, and metanotum coarsely and deeply punctate, interspaces between punctures with distinct carinae and reticulate, epicnemial carina present, not strong; mesoscutum weakly convex, scutellum flat, in lateral view at same level as mesoscutum, strongly depressed along anterior margin with some short longitudinal carinae, and without a medial longitudinal furrow from middle to apex; metanotum sloping down to apical margin; propodeum (Fig. 90) without horizontal area behind midline of metanotum, dorsal face of propodeum coarsely punctate, punctures large, shallow, flat bottomed and interspaces with reticulate carinate, superior carinae (Fig. 90) of propodeum well developed and on top forming a pair of large triangular teeth behind metanotum, carinae curved, posterior surface distinctly concave, with few faint striae, and bordered by superior carina with wide V-shaped incision in middle above; tegula shorter than parategula posteriorly.

Metasoma. T1 wider than long, width 1.63× its length and 0.83× width of T2, vertical anterior faces distinctly coriaceous and separated from horizontal surface, horizontal surface without transverse carina and moderately punctate, punctures much sparser and smaller than those of head and mesosoma, apex with a wide, smooth and shiny preapical band (Fig. 91); T2 1.29× as wide as long, with a row of larger and denser punctures at about 1/5 of their length from apical margin and forming a broad



**Figures 86–97.** *Orientalicesa nigra* sp. nov., female **86** habitus (lateral view) **87** habitus (dorsal view) **88** head (frontal view) **88** face (frontal view) **89** dorsal view of vertex **90** propodeum (dorsal view) **91** metasoma (dorsal view) **92–94** *Paraleptomenes kosempoensis*, female **92** habitus (lateral view) **93** habitus (dorsal view) **94** head (frontal view) **95–97** *Parancistrocerus hongkongensis*, female **95** habitus (lateral view) **96** habitus (dorsal view) **97** head (frontal view).



smooth and shiny preapical band (Fig. 91) and with another row of sparse punctures close to the apical edge, other punctures of T2 slightly sparser than those of T1, sub-apex of T2 not swollen; S2 sparsely punctate and regularly convex; visible apexes of T3–T5 with the similar preapical bands to that of T2; lateral margins of T2–T4 clearly marginalized.

Male. Unknown.

**Distribution.** \*China (\*Hong Kong).

**Remarks.** This species is similar to *O. bicolorata* (Giordani Soika, 1994) from Indonesia in superior carinae of propodeum well developed and forming a pair of large triangular teeth behind metanotum, punctures of T2 moderately dense and not larger than those of mesoscutum, and apex of T2 with another row of sparse punctures close to the apical edge. It can be distinguished from the related species and all other members of the genus by the combination of following characters: mesosoma not visibly depressed, and the body (Figs 86–87) almost wholly black and without yellowish or reddish-ferruginous spots or bands.

**Etymology.** The specific name refers to the body almost wholly black.

## 17. Genus *Paraleptomenes* Giordani Soika, 1970

*Paraleptomenes* Giordani Soika, 1970. Type species: *Paraleptomenes nurseanus* Giordani Soika, 1970: 79, Fig.16, pl.V, by original designation and monotypy.

### (27) *Paraleptomenes kosempoensis* (von Schulthess, 1934)

Figs 92–94

*Odynerus kosempoensis* von Schulthess, 1934: 102, “Formosa”, NMW. Type: male.

**Material examined.** CHINA: Hong Kong: 2♀, Tai Tam, Malaise trap, 23–30.x.2017, 22.24614N, 114.22334E, 2m, ref.: 0682.Y.Hy.1, leg. C. Taylor [CBC].

**Distribution.** China (\*Hong Kong, Taiwan).

**Remarks.** Species collected in mangroves.

## 18. Genus *Parancistrocerus* Bequaert, 1925

*Parancistrocerus* Bequaert, 1925: 64. Type species: *Odynerus flavipes* de Saussure, 1855: 205 [= *O. “flavipes* Fabricius” *sensu* de Saussure, 1852, non *Vespa flavipes* Fabricius, 1775], by original designation.

**(28) *Parancistrocerus hongkongensis* Gusenleitner, 2002**

Figs 95–97

*Parancistrocerus hongkongensis* Gusenleitner, 2002: 1091, 1095, “Hong Kong, Lantau I., Shui Hau, 20–50 m, 22.22N, 113.92E”, LACM. Type: Holotype female, male.

**Material examined.** CHINA: Hong Kong: 2♀, Sha Lo Tong & Pak Sha O, hand net, 01.v.2006 & 01.v.2009, UTM: 50Q KK 101 884 & 50Q KK 242 849, 160 m & 70m, refs.: 0177.B.Hy.1, leg. C. Barthélémy [AMNH] & 0328.E.Hy.2 [CBC]; 1♀, Pak Sha O, Malaise trap, 23.viii.–12.ix.2014; UTM: 50Q KK 242 849, 70m, ref.: M173.C.Hy.4 [CBC]; 2♀, Mang Kung Wo, hand net, 21.viii.18 & 02.ix.18, UTM: 50Q KK 174 760, 60m, Refs.: 0659.C.Hy.3 & 0662.C.Hy.1 [CBC].

**Distribution.** China (Hong Kong).

**Remarks.** A frequent wasp in Hong Kong, known to visit flowers of *Vitex negundo* Linn.

**(29) *Parancistrocerus yachowensis* Giordani Soika, 1986**

Figs 98–100

*Parancistrocerus yachowensis* Giordani Soika, 1986: 125, figs. 31, 33, “Cina: Szechuan, Tachow”, USNM. Type: female.

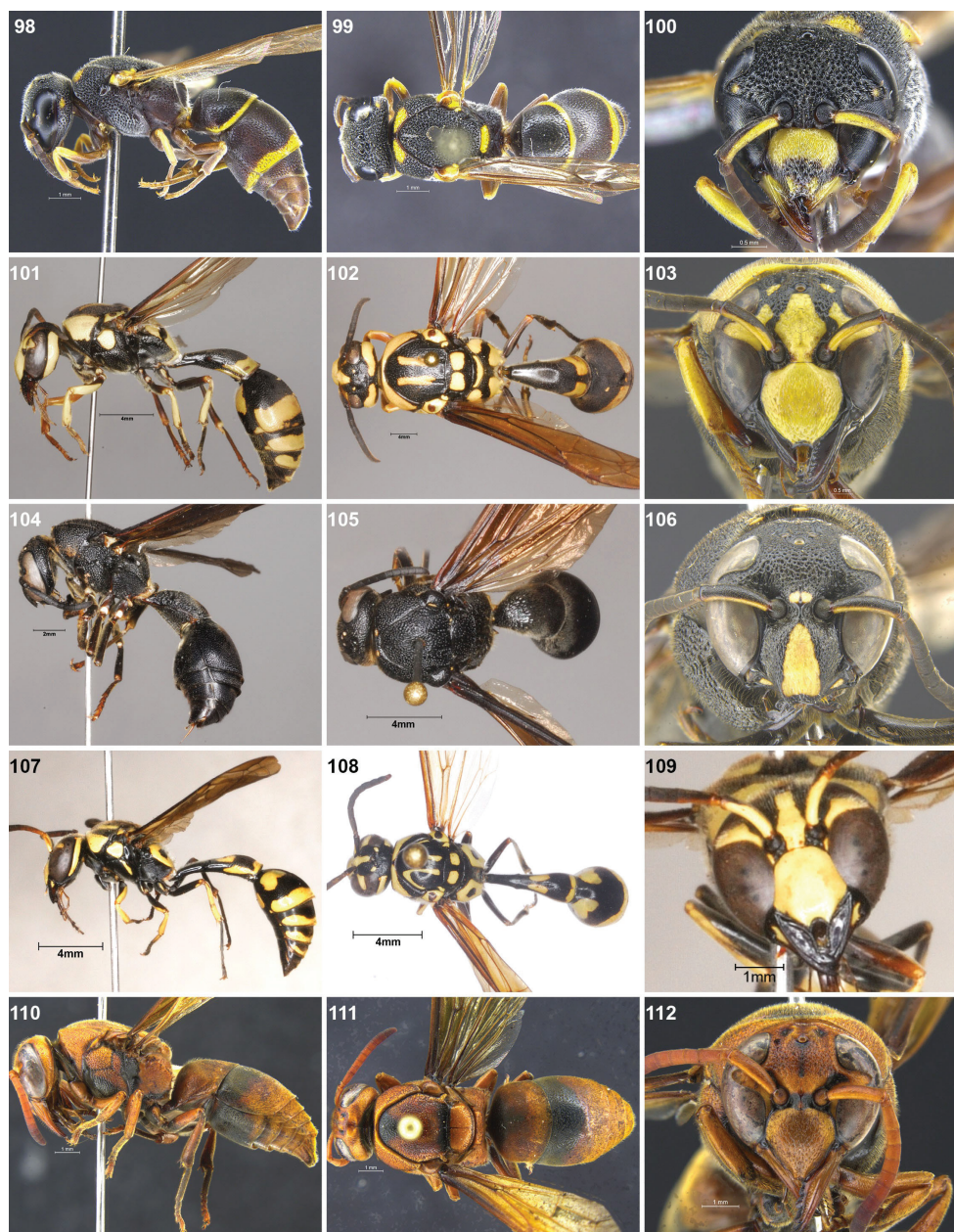
**Material examined.** CHINA: Hong Kong: 2♀, Fung Yuen Li & Pak Sha O, hand net, 31.viii.2006 & 17.iv.2011, UTM: 50Q KK 097 873 & 50Q KK 242 849, 30m & 70m, Refs.: 0228.E.Hy.4 & 0435.A.Hy.1 [CBC]; 1♀, Pak Sha O, Malaise trap, 27.iv.–14.v.2009, UTM: 50Q KK 242 849, 70m, Ref.: M061.C.Hy.13 [CBC]. INDONESIA: North Sulawesi: 1♀, Tomohon, hand net, 08.vi.2008, 01°20'N, 124°50'E, 720m, Ref.: 0290.C.Hy.1 [CBC].

**Distribution.** China (\*Hong Kong, Sichuan, Taiwan); \*Indonesia (North Sulawesi: Tomohon); Laos.

**Remarks.** Two subspecies are recognized, *P. y. konkunesis* Giordani Soika, 1994 and *P. y. yachowensis* Giordani Soika, 1986. The Hong Kong material shows a mix of characters used by Giordani Soika (1994) and Li and Carpenter (2018) between the nominotypical form and *P. y. konkunesis* which does not allow us to conclude the sub-specific placement of our Hong Kong material. In addition, a specimen from Sulawesi collected by CB and examined by JC, is recognized as similar to the Hong Kong material, increasing substantially the biogeographic range of this taxon.

**19. Genus *Pareumenes* de Saussure, 1855**

*Pareumenes* de Saussure, 1855. Type species: *Eumenes quadrispinosus* de Saussure, 1855: 133, by subsequent designation of Bequaert, 1918: 271.



**Figures 98–112.** *Parancistrocerus yachowensis*, female **98** habitus (lateral view) **99** habitus (dorsal view) **100** head (frontal view) **101–103** *Pareumenes quadrispinosus acutus*, female **101** habitus (lateral view) **102** habitus (dorsal view) **103** head (frontal view) **104–106** *Pseudozumia indica indica*, female **104** habitus (lateral view) **105** habitus (dorsal view) **106** head (frontal view) **107–109** *Pseumenes depressus depressus*, male **107** habitus (lateral view) **108** habitus (dorsal view) **109** head (frontal view) **110–112** *Rhynchium brunneum brunneum*, female **110** habitus (lateral view) **111** habitus (dorsal view) **112** head (frontal view).

**(30) *Pareumenes (Pareumenes) quadrispinosus acutus* Liu, 1941**

Figs 101–103

*Pareumenes acutus* Liu, 1941: 255, 262, “South China”, Coll. Liu. Type: female.

**Material examined.** CHINA: Hong Kong: 3♀, Pak Sha O, hand net, 19.ix. 2001, 27.vi.2006 & 29.vi.2009, UTM: 50Q KK 242 849 70m, refs.: 0058.A.Hy.1, 0203.B.Hy.2 [CBC] & 0351.A.Hy.1, leg. C. Barthélémy [AMNH]; 1♂, same location, reared, 13.iv.2009, ref.: 0317.A.Hy.7 [CBC]; 2♀, same location, Malaise trap, 26.iv.–03.v.2004 & 2–14.v.2011, refs.: M012.C.Hy.22 & M091.C.Hy.3 both [CBC]; 2♀, Ping Shan Chai, hand net, 27.vi.2006 & 27.vi.2015, UTM: 50Q KK 104 891, 180m & 140m, refs.: 0203.B.Hy.1 & 0550.B.Hy.2 both [CBC].

**Distribution.** China (Guangdong, Guangxi, Hong Kong, Yunnan); India; Bhutan; Vietnam.

**Remarks.** A frequent wasp in Hong Kong, known to visit flowers of *Vitex negundo* Linn. Nesting biology was reported by Barthélémy (2012). Dover (1926) recorded *Pareumenes quadrispinosus* Sauss. from the SAR, however, as mentioned in the introduction, none of his examined material survives today, in consequence we are unable to ascertain that he saw *P. q. acutus*, but because no other subspecies have been collected from Hong Kong since then, there is great probability that it was in fact *P. q. acutus*. Dissected cells were mass-provisioned with caterpillars in the family Thyrididae (CB pers. obs., det. Dr. Roger Kendrick, Hong Kong).

**20. Genus *Pseudozumia* de Saussure, 1875**

*Pseudozumia* de Saussure, 1875: 128. Type species: *Montezumia indica* de Saussure, 1855: 167, by monotypy.

**(31) *Pseudozumia (Pseudozumia) indica indica* (Saussure, 1855)**

Figs 104–106

*Montezumia indica* de Saussure, 1855: 167, pl. 9 figs. 4, 4a, “Java”, MRSN. Lectotype: female.

**Material examined.** CHINA: Hong Kong, 1♀, Sha Lo Wan, Lantau Isl., hand net. 30.xii.2015, 22.17N 113.54E, 60m, ref.: 0582.B.Hy.1, leg. C. Barthélémy [AMNH]; 1♀, Ping Shan Chai, Malaise trap, 30.v.–13.vi.2015, UTM: 50Q KK 106 893, 140m, ref.: M206.D Hy.1 [CBC].

**Distribution.** China (Guangxi, \*Hong Kong, Taiwan); India; Sri Lanka; Malaysia; Vietnam; Indonesia.

**Remarks.** A scarce wasp in Hong Kong.



## 21. Genus *Pseumenes* Giordani Soika, 1935

*Pseumenes* Giordani Soika, 1935: 145. Type species: *Eumenes eximius* Smith, 1861: 126, by original designation.

### (32) *Pseumenes depressus* (Saussure, 1855)

Figs 107–109

*Eumenes depressus* de Saussure, 1855: 135, “Les Indes Orientales”, MNHN. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, hand net, 14.viii.2009, UTM: 50Q KK 242849, 70m, ref.: 0371.C.Hy.1 [CBC]; 1♀, same location, Malaise trap, 1–24.vii.2011, ref.: M095.C.Hy.1, [CBC]; 1♀, Sha Lo Tong, hand net, 29.vi.2014, UTM: 50Q KK 102 883, 180m, ref.: 0524.B.Hy.3 [CBC].

**Distribution.** China (Anhui, Fujian, Guangxi, Hong Kong, Jiangsu, Taiwan, Yunnan, Zhejiang); India; Myanmar; Thailand; Malaysia; Vietnam.

**Remarks.** A frequent wasp in Hong Kong. Firstly recorded from Hong Kong by Dover (1926) as *Pareumenes depressa* Sauss.

## 22. Genus *Rhynchium* Spinola, 1806

*Rhynchium* Spinola, 1806: 84. Type species: *Rygchium europaeum* Spinola, 1806 [= *Vespa oculata* Fabricius, 1781], by monotypy.

### (33) *Rhynchium brunneum brunneum* (Fabricius, 1793)

Figs 110–112

*Vespa brunnea* Fabricius, 1793: 264, “Tranquebariae” (Tharangambadi, Tamil Nadu, India), ZMUC. Type: sex not stated.

**Material examined.** CHINA: Hong Kong: 2♀, Pak Sha O, hand net, 11.vii.03 & 12.vi.2011, UTM: 50Q KK 242852, 70m, refs.: 0091.A.Hy.1 [CBC] & 0440.A.Hy.1, leg. C. Barthélémy [AMNH]; 1♂1♀, Mai Po Nature Reserve, hand net, 19.vii.2014, UTM: R. 50Q JK959903, 1m, refs.: 0527.G.Hy.3 & 0527.G.Hy.6 both [CBC].

**Distribution.** China (Guangdong, \*Hong Kong, Taiwan, Yunnan); Pakistan; Seychelles; India; Bangladesh; Myanmar; Thailand; Cambodia; Laos; Vietnam; Malaysia; Indonesia; New Britain; Marianas; Palau.

**Remarks.** An occasional wasp in Hong Kong. Easily confused with *Rhynchium quinquecinctum quinquecinctum* and only minor colour differences of the scutellum permit differentiation.

**(34) *Rhynchium quinquecinctum quinquecinctum* (Fabricius, 1787)**

Figs 113–115

*Vespa quinquecincta* Fabricius, 1787: 288, “in China”, ZMUC. Type: sex not indicated.

**Material examined.** CHINA: Hong Kong: 1 ♀, Mang Kung Wo, hand net, 29.v.2017, UTM: 50Q KK 174 760, 60m, ref.: 0629.A.Hy.1 [CBC].

**Distribution.** China (Hong Kong, Shaanxi, Sichuan, Taiwan, Yunnan); Pakistan; Bhutan.

**Remarks.** A scarce wasp in Hong Kong. First recorded from Hong Kong by Dover (1926) as *Odynerus haemorrhoidalis* var. *quinquecincta* Fabr. Known from a single specimen.

**23. Genus *Subancistrocerus* de Saussure, 1855**

*Subancistrocerus* de Saussure, 1855: 206. Type species: *Odynerus sichelii* de Saussure, 1855, by subsequent designation of Bequaert 1925: 61.

**(35) *Subancistrocerus camicrus* (Cameron, 1904)**

Figs 116–118

*Odynerus camicrus* Cameron, 1904a: 259, in “Darjeeling”, NHMUK. Type: male.

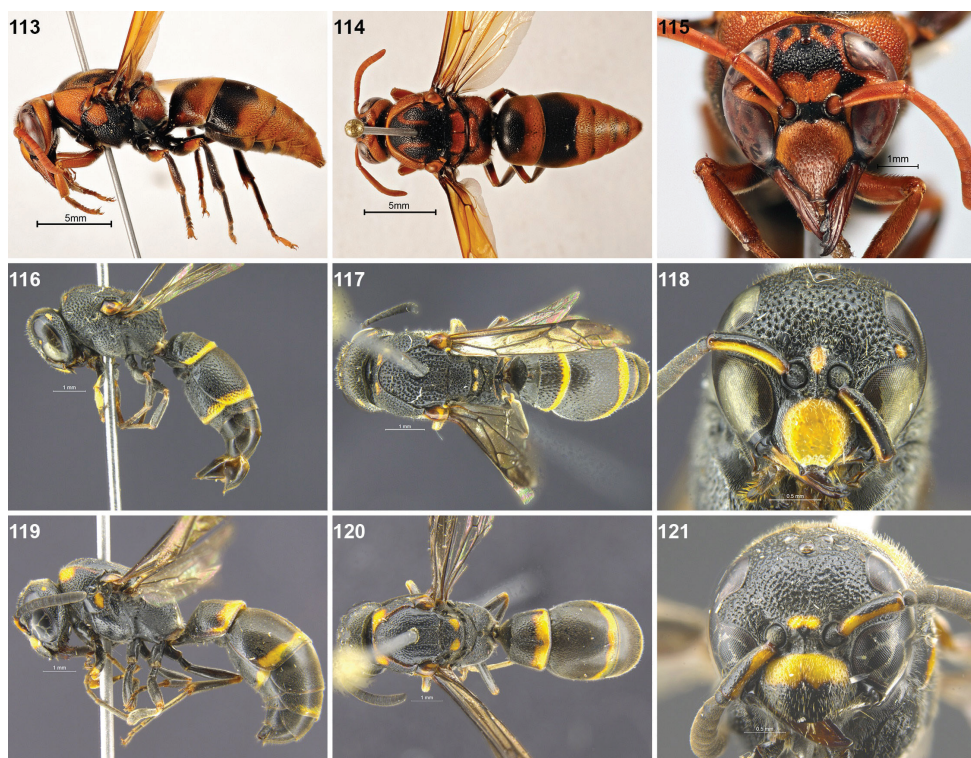
**Material examined.** CHINA: Hong Kong: 1 ♀, Mang Kung Wo, hand net, 15.ix.2018, UTM: 50Q KK 174 760, 60m, ref.: M365.C.Hy.1 [CBC]

**Distribution.** China (Chongqing, \*Hong Kong, Sichuan, Yunnan); India; Nepal; Thailand; Myanmar; Laos; Malaysia.

**Remarks.** A scarce wasp in Hong Kong.

**24. Genus *Symmorphus* Wesmael, 1836**

*Symmorphus* Wesmael, 1836: 45. Type species: *Odynerus elegans* Wesmael, 1833, by subsequent designation of Richards, 1935: 162.



**Figures 113–121.** *Rhynchium quinquecinctum quinquecinctum*, female **113** habitus (lateral view) **114** habitus (dorsal view) **115** head (frontal view) **116–118** *Subancistrocerus camicrus*, female **116** habitus (lateral view) **117** habitus (dorsal view) **118** head (frontal view) **119–121** *Symmorphus tsushmanus*, female **119** habitus (lateral view) **120** habitus (dorsal view) **121** head (frontal view).

**(36) *Symmorphus tsushmanus* Yamane, 1990**

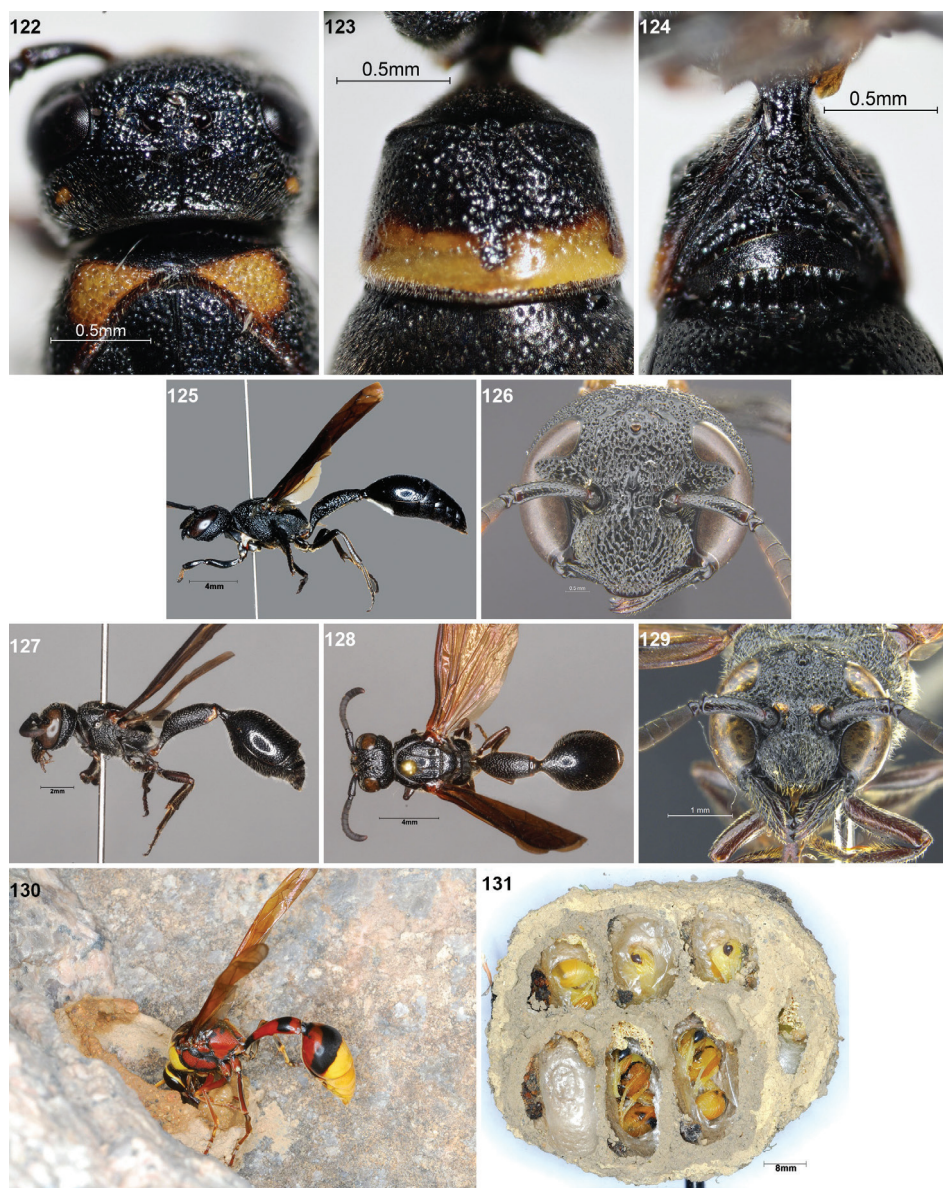
Figs 119–124

*Symmorphus tsushmanus* Yamane, 1990: 1, 115, “top of Ariake-san (558 m. alt.), Tsushima Is.” [Japan], OCMNH. Type: male.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, Malaise trap, 08–21. iv.2018, UTM: 50Q KK 242 849, 70m, ref.: M340.C.Hy.4 [CBC].

**First description of female.** Body length 7.5 mm, fore wing length 8.5 mm. Black (Figs 119–120), with yellow to orange yellow markings as follows: basal half of clypeus (Fig. 121), a spot above interantennal space, a large band on antennal scape ventrally, a small spot on upper part of gena, a pair of big triangular spots on pronotum anteriorly, a spot on dorsal mesepisternum, a pair of spots on scutellum, wide apical band of T1 (laterally narrower and mesally with anterior incision), wide apical band of T2 (somewhat sinuate), medially interrupted apical band on S2, a narrow apical band on





**Figures 122–131.** *Symmorphus tsushmanus*, female **122** vertex (dorsal view) **123** T1 (dorsal view) **124** S1 (ventral view) **125–126** *Calligaster himalayensis*, female **125** habitus (lateral view) **126** head (frontal view) **127–129** *Zethus dolosus*, female **127** habitus (lateral view) **128** habitus (dorsal view) **129** head (frontal view) **130–131** *Delta pyriforme* **130** female constructing a cell **131** ventral side of a nest showing seven cells with brood, most at advanced pupal stage.

T4 (not extending to lateral margin), apices of fore and mid femur, ventral face of fore tibia, and a spot of tegula posteriorly; mandible and tegula (except yellow spot) dark ferruginous; legs except yellow parts blackish brown.



Head about as wide as long in front view; clypeus (Fig. 121) wider than long, minutely and sparsely punctate, apical margin almost truncated, apical width equal to interantennal distance; frons coarsely punctuate, interspaces between punctures reticulate; punctures on vertex and gena slightly sparser than those of frons; two cephalic foveae (Fig. 122) right behind posterior ocelli, just a little smaller than posterior ocelli and bearing brownish setae; occipital carina complete, without incision. Pronotal carina (Fig. 122) complete, front corner slightly produced, pronotum coarsely punctate and somewhat striate on lateral side; punctures on mesoscutum and scutellum sparsely bigger and a little sparser than those of pronotum, interspaces between punctures with minute punctures, notaulices of mesoscutum complete and median scutalline present at base; scutellum with a median furrow; epicnemial carina present and strong; mesopleuron just obviously with a few sparse punctures, interspaces between punctures polished; metanotum coarsely punctate in basal half and coriaceous in apical part; metapleuron finely striate; propodeal shelf narrow and indistinct, and with a deep median orifice; dorsal face of propodeum coarsely punctate, punctures large, shallow, flat bottomed and interspaces between punctures obviously with reticulate carinae; posterior side of propodeum finely striate and with strong median carina; lateral side of propodeum striate, sparsely with a few large punctures posteriorly. Anterior vertical face of T1 with ill-defined punctures except for upper part, without vertical carina; transverse carina mesally with a deep U-formed incision; dorsal horizontal part of T1 (Fig. 123) distinctly wider than long, coarsely punctate excluding apical yellow, smooth band; without apical lamella as that of Japanese male (Yamane 1990); S1 (Fig. 124) punctate and carinate almost as that in male (Kim and Lee 2006); other tergites and sternites much more finely punctate. Anterior faces of coxae and femora below with silver setae.

**Distribution.** \*China (\*Hong Kong); South Korea; Japan.

**Remarks.** A scarce wasp in Hong Kong, known from a single specimen. The species has Palearctic affinities.

## Tribe ZETHINI

### 25. Genus *Calligaster* de Saussure, 1852

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

#### (37) *Calligaster himalayensis* (Cameron, 1904)

Figs 125–126, 159–160

Type species: female, *Zethus himalayensis* Cameron, 1904b: 13, “Sikkim”, NHMUK.

**Material examined.** CHINA: Hong Kong: 1♀, High Island Reservoir, Sai Kung, hand net, 01.viii.2012, UTM: 50Q KK 266 791, ref.: 0655.B.Hy.1, leg. John X.Q. Lee [CBC].

**Distribution.** China (Guangdong, \*Hong Kong); India; Laos; Vietnam.

**Remarks.** A scarce wasp in Hong Kong, it also probably has a restricted distribution in the territory. Nesting sites have been observed over several years in the same location(s).

## 26. Genus *Zethus* Fabricius, 1804

*Zethus* Fabricius, 1804. Type species: *Zethus coeruleo-pennis* Fabricius, 1804: 282, [= *Vespa coeruleopennis* Fabricius, 1798: 263], by subsequent designation of Latreille, 1810: 328, 438.

### (38) *Zethus dolosus* Bingham, 1897

Figs 127–129, 161–164

*Zethus dolosus* Bingham 1897: 332, 333 “Burma (Pegu Hills); Tenasserim”, NHMUK. Type: female.

**Material examined.** CHINA: Hong Kong: 1♀, Pak Sha O, hand net, 11.vii.2007, UTM: 50Q KK 242852 70m, ref.: 0267.C.Hy.2 [CBC]: same location, 1♂, hand net, 27.vii.2009, ref.: 0366.C.Hy.3 [CBC]; same location, 5♀, reared, 07.xii.2010, 21.iv.2010, 19.v.2013, 24.iv.2016 & 28.iv.2016, refs.: 0380.A.Hy.1 [CBC], 0396.A.Hy.1 leg. C. Barthélémy [AMNH], 0503.A.Hy.1 [CBC], 0584.C.Hy.1 [CBC] & 0585.C.Hy.1 [CBC]; same location, 10♂, 22.iv.2010, 27.iv.2010, 27.vii.2011, 31.v.2013, 16.iv.20016, 17.iv.2016 & 23.iv.2016, refs.: 0397.A.Hy.1 [CBC], 0399.A.Hy.1 [CBC], 0445.A.Hy.1 leg. C. Barthélémy [AMNH], 0505.A.Hy.1 [CBC], 0576.C.Hy.1 (2 Nos.) [CBC], 0577.C.Hy.1 (3 Nos.) [CBC] & 0580.C.Hy.1 [CBC].

**Distribution.** China (Guangdong, Hong Kong); India; Bhutan; Myanmar; Thailand; Vietnam.

**Remarks.** A frequent wasp in Hong Kong. Barthélémy (2012) reported on the nesting biology of this species under the name of *Zethus* sp.1. Cells are mass-provisioned with caterpillars belonging to the family Geometridae and Noctuidae (Barthélémy, 2012). It is expected that *Zethus malayanus* Gusenleitner, 2010 distributed from Malaysia to Guangdong will also be recorded in Hong Kong.

## SPECIES DUBIAE

### *Eumenes architectus* Smith, 1859

*Eumenes architectus* Smith, 1859: 20, “Celebes”, NHMUK (?). Type: female.

**Distribution.** China (Hong Kong [?]); India[?]; Myanmar; Malaysia; Singapore; Indonesia; Philippines.

**Remarks.** Reported by Dover (1926) from Hong Kong. In the past 92 years, no specimen has been found in Hong Kong or even other areas of China, but it has been recorded from Myanmar so it may still be discovered from China, but its presence in Hong Kong is doubtful. Additionally, the name has been previously used erroneously by some workers (Yasumatsu 1936; Schulz 1912) and this may have been the case for Dover.

### *Antepipona bipustulata* (de Saussure, 1855)

*Odynerus bipustulatus* de Saussure, 1855: 277, pl. XII fig. 10, locality unknown, MNHN. Type: Male & Female.

**Distribution.** China (Hong Kong [?]); India; Sri Lanka; Myanmar; Thailand; Laos; Malaysia; Singapore; Indonesia.

**Remarks.** Reported from Hong Kong by Dover (1926) as *Odynerus bipustulatus* Sauss. Giordani Soika (1982) in his revision of the genus does not list this taxon from Hong Kong nor does he mention Dover. Also, according to the latter the taxon is “Common”, yet we have not collected it and we suspect that Dover may have misidentified this species, probably with the superficially similar (colour markings) *Apodynerus formosensis formosensis*.

### *Anterhynchium flavopunctatum flavopunctatum* (Smith, 1852)

*Ancistrocerus flavo-punctatus* Smith, 1852: 36, “Ning-po” (China), NHMUK. Type: female.

**Distribution.** Laos; China (Hong Kong [?]); Taiwan; Korea; Japan

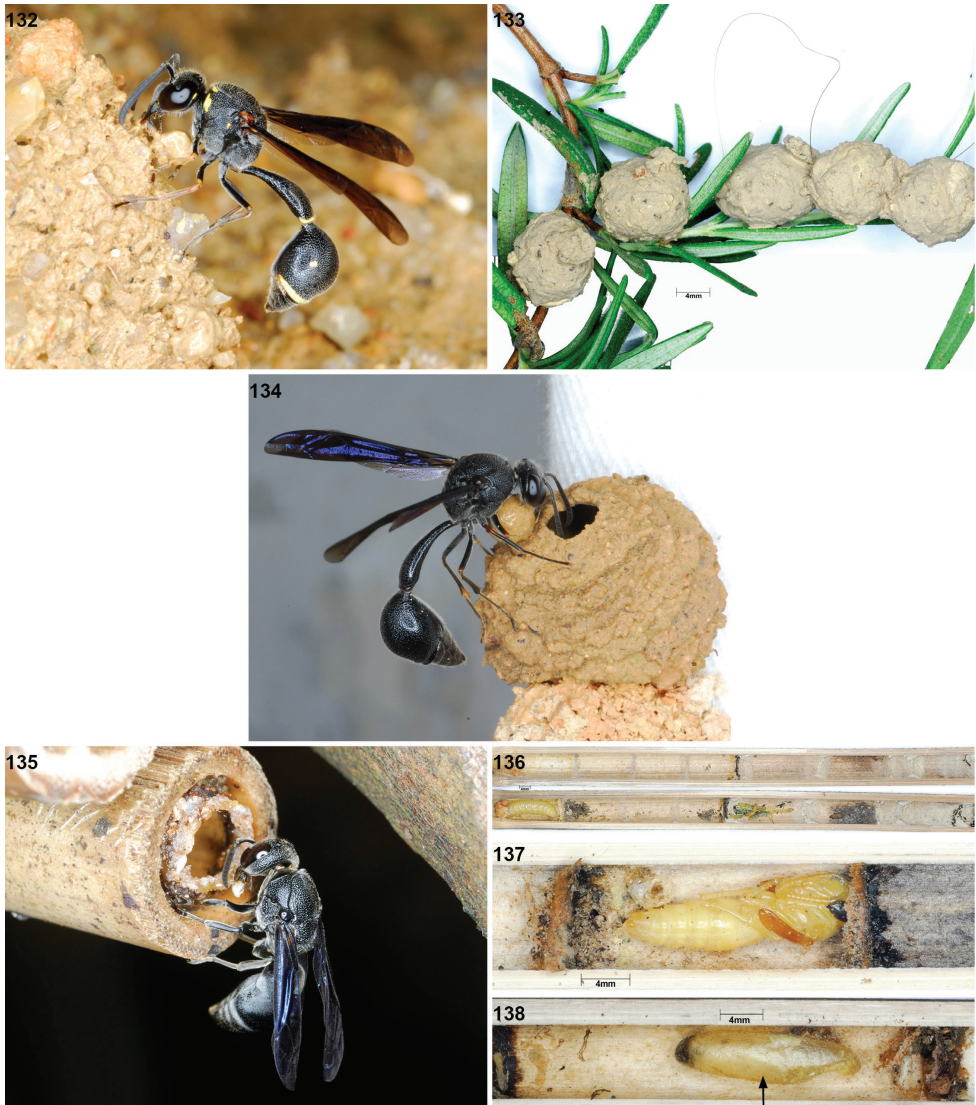
**Remarks.** Reported from Hong Kong by Dover (1926) as *Odynerus* (R.) *flavopunctatum* Smith, however, this species is very similar to one of the colour variants of *Anterhynchium flavomarginatum* (Smith 1852) and we believe Dover may have identified a color variant of this species as *Anterhynchium flavopunctatum flavopunctatum*.

### *Labus exiguus* (de Saussure, 1855)

*Eumenes exiguus* de Saussure, 1855: 150, “Les Indes-Orientales” (? OUM). Type: male.

**Distribution.** China (Hong Kong [?]); Singapore; Malaysia.

**Remarks.** This species was recorded by Dover (1926) from Hong Kong, however the concept of this species in this author's publications was rather broad and we believe that Dover actually saw *Labus edenticulus* Li & Carpenter, 2018 but misidentified his material.



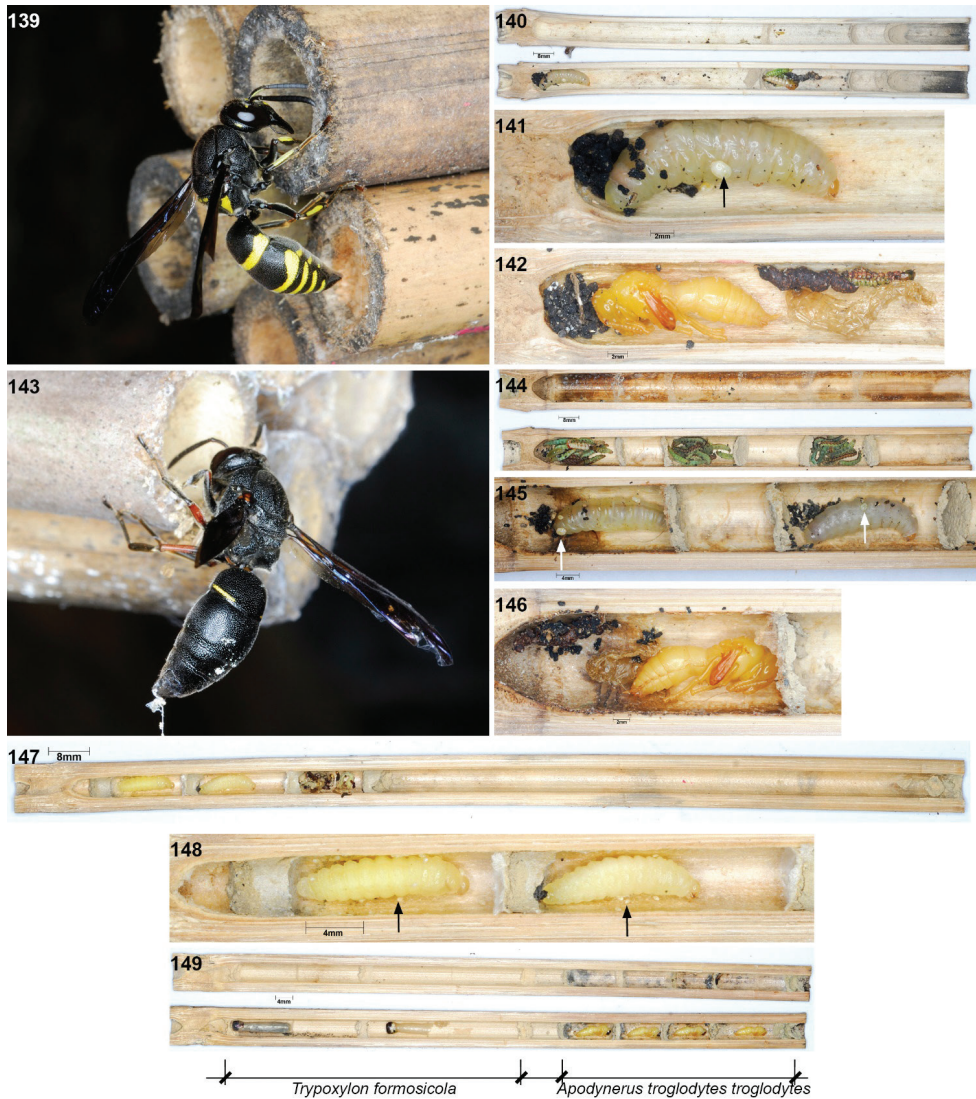
**Figures 132–138.** *Eumenes punctatus* **132** female collecting construction material **133** group of cells on a branch of Rosemary **134** *Eumenes quadratus quadratus* **134** female completing a brood cell **135–138** *Allorhynchium chinense* **135** female at nest building the resin collar at the entrance **136** typical nest in a bamboo segment showing two cells. The first cell with post feeding larva, the second cell with feeding larva with prey, cell un-closed **137** a pupa **138** cocoon of a Chrysididae inside a nest.

***Paraleptomenes miniatus miniatus* (de Saussure, 1855)**

*Odynerus miniatus* de Saussure, 1855: 249, pl. XI fig. 6, “Les Indes orientales”, NHMUK. Type: female.

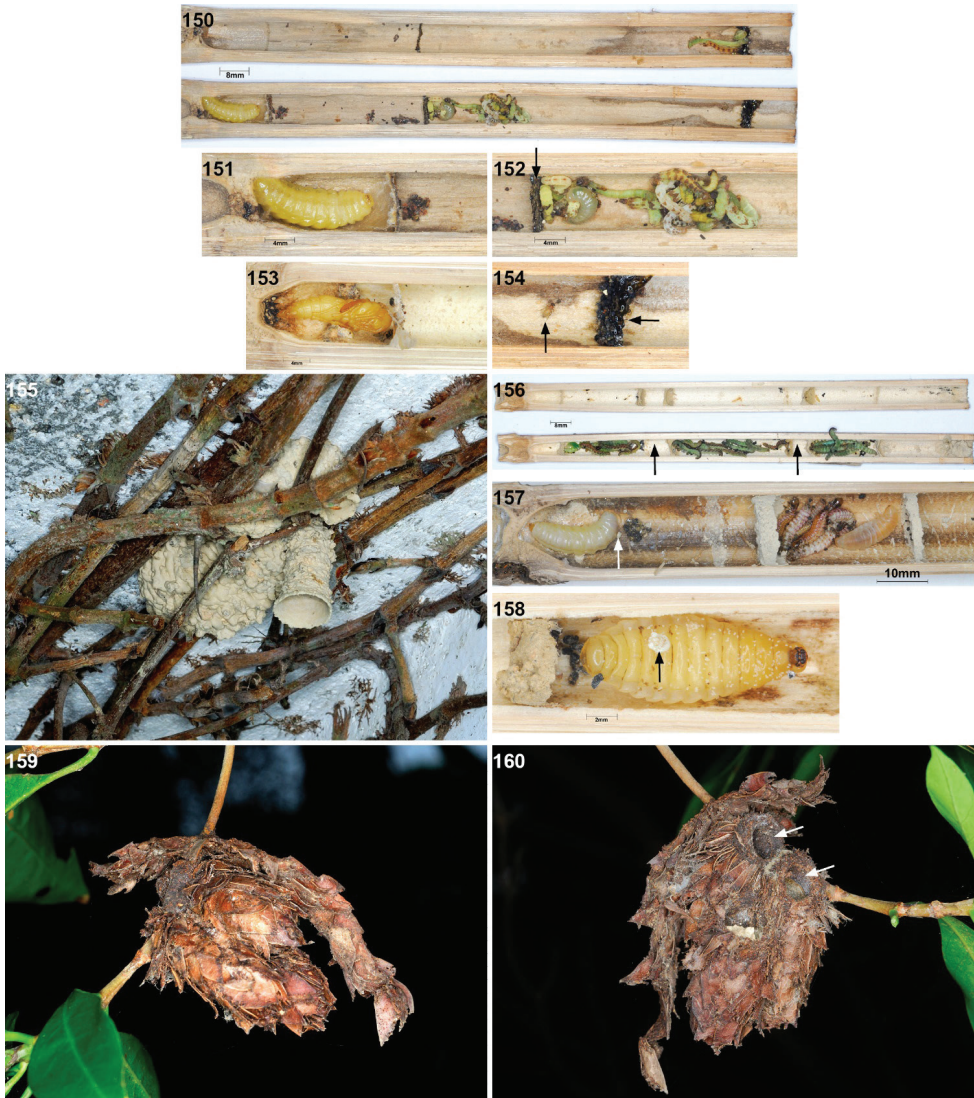
**Distribution.** China (Taiwan, Hong Kong [?]); India; Pakistan; Iran; Mauritius.



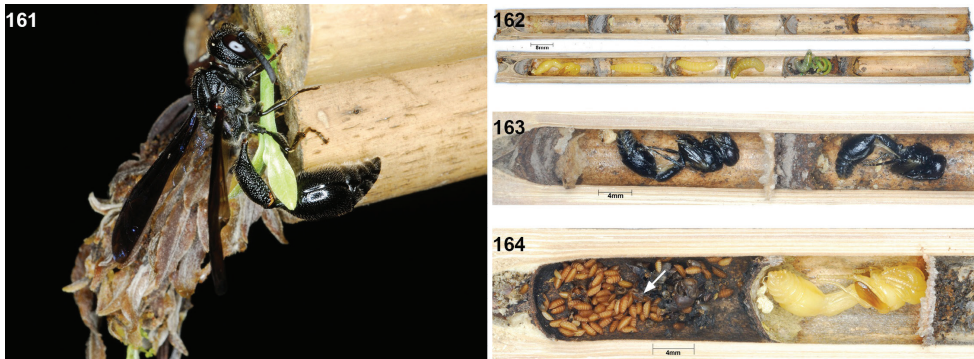


**Figures 139–149.** *Anterhynchium flavolineatum* **139** female at nest **140** typical nest containing two cells two vestibular cells. Cell 1 with post-feeding larvae. Cell 2 with feeding larva and prey **141** post feeding larva with gravid female symbiotic mite **142** pupa **143–146** *Anterhynchium flavomarginatum* **143** female at nest **144** typical nest showing three cells, and 2 intercalary cells. All cells with early instar boor and preys **145** two post feeding larvae, with gravid female symbiotic mites **146** pupa **147–149** *Apodynerus troglodytes troglodytes*, nest contents **147** bamboo nest-trap at opening, containing three cells with two post feeding larva and a fully provisioned cell **148** the post feeding larvae with symbiotic mite nymphs **149** superseedure of a nest of *Trypoxylon petiolatum* Smith, 1858 by *A. t. troglodytes*.

**Remarks.** Species recorded on i-Naturalist only at: <https://www.inaturalist.org/observations/8916317> and <https://www.inaturalist.org/observations/2603869>. Accessed on 17 March 2019. Without a voucher specimen we cannot ascertain the existence of this taxon locally and we place it in *Species dubiae* until further elucidation.



**Figures 150–160.** *Lissodynerus septemfasciatus feanus*, nest content **150** typical nest in a bamboo nest-trap, showing two cells partitioned with a resin operculum containing one post-feeding larva and a feeding larva with mass provision of preys **151** post-feeding larva and silk pupal chamber, the meconium is not yet voided **152** resin cell partition and feeding larva and mass prey provision **153** pupa **154** entrance resin plug and Phorid fly **155–158** *Orancistrocerus aterrimus erythropus*, nest and nest contents **155** nest affixed on the underside of a roof showing a tubular entrance vestibule to a cell under provisioning **156** typical nest in bamboo nest-trap showing three cells with fully provisioned cells and feeding larvae and the two intercalary cells **157** post-feeding larva with symbiotic mite **158** diapausing post-feeding larva with gravid symbiotic mite and numerous nymphs **159–160** *Calligaster himalayensis*, nest affixed to a hanging substrate **159** normal view, in **160** nest is rotated approximately 180 degree to show two new cell entrances.



**Figures 161–164.** *Zethus dolosus* **161** female at nest fixing plant material on the vicinity of the nest entrance **162** typical nest in a bamboo segment showing five cells. The first four cells with post-feeding larvae and the fifth cell with a feeding larvae **163** two advanced pupae **164** cell attacked by Phorid flies with numerous fly cocoons.

### Key to the species of the subfamily Eumeninae from Hong Kong

- 1 Mid tibia apically with two spurs ..... **2**
- Mid tibia apically with one spur..... **3**
- 2 Width of T1 in dorsal view more or less constant; dorsal part with faint longitudinal groove, T1 rounded dorsally..... *Zethus dolosus* **Bingham**
- T1 in dorsal view wider at level of spiracles than apically; no groove dorsally, T1 flattened dorsally..... *Calligaster himalayensis* (**Cameron**)
- 3 T1 slender, distinctly petiolate, distinctly more than 2× as long as wide (Figs 1–2, 4–5, 7–8, 12–13, 24–25, 27–28, 62–63, 65–66, 77–78, 101–102, 104–105, 107–108)..... **4**
- T1 short and robust, not petiolate, usually less than wide (all other figs.)..... **17**
- 4 Mesepisternum with epicnemial carina ..... **5**
- Mesepisternum without epicnemial carina or epicnemial carina obsolete ..... **7**
- 5 T1 basally with transverse carina (Fig. 66).... *Ectopioglossa ovalis* **Giordani Soika**
- T1 basally without transverse carina..... **6**
- 6 Apical half of S1 densely punctuate and small area post medio-basally with small transverse striae; mesoscutum with prescutal grooves..... *Pseudozumia indica indica* (**Saussure**)
- S1 basally smooth, and with rather regular and transverse striae at 2/3 apex; mesoscutum without prescutal grooves..... *Coeleumenes burmanicus* (**Bingham**)
- 7 Propodeal valvula elongate, or more or less rectangular; metanotum with a single medial tooth dorsally second submarginal cell of fore wing basally truncate ..... *Labus edentatus* **Li & Carpenter**
- Propodeal valvula rounded, short; metanotum non-dentiform; second submarginal cell of fore wing basally acute..... **8**



- 8 Propodeum dorsally with elongate fovea mesally..... **9**
- Propodeum dorsally without elongate fovea mesally..... **10**
- 9 Prestigma of fore wing shorter than stigma; female without cephalic foveae; mesoscutum without prescutal grooves..... *Pseumenes depressus* (Saussure)
- Prestigma of fore wing longer than stigma; female with cephalic foveae; mesoscutum with deep prescutal grooves ..... *Pareumenes quadrispinosus acutus* Liu
- 10 T1 impunctate or sparsely with small punctures (Figs 2, 5); T2 without lamella (Figs 1, 4)..... **11**
- T1 coarsely and densely punctate (Figs 8, 22); T2 with apical lamella (Figs 19–20, 24) ..... **13**
- 11 T1 less than 1.5× mesosomal length; propodeum laterally more or less punctate, not shining; terminal sternum with a longitudinal furrow in male ..... **12 Delta de Saussure**
- T1 1.5× or more mesosomal length; lateral part of propodeum almost impunctate, shining; terminal sternum without longitudinal furrow in male ..... *Phimenes flavopictus* (Blanchard)
- 12 Body relatively smaller than the below species; T2 in dorsal view gradually diverging from base to the middle and gradually narrowing to the apical margin (Fig. 2); S2 without longitudinal depression in the middle..... *D. campaniforme campaniforme* (Fabricius)
- Body bigger; T2 in dorsal view abruptly diverging from base to the middle and strongly narrowing to the apical margin (Fig. 5); S2 with shallow longitudinal depression mesally..... *D. pyriforme pyriforme* (Fabricius)
- 13 Apical margin of clypeus truncated in female (Fig. 26); lateral side of propodeum clearly separated from its posterior face; A13 small and straight in male..... *Oreumenes decoratus* (Smith)
- Apical margin of clypeus emarginated in female (Figs 9–11, 14, 23); lateral margin of propodeum rounded, without an edge between lateral and posterior faces; A13 medium-sized and forming a recurved hook in male ..... **14 Eumenes Latreille**
- 14 T1 in dorsal view long, triangular, more than 4× as long as wide, basal ½ of lateral margins sub-parallel, widening gradually toward apex (Fig. 13)..... *E. quadratus quadratus* Smith
- T1 in dorsal view shorter, thread-like at base, less than 3× as long as wide, then visibly widening sharply toward the middle, the lateral post-medial margins being parallel (Figs 8, 22) ..... **15**
- 15 T1 in dorsal view more elongate; T2 in lateral view basally acute; apical margin of T2 almost straight..... *E. atrophicus* (Fabricius)
- T1 in dorsal view stumpy; T2 in lateral view basally right angle or obtuse; apical margin of T2 emarginated..... **16**
- 16 Mesoscutum and mesopleuron with dense punctures, interspaces between punctures less than puncture diameter and slightly carinate; tibiae dark but often partly ferruginous, apical end darker ..... *E. punctatus de Saussure*
- Mesoscutum and mesopleuron with large, deep, round punctures, interspaces between punctures more than or at least equal to puncture diameter; hind tibia



- always black ..... *E. rubronotatus* Pérez
- 17 T1 basally with transverse carinae close to edge of declivity (Figs 37, 81, 84, 95, 116) ..... 18
- T1 basally without transverse carinae ..... 24
- 18 T1 basally with two transverse carinae (Figs 116–117), both transverse carinae close to each other at the crest of the declivity ..... *Subancistrocerus camicus* (Cameron)
- T1 basally with one transverse carina ..... 19
- 19 Vertex with a pair of cephalic foveal pits behind posterior ocelli in female; T2 with a median longitudinal depression or furrow (Fig. 120) ..... *Symmorphus tsushimanus* Yamane
- Vertex with or without cephalic foveal pits behind posterior ocelli in female; T2 without a median longitudinal depression or furrow ..... 20
- 20 Anterior sloping face of pronotum mesally with two impressed foveae ..... 21 *Parancistrocerus* Bequaert
- Anterior sloping face of pronotum mesally without impressed foveae ..... 22
- 21 Apex of T3 prolonged mesally ..... *P. yachowensis* Giordani Soika
- Apex of T3 not prolonged mesally ..... *P. hongkongensis* Gusenleitner
- 22 T2–T4 apically with well developed lamella (Fig. 80) ..... *Lissodynerus septemfasciatus feanus* (Giordani Soika)
- T2–T4 apically without lamella ..... 23
- 23 Apex of clypeus widely emarginated, lip wide and covered with long brown bristles (Fig. 85) ..... *Orancistrocerus aterrimus erythropus* (Bingham)
- Apex of clypeus narrowly emarginated, lip narrower and without long brown bristles (Fig. 35) ..... *Allorhynchium radiatum* sp. nov.
- 24 T1 obviously narrower than T2 and much wider at the apex than at the base (Figs 41, 57) ..... 25
- T1 slightly narrower than T2 and a little wider at the apex than at the base (Figs 31, 44, 47, 69, 72, 91, 111) ..... 27
- 25 Pronotal carina widely arched on shoulder ..... *Paraleptomenes kosempoensis* (von Schulthess)
- Pronotal carina sharply angled on shoulder ..... 26 *Apodynerus*
- 26 S2 largely depressed basally and with a thin, more or less developed median furrow; clypeus higher than wide; often with yellow spot on baso-lateral sides of T2 ..... *A. formosensis formosensis* (von Schulthess)
- S2 distinctly convex basally and not crossed baso-medially; clypeus wider or subequal to height; no yellow spot on baso-lateral sides of T2 ..... *A. troglodytes troglodytes* (de Saussure)
- 27 Metanotum dorsally with two distinct sharp teeth (Fig. 41) ..... 28 *Antepipona*
- Metanotum dorsally without sharp teeth or just with tiny teeth ..... 29
- 28 T1 except yellow apical band and S1 ferruginous ..... *A. rufescens* (Smith)
- T1 and S1 black ..... *A. menkei* Giordani Soika

- 29 Propodeum with well developed superior carinae (Fig. 90); each of T2–T5 with a row of large and dense punctures at a certain distance from the apical margin and forming a broad smooth and shiny preapical band, and with another row of sparser punctures close to the apical edge, respectively (Fig. 91) ..... *Orientalicesa nigra* sp. nov.
- Propodeum without superior carinae; T2–T5 without above apical band.....30
- 30 Axillary fossa in dorsal view at least as wide as long, oval.....31 *Euodynerus*
- Axillary fossa in dorsal view much narrower than long, often slit-like.....32
- 31 Posterior margin of horizontal surface of metanotum with large denticles; dorsal surface of propodeum behind metanotum without teeth; ocellar triangle without tubercles (Fig. 73) .....*E. (Euodynerus) dantici violaceipennis* Giordani Soika
- Posterior margin of horizontal surface of metanotum with small denticles; dorsal surface of propodeum behind metanotum with two teeth; ocellar triangle with three bifid tubercles (Fig. 76) .....*E. (Pareuodynerus) trilobus* (Fabricius)
- 32 T2 apically with a transparent lamella (Fig. 68) .. *Epsilon dyscherum* (de Saussure)
- T2 apically without a transparent lamella.....33
- 33 Propodeum nearly at level of metanotum; body wholly black (Figs 30–32) ..... *Allorhynchium chinense* (de Saussure)
- Propodeum below level of metanotum; body with colorful marks (Figs 43–55, 110–115).....34
- 34 Scutellum and posterior part of mesoscutum finely and sparsely punctate, slightly polished; in male mid femur distinctly emarginated basally..... 35 *Rhynchium*
- Scutellum and posterior part of mesoscutum coarsely and densely punctate, dull; in male mid femur not emarginated basally.....36 *Anterhynchium*
- 35 Mesoscutum mostly to entirely reddish brown (Fig. 111) ..... *R. brunneum* (Fabricius)
- Mesoscutum mostly to entirely black (Fig. 114) ..... *R. quinquecinctum quinquecinctum* (Fabricius)
- 36 Narrow basal part of S1 smooth; gastral tergites only finely punctate at base; mandibles of male deeply emarginate on inner side near the middle; metasomal terga except T1 and basal part of T2 ferruginous (Figs 43–44)..... *A. (Anterhynchium) mellyi* (de Saussure)
- Narrow basal part of S1 densely transversely striate over almost its entire width; third and following gastral tergites very coarsely punctate at base (visible only when the segments are unusually extended); mandibles of male not deeply emarginate on inner side; metasomal terga without ferruginous marks .....37
- 37 Mesoscutum posteriorly weakly punctate, interspaces not carinate; each of T1–T5 with a yellow complete apical band (Figs 46–47)..... *A. (Dirhynchium) flavolineatum flavolineatum* (Smith)
- Mesoscutum posteriorly very densely punctate, interspaces with distinct irregular longitudinal carinae; metasoma black except T1 or T1–T2 with narrow pale yellow apical band (Figs 49–50, 52–53) ..... *A. (Dirhynchium) flavomarginatum flavomarginatum* (Smith)

## Conclusion

This study produces some remarkable additions; besides the two new species, to the local and Chinese hymenopterous fauna such as *Symmorphus tsushmanus* Yamane, 1990 and *Epsilon dyscherum* (Saussure, 1852) both new to China or occurrences that expand the known geographical distribution of the taxon as with *Calligaster himalyensis* or *Parancistrocerus yachowensis*. These results show the persistence of Palearctic elements in the fauna of Hong Kong, such as three out of four recorded *Eumenes* spp., the two *Euodynerus* listed below or *Symmorphus tsushmanus* and 11 other species. Whilst Hong Kong lies well inside the geographical tropical zone it is influenced by surges of northern cold air, and this may partially explain the presence of species that are known to cross the climatological divide between Palearctic and tropical Oriental regions.

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# Ants trapped for years in an old bunker; survival by cannibalism and eventual escape

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## Abstract

Successful evacuation of a peculiar ‘colony’ of the wood ant *Formica polyctena* Först., for years trapped within an old bunker previously used for storing nuclear weapons (see Czechowski et al. 2016), is reported. Using an experimentally installed boardwalk, the imprisoned ants managed to get through the ventilation pipe to their maternal nest on the top of the bunker. In our previous report, we left open the question of how the ‘colony’ could survive seemingly without food. Here we show that the ‘colony’ in the bunker survived and grew thanks to an influx of workers from the source nest above the bunker and mass consumption of corpses of the imprisoned nestmates.

## Keywords

Adaptability, *Formica polyctena*, marginal habitats, scarce food resources, wood ants

## Introduction

In a recent paper (Czechowski et al. 2016), we described a unique accumulation of workers (for convenience called a ‘colony’) of the wood ant *Formica polyctena* Först., trapped within an old bunker in western Poland, used in the Soviet time for storing

nuclear weapons. The source of this ‘colony’ was a large colony nesting outdoors, on top of the bunker. The nest was located on the outlet of the bunker’s ventilation pipe. Ants which had dropped through the pipe to the bunker were not able to reach the outlet, located in the ceiling, to return to the mother nest. The size of the bunker ‘colony’ of *F. polyctena*, known since 2013, has been estimated at close to a million, and the contents of ‘cemeteries’ at ca. two million corpses. Neither before (Czechowski et al. 2016), nor in the time considered here were queens or offspring seen in the bunker, not even empty cocoons – only workers were present.

After our previous study (Czechowski et al. 2016), we started to contemplate on possible means to help the imprisoned ants to find their way out of the bunker. In practice, the only way to free the ants from the bunker would be to enable their spontaneous return migration to the maternal nest through the ventilation pipe – assuming that the rusty pipe interior is coarse enough for that (see fig. 5 in Czechowski et al. 2016). We were helped by a serendipitous observation: we noticed that a piece of board accidentally leaning against the wall became a starting point of an ant route leading up along the wall (Fig. 1), ending just under the ceiling where the ants dispersed, not reaching the pipe outlet (Fig. 2). Thus it might suffice to provide the ants with direct access to the outlet.

Our previous study also left open, how the bunker colony could survive and grow without access to foraging grounds. One evident means could be cannibalism. It is known that wood ants consume dead bodies of their conspecifics left in masses on the ground during spectacular ‘ant wars’ early in the season. The function of such wars is to settle the borders of neighbouring conspecific colonies, but the corpses also add substantially to the scarce food resources available when the colony lives commence after winter (Mabelis 1979).

Here we report our successful trial to re-connect the imprisoned ants with their maternal colony. We also studied possible consumption by the bunker ants of their dead nestmates which seemed to be the only food resource available to keep the ‘colony’ alive such that it could grow through the years.

## Methods

As a first step in freeing the captive ants, in spring 2016, we took a group of ca 100 ants from the bunker and let them free on the outskirts of the mother nest, to check relations between the two partly isolated entities. As expected, no aggressive behaviour was observed. Subsequently, on 18<sup>th</sup> September 2016, we constructed a ca 3-metre long vertical boardwalk with one end burrowed in the earthen mound of the bunker colony and the other one tucked inside the ventilation pipe (Fig. 3). It was meant to serve as an escape route, allowing the ants to leave the bunker. At that time, the mound in the bunker was fully inhabited by ant workers (Fig. 4) – as in previous years (see figs 2 and 6 in Czechowski et al. (2016).

To study possible cannibalism as a means of survival in the resource-scarce bunker, we collected corpses of *F. polyctena* from waste piles (‘cemeteries’) in the bunker,



**Figure 1.** A piece of board leaning against the wall initiated an ant trail leading upwards. Photo taken on 18.09.2016 (Wojciech Stephan).





**Figure 2.** The upper part of the ant trail in Fig.1; the ants (on the left) were unable to move along the ceiling and thus could not reach the outlet of the ventilation pipe. Photo taken on 18.09.2016 (Wojciech Stephan).

to be analysed in the laboratory for signs of cannibalism. More than 150 workers were investigated carefully under a binocular (Olympus DF Planapo IX SzH 10, using a magnification of 10×). By identifying the presence of a gnawed hole (mostly on the abdomen) and signs of biting we could recognise a corpse as consumed. Only corpses with abdomen, or detached abdomens, were counted, to avoid recording the same corpses twice. If a corpse was highly destroyed or broken into very small pieces, it was not considered.

## Results

Soon after the boardwalk had been installed, single ants started to inspect it. The next opportunity to check the situation of *F. polycтена* in the underground arose when bats overwintering in the bunkers were counted. On 11<sup>th</sup> February 2017, the mound was almost deserted, only a few ants being present close to the base of the boardwalk (Fig. 5); no live ants were seen elsewhere in the bunker chamber. To compare the situation with that in the former winter, when the bunker mound and the whole chamber was filled with ants, see figs 2 and 7 in Czechowski et al. (2016).

Of the corpses collected from ‘cemeteries’, a vast majority (93%) bore traces of bites, and also fret holes were seen on their abdomens – typical signs left when the contents have been consumed.





**Figure 3.** The boardwalk just assembled, to provide the ants a means to reach the ventilation pipe. Photo taken on 18.09.2016 (Wojciech Stephan).





**Figure 4.** On the earth mound in the bunker, the density of ants was high on the day when the boardwalk was put. Photo taken on 18.09.2016 (Wojciech Stephan).



**Figure 5.** The earth mound, almost deserted by the ants, at the bottom of the bunker in winter, four months after setting the boardwalk. 'Ant cemeteries' are visible around the mound and next to the walls. Photo taken on 11.02.2017 (Wojciech Stephan).

## Discussion

The most interesting lesson taught by the *F. polycтена* 'colony' studied here is, how monumental potential wood ants have to maintain self-organisation even under conditions going far beyond the limits of the survival of the species (for details see Czechowski et al. 2016). More generally, the present case adds a dimension to the great adaptive ability of ants to marginal habitats and suboptimal conditions, as the key to understanding their unquestionable eco-evolutionary success (see Hölldobler and Wilson 1990).

A pivotal question, considered in this report, is what the ants in the bunker ate to survive, as the only possible food source that seemed to occur there in a sufficient amount (not counting occasional dead mice or bats) consisted of corpses of dead nestmates. Cannibalism may serve as a means of survival when other food is scarce. Despite being widely documented in the animal kingdom, cannibalism is relatively poorly known in social insects (Lopez-Riquelme and Fanjul-Moles 2013; Sun and Zhou 2013). In termites, besides corpse burial, cannibalism is one of the most important ways of corpse disposal (Lopez-Riquelme and Fanjul-Moles 2013; Sun and Zhou 2013) – in this way the consumer also benefits from important protein and nitrogen of the corpses consumed (Chouvenc and Su 2012; Sun et al. 2017). Among ants, wood ants are notoriously well known of their 'ant wars'; e.g. in *F. polycтена*, intraspecific territorial fights often occur in early spring when protein food is scarce and fresh corpses resulting from the conflicts are dragged in large numbers into the nests, to feed the developing offspring (De Bruyn and Mabelis 1972; Mabelis 1979; Driessen et al. 1984). Recent research has also shown that corpse consumption in *F. polycтена* is more common than it was previously thought, and nestmate corpses can serve as an important food source not only in periods of food shortage (Maák et al., in press). In the light of the above, and the clear signs of mass consumption of the *F. polycтена* corpses in the bunker with practically no other organisms able to do it (see Czechowski et al. 2016), we can safely deduce that the bunker 'colony' survived on cannibalism, by consuming dead nestmates.

Summing up, the ecological and behavioural flexibility of the wood ants (Seifert 2018) may allow them survival even in unexpectedly suboptimal conditions (e.g. Czechowski and Vepsäläinen 2009). The survival and growth of the bunker 'colony' through the years, without producing own offspring, was possible owing to continuous supply of new workers from the upper nest (Czechowski et al. 2016) and accumulation of nestmate corpses. The corpses served as an inexhaustible source of food which substantially allowed survival of the ants trapped down in otherwise extremely unfavourable conditions.

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