Deutsche Entomologische Zeitschrift 67 (1) 2020





Deutsche Entomologische Zeitschrift

An International Journal of Systematic Entomology

Editor-in-Chief

Dominique Zimmermann

Natural History Museum Vienna dominique.zimmermann@nhm-wien.ac.at

Managing Editor

Lyubomir Penev Pensoft Publishers, Sofia, Bulgaria phone: +359-2-8704281 fax: +359-2-8704282 e-mail: penev@pensoft.net

Editorial Secretary

Boryana Ovcharova Pensoft Publishers, Sofia, Bulgaria e-mail: journals@pensoft.net

Editorial Board

Ulrike Aspöck, Vienna, Austria Roger L. Blackman, London, United Kingdom Jose Fernandez-Triana, Ottawa, Canada Claudia Hemp, Bayreuth, Germany Harald Letsch, Vienna, Austria James Liebherr, Ithaca, United States of America Wolfram Mey, Berlin, Germany Alessandro Minelli, Padova, Italy Michael Ohl, Berlin, Germany Ralph Peters, Bonn, Germany Susanne Randolf, Vienna, Austria Dávid Rédei, Tianjin, China Nikolaus Szucsich, Vienna, Austria Sonja Wedmann, Messel, Germany Frank Wieland, Bad Dürkheim, Germany Michael Wilson, Cardiff, United Kingdom Dominique Zimmermann, Vienna, Austria

Deutsche Entomologische Zeitschrift

2020. Volume 67. Issue 1

ISSN: 1435-1951 (print), 1860-1324 (online) Abbreviated keys title: Dtsch. Entomol. Z.

In Focus

The cover picture shows Tenthredo atra Linnaeus, 1758 larvae

See paper of **Liston A**, **Altenhofer E**, **Netzberger R**, **Prous M** Biology of two European *Tenthredo* species (Hymenoptera, Tenthredinidae) feeding on *Gentiana*

Cover design Pensoft



Deutsche Entomologische Zeitschrift

An International Journal of Systematic Entomology

Content of volume 67 (1) 2020

El-Sonbati SA, Wilson MR, Al Dhafer HM The Tamarix feeding Leafhopper genus <i>Opsius</i> Fieber, 1866 (Hemiptera, Cicadellidae, Deltocephalinae, Opsiini) in the Kingdom of Saudi Arabia, with description of a new species	1
Liston A, Altenhofer E, Netzberger R, Prous M Biology of two European <i>Tenthredo</i> species (Hymenoptera, Tenthredinidae) feeding on <i>Gentiana</i>	13
Nazari V, ten Hagen W Molecular taxonomy of <i>Tomares</i> hairstreaks (Lepidoptera, Lycaenidae, Theclinae)	19
Jia F, Liang Z, Fikáček M A review of <i>Himalcercyon</i> stat. nov., with description of a new species from the Chinese Himalaya and an updated key to Asian genera of Megasternini (Coleoptera, Hydrophilidae)	35
Willsch M, Friedrich F, Baum D, Jurisch I, Ohl M A comparative description of the mesosomal musculature in Sphecidae and Ampulicidae (Hymenoptera, Apoidea) using 3D techniques	51
Shimizu S The Nepalese species of the genus <i>Enicospilus</i> Stephens, 1835 (Hymenoptera, Ichneumonidae, Ophioninae): a preliminary revision and identification key to species	69

Abstract & Indexing Information

Biological Abstracts® (Thompson ISI) BIOSIS Previews® (Thompson ISI) Camgridge Scientific Abstracts (CSA/CIG) Web of Science® (Thompson ISI) Zoological Record™ (Thompson ISI)

PENSOFT.



The Tamarix feeding Leafhopper genus *Opsius* Fieber, 1866 (Hemiptera, Cicadellidae, Deltocephalinae, Opsiini) in the Kingdom of Saudi Arabia, with description of a new species

Saad A. El-Sonbati¹, Michael R. Wilson², Hathal M. Al Dhafer¹

2 Department of Natural Sciences, National Museum of Wales, Cardiff, CF10 3NP. Wales, UK

http://zoobank.org/DEEE35C5-0597-4778-840E-D3D9DA1F996E

Corresponding author: Saad A. El-Sonbati (anase24@yahoo.com; ssonbati@ksu.edu.sa)

Academic editor: D. Zimmermann • Received 17 September 2019 • Accepted 19 December 2019 • Published 14 January 2020

Abstract

The leafhopper genus *Opsius* Fieber, 1866 is revised for the Kingdom of Saudi Arabia. Seven species are treated, including three that previously were reported by Dlabola (1979), *O. pallasi* (Lethierry, 1874), *O. tigripes* (Lethierry, 1876), and *O. versicolor* (Distant, 1908). *Opsius heydeni* (Lethierry, 1876), *O. richteri* Dlabola 1960, and *O. scutellaris* (Lethierry, 1874) are reported for the first time from the Kingdom. A new species, *O. wilsoni* El-Sonbati, **sp. nov.** is described from the southwestern region of the Kingdom of Saudi Arabia. A key to the species of *Opsius* of the Kingdom is also provided.

Key Words

Auchenorrhyncha, Cicadellidae, Deltocephalinae, distribution, Hemiptera, leafhopper, Opsiini

Introduction

The Cicadellidae is the largest family of the suborder Auchenorrhyncha, and the Deltocephalinae is the largest leafhopper subfamily with more than 6,700 valid species (Zahniser and Dietrich 2013). The tribe Opsiini is divided into four subtribes including more than 300 species. Recently, the subtribe Opsiina has had additional genera (El-Sonbati et al. 2016, 2017) and species (El-Sonbati et al. 2015, 2018, 2019) added, doubling the known genera from the Arabian Peninsula.

The genus *Opsius* Fieber, 1866 (Opsiini; type species *Opsius stactogalus* Fieber, 1866) includes at least 20 valid species distributed worldwide. This study records seven species of *Opsius* from the Kingdom of Saudi Arabia (KSA), including three previously reported by Dlabola (1979, 1980). Three additional species are reported herein for the first time from KSA and a new species is also proposed from the southwestern region

of the country. This region has strong Afrotropical affinities (von Kéler 1955).

Among the 20 species of *Opsius*, 17 have been recorded from the Palaearctic Region, with only three shared with other regions, *O. stactogalus* Fieber, 1866, *O. versicolor* (Distant, 1908) and *O. cypriacus* Lindberg, 1958. Only *O. stactogalus* is considered cosmopolitan (Zahniser 2019). *Opsius* species are apparently restricted to moist habitats with *Tamarix* spp. (Tamaricaceae), and especially river valleys. *Tamarix* spp. are known to be salt tolerant (Newete et al. 2019) and are difficult to identify with many species known. KSA is the center of diversity of the *T. nilotica* (Ehrenb.) Bunge group and *T. aphylla* (L. Karst) (Guba and Glennie 1998). Due to their feeding activity, *Opsius* leafhoppers are well-known honeydew producers on *Tamarix* spp. (Wiesenborn 2004; Virla et al. 2010; Siemion and Stevens 2015).

King Saud University Museum of Arthropods, Plant Protection Department, College of Food and Agriculture Science, King Saud University, P.O. Box 2460, Riyadh 11451, Saudi Arabia

The purpose of this study is to clarify the taxonomy of *Opsius* species of KSA. The morphological characters and global distributions of each species occurring in KSA are presented.

Material and methods

The holotype and paratypes of the new species are deposited in King Saud University Museum of Arthropods (KSMA), College of Food and Agriculture Sciences, King Saud University, Riyadh, KSA and in the National Museum of Wales, Cardiff (NMWC). Other specimens examined are deposited in KSMA.

The morphological terminology follows Dietrich (2005). Measurements are given in millimeters (mm) and are the mean value of 20 specimens of each species; if

fewer than 20 specimens were available, all were measured. Genitalia preparations were made by soaking the terminalia in hot 10% KOH solution for 8–10 minutes, and then washed in distilled water. The cleared terminalia were transferred to glycerol for further dissection and examination. After examination, genitalia were moved to fresh glycerol and stored in a micro vial pinned below each specimen.

All specimens were examined with a Leica LABO-PHOT-2 stereomicroscope. Illustrations of the male genitalia were prepared using a NIKON microscope with a drawing tube attachment. Images were taken with a Canon 70D DSLR attached to a Leica Z6 microscope. Individual source images were then stacked using Helicon Focus v. 6.22 software, with calibrated scale bars added using Syncroscopy Automontage v. 5.4. The maps (Figs 75, 76) were created using ArcGIS 10.3 software.

Key to males of Opsius species in the Arabian Peninsula

1	Aedeagus and phallobase with two pairs of processes O. stactogalus Fieber*
_	Aedeagus and phallobase with one pair of processes
2	Aedeagal shafts substantially shorter than basal appendages
-	Aedeagal shafts and basal appendages equal or only slightly different lengths
3	Process branches almost contiguous, processes and aedeagal shafts distant from each other (Fig. 32)
_	Process branches parallel or divergent, processes and aedeagal shafts close to each other
4	Aedeagal shafts and basal process distinctly divergent throughout its length5
-	Aedeagal shafts and basal process parallel or slightly divergent throughout its length
5	Aedeagal shafts and basal processes distinctively curved backward to connective; apex of processes arched to base,
	close to each other, longer than aedeagal shafts (Fig. 26)
-	Aedeagal shafts and basal process slightly curved but not backward; apex of process curved outward, distant from each
	other, shorter than aedeagal shafts; apex of aedeagus forming a hump or lamellate (Fig. 29) O. scutellaris (Lethierry)
6	Aedeagal shafts and basal process parallel throughout its extent, aedeagal shafts equal to basal process (Fig. 35)
-	Aedeagal shafts and basal process slightly divergent throughout its extent, aedeagal shafts shorter than basal process7
7	Basal process straight but without any curvature (Fig. 23)
_	Basal process not straight, curved preapicallyO. tigripes (Lethierry)

Results and discussion

Genus Opsius Fieber

Opsius Fieber 1866: 505 (Type: *Opsius stactogalus* Fieber, 1866) *Cestius* Distant 1908: 309 (Type: *Cestius versicolor* Distant, 1908) *Opsius* Dlabola 1981: 247; Khatri and Webb 2010: 14

Description. The genus *Opsius* can be recognized by the following combination of features:

Head. Head as wide as or slightly wider than pronotum; crown parallel in length or slightly produced, more than or equal to two times the width of eye; ocelli on crown posterad of anterior margin and close to eyes; gena slightly

incised; antenna short, near upper corner of eye; Frontoclypeus shorter than wide, with fine erect seta on gena close to lateral frontal suture; lateral frontal suture reaching ocellus, shorter than clypeogenal suture, toward middle of ocelli; ratio of frontoclypeal loral suture to clypellar loral suture more than ¹/₃; lorum extended nearly to genal margin, wider than clypellus at base; clypellar suture complete and arcuate; clypellus, not inflated, expanded apically ovoid, not protruding beyond the curve of gena, straight or convex apically.

Thorax. Thorax yellowish green in colour, pronotum more than two times the length of vertex, wider than long, short lateral margin, anterior margin convex, posterior margin concave or slightly straight, about two times as long as scutellum; scutellum wider than long.

* O. stactogalus Fieber and O. cypriacus Lindberg are not known from the Arabian Peninsula but known from neighboring countries and are potential species of the region

Wings. Forewings more than three times as long as wide, appendix restricted to anal margin with A veins gently curved distally, A1 crossvein present or absent, A1–A2 crossvein present or absent, two closed anteapical cells, inner anteapical cell open. Hind wing submarginal vein complete.

Legs. Legs generally yellowish green with brown spots, with brown setal areolae; profemur row AM with AM1, profemur with two dorsoapical setae; intercalary row with 8 fine scattered setae gradually reduced apically; AV row with numerous long setae. Protibia dorsal margin rounded, AD row with 1 macrosetae, PD row with 4 macrosetae, AV row with numerous macrosetae, PV row with 1 to 4 macrosetae. Mesofemur AV row with numerous setae, two dorsoapical seta, short and reduced. Metafemur setal formula 2+2+1, setae of penultimate pair set close to each other. Metatibia arched throughout its length, PD row with long and short macrosetae alternating or subequal in length, AD row with macrosetae and one smaller intercalary seta between each pair, AV row with numerous macrosetae and extending nearly to base, gradually increasing in size apically. Metatarsomere I length equal or shorter to tarsomeres II and III combined.

Male genitalia. Pygofer broadly rounded posteriorly, without process, and with well differentiated macrosetae into several rows; valve triangular, laterally, short and pointed articulation with pygofer and free to subgenital plates; subgenital plates triangular, with one row of macrosetae laterally, apex often fingerlike, membranous, with rounded, stout or tapered end; style broadly bilobed basally, with preapical lobe, apophysis not elongate; connective anterior arms linear, contiguous, Y- or U-shaped, not fused, articulated with aedeagus; abdominal apodemes broad, narrow, or tiny, extended to 1st, 2nd visible segments, with distance between two branches, posterior margin angled, acute rounded, gradually tapering externally and gradually tapering or tapered internally; aedeagus not hinged at base, with atrium not extending ventrad of shafts, with basal process, basal processes diverging or slightly diverging or parallel or converging, close to each other or distant, arising from socle, divided near base or from middle, aedeagal shafts parallel or diverging or converging or a hump or lamellate, with or without pair of ventral processes at base, aedeagal socle swollen and bulbous.

Female genitalia. Pygofer with scattered macrosetae, ovipositor not protruding far beyond pygofer apex; first valvula convex; second valvula broad, gradually tapered or slender throughout, teeth on apical 1/3 or more, regularly or irregularly shaped, large and prominent.

Distribution. Palaearctic, Oriental (Oman et al. 1990), Afrotropical (Lindberg 1958; Metcalf 1967) (Figs 75, 76), Nearctic (adventive) (Metcalf 1967), Neotropic (adventive) (Virla et al. 2010).

Diagnosis. The genus *Opsius* can be distinguished by general colour pattern often greenish brown patches, anterior margin of head without carinae, not angularly curved to the face, face convex, and neither horizontal nor concave, face not elongate; pronotum without longitudinal dark bands or transverse dark markings; aedeagus not

hinged at base, with atrium not extending ventrad of shafts, with basal process, basal processes diverging or slightly diverging or parallel or converging, close to each other or distant, arising from socle, divided near base or from middle, aedeagal shafts parallel or diverging or converging or a hump or lamellate, with or without pair of ventral pro-

cesses at base, aedeagal socle swollen and bulbous.

Comment. *Opsius* was described by Fieber (1866) with *O. stactogalus* designated as a type species. Species have been subsequently described, but unfortunately several species have been described only from females, with descriptions often incomplete, lacking illustrations, and without the examination of types of other species. In our examination of available material of the genus, the following morphological characters in males can be used to characterize the genus: the relative lengths of the pairs of basal processes; and the relative lengths of the pair of aedeagal shafts; the relative lengths and distance between aedeagal shafts and pairs of processes at mid-length and tip length. A comprehensive revision of the genus is required to develop a key for all *Opsius* species.

Opsius heydeni (Lethierry)

Figs 1-4, 23-25, 38-40, 53-57

Opsius heydeni Lethierry and Puton 1876: 51 Athysanus heideni de Bergevin 1931: 429 Euscelis heydeni Lindberg 1936: 2 Opsius lethierryi Wagner 1942: 121

Description. In addition to generic characters, with the following characteristics.

Male genitalia. Subgenital plates with rounded apex (Fig. 38); connective linear, contiguous (Fig. 40); apodemes broad, extending to mid-length or the end of second abdomen segments, apodeme width 1.5 times the distance between each apodeme, posterior margin angled externally and tapered internally (Fig. 54); aedeagus with only dorsal process, both slightly curved inward preapically but not bent, aedeagal shafts with diverging branches, ratio of distance between two shafts at mid-length to tip length 5/9, straight, shorter than basal process, as wide as basal process, basal process extending close to shafts branches, pointed; phallobase not inflated (Figs 23, 24).

Female genitalia. Female 7th sternite 2.5 times as broad at base as long medially, posterior margin concave, acutely sinuous with V-shaped notch in middle, posterolateral angles rounded (Fig. 55); first valvula slightly convex; second valvula gradually tapered apically with rather small and serrate teeth on dorsal surface (Figs 56, 57).

Measurement. \bigcirc 3.6 mm; \bigcirc , 4 mm; pygofer, 0.70 mm; valve, 0.26 mm; subgenital plate, 0.55 mm; style, 0.33 mm; connective, 0.39 mm; apodemes, 0.33 mm; aedeagus to process, 0.51 mm; aedeagus to shaft, 0.48 mm; distance at top of aedeagal shafts, 0.14 mm; distance at mid-length of aedeagal shafts, 0.08 mm; female 7th sternite, 0.47 mm.



Figures 1–22. Habitus of *Opsius* spp. 1–4. *O. heydeni* (Lethierry), \Diamond , 1. dorsal view; 2. lateral view; 3. dorsal view of head and thorax; 4. face; 5–8. *O. richteri* Dlabola, \Diamond , 5. dorsal view; 6. lateral view; 7. dorsal view of head and thorax; 8. face; 9–12. *O. scute-llaris* (Lethierry), \Diamond , 9. dorsal view; 10. lateral view; 11. dorsal view of head and thorax; 12. face; 13–18. *O. versicolor* (Distant), \Diamond , 13. dorsal view; 14. lateral view; 15. dorsal view; 20. lateral view; 21. dorsal view of head and thorax; 22. face.

Specimens examined. $21 \[mid] 19\[d]$, KSA: **Asir**: Wadi Qounonah: 19°24.67'N, 041°36.39'E, 348 m, Light trap, 11.III.2012, El-Sonbati, S. & Al Dhafer, H.; 1 $\[d]$, same but Wadi Yabah: 19°20.52'N, 041°55.73'E, 411 m, 12.III.2012, Abdel-Dayem, M. & El Torky, A.; 1 $\[c]$, same but Wadi Targ: 19°37.38'N, 042°18.02'E, 1317 m, 14.III.2012, Fadl H., Setyaningrum H.; $2\[c] 1\[d]$, same but Wadi Baqrah: 18°47.48'N,

041°56.31'E, 331 m, 4.VI.2014, El-Sonbati, S.; $2 \subseteq 1$ ³, same but Khamis Mushayt, Wadi Bisha: 18°20.02'N, 042°42.22'E, 1990m, Sweep net, 27.IV.2011, Sharaf, M., Al Ansi, A. & Setyaningrum, H.; $1 \subseteq 1$ ³, KSA: **Bahah**, Shada, Wadi Neera: 19°44.87'N, 041°20.01'E, 471 m, Vacuum, 10.XII.2014, Al Dhafer, H., Fadl, H., Abdel-Dayem, S. & El Torky, A.; $1 \subseteq$, KSA, **Riyadh**, Al Ammariyah:

24°40.00'N, 043°40.00'E, Beating, 22.II.2012, Drayhim, Y., Al Dhafer, H., El-Gharbawy, A. & El-Sonbati, S.

Distribution. Azores, Armenia, Austria, Belgium, Canary Islands, Egypt, European Russia, France, Germany, Italy, Kazakhstan, Kyrgyzstan, Libya, Morocco, Sardinia, Sweden, Tadzhikistan, Turkmenistan, Uzbekistan (Metcalf 1967); Saudi Arabia (present study) (Figs 75, 76).

Ecology and biology. This species is widespread and common in southwestern KSA and is often associated with the wadies of Asir Province, a habitat that has one of the most diverse floras of the region. In five of these Asir wadies and also in Baha Province, KSA, *O. heydeni* became common in March, particularly in Wadi Qouno-nah. Although *Opsius* is host-specific on *Tamarix* spp., this species was collected from other plants at these sites including *Acacia* spp. (Fabaceae) (Figs 77–79).

Diagnosis. Opsius heydeni is similar to O. wilsoni sp. nov. but males of the species can be distinguished easily by the aedeagus and dorsal process slightly curved inward preapically, aedeagal shafts with diverging branches and straight, shorter than basal process, as wide as the basal process, ratio of distance between two shafts at mid-length to tip length 5/9; and the basal process extending close to shafts branches.

Opsius pallasi (Lethierry)

Athysanus pallasi Lethierry 1874: 449 Opsius pallasi Lethierry 1874: 449 Athysanus pallasii Puton 1875: 138 Opsius pallasi Dlabola 1979: 131 Opsius distantiatus Dlabola 1960a: 2

Specimens examined. No specimens were examined from KSA. Several specimens of this species from Iran were studied but not illustrated.

Distribution. European Russia, Tajikistan (Dlabola 1960a; Metcalf 1967) Algeria, Armenia, Azerbaijan, France, Georgia, Greece, Kazakhstan, Kyrgyzstan, Spain, Tadzhikistan, Tunisia, Turkey, Turkmenistan, Uzbekistan (Metcalf 1967); Saudi Arabia (Dlabola 1979); Iran (Dlabola 1981) (Figs 75, 76).

Diagnosis. The males of this species can be easily distinguished from all other members of the genus by the aedeagus and phallobase with one pair of processes; and the aedeagal shafts substantially shorter than the basal appendages.

Opsius richteri Dlabola

Figs 5-8, 26-28, 41-43, 58-62

Opsius richteri Dlabola 1960b: 15

Description. In addition to generic characters, with the following characteristics.

Male genitalia. Pygofer slightly angled posteriorly (Fig. 58); subgenital plates with rounded apex (Fig. 41); connective linear, contiguous (Fig. 43); apodemes nar-

row, extend to mid-length or the end of first abdomen segments, apodeme width three times as distance between each apodeme, posterior margin angled externally and tapered internally (Fig. 59); aedeagus with only dorsal process, both distinctively curved or bent inward at base, aedeagal shafts with diverging branches, ratio of distance between two shafts at mid-length to tip length 5/11, bent inward at base, shorter than basal process, two times as

shaft branches, distinctively curved to form distinctive inward pointed tips; phallobase not inflated (Figs 26, 27). *Female genitalia.* Female 7th sternite three times as broad at base as long medially, posterior margin concave, slightly produced with V-shaped notch in middle, posterolateral angles acutely rounded (Fig. 60); first valvula slightly convex; second valvula slender throughout their length with rather small and serrate teeth on dorsal surface (Figs 61, 62).

wide as basal process, basal process extending close to

Measurement. \bigcirc 2.8 mm; \bigcirc , 3.2 mm; pygofer, 0.39 mm; valve, 0.25 mm; subgenital plate, 0.46 mm; style, 0.32 mm; connective, 0.39 mm; apodemes, 0.22 mm; aedeagus to process, 0.16 mm; aedeagus to shaft, 0.16 mm; distance at top of aedeagal shafts, 0.17 mm; distance at mid-length of aedeagal shafts, 0.08 mm; female 7th sternite, 0.61 mm.

Specimens examined. 74♀57♂, KSA: Asir, Wadi Qounonah: 19°24.67'N, 041°36.39'E, 348 m, Light trap, 11.III.2012, El-Sonbati, S., Al Dhafer, H., Fadl, H., Abdel-Dayem, M., El- Torky, A. & Al Ansi, A.; 1♀1♂, same but Al Mandaq, Wadi Tourabah: 20°14.37'N, 041°15.23'E, 1757 m, 9.III.2012; 7 $\bigcirc 23$, same but Thalooth Al Mandhar, Wadi Baqrah: 18°47.98'N, 042°01.38'E, 425 m, 4.VI.2014, El-Sonbati, S.; 1♀, same but Al Dhafer H. & Fadl H.; 17 \bigcirc 3 \bigcirc , KSA: Jazan, Baish, Wadi Baish: 17°22.46'N, 042°32.24'E, LT, 30.I.015, Mashry, H. & Iftekhar, R.; 13, same but Abo Arish Road, Al Ariydah: 17°02.39'N, 042°58.47'E, sweep net, 12.II.2010, Al Dhafer, H. & A. El-Gharbawy; 7Å, same but Wadi Jizan: 17°01.28'N, 042°59.19'E, 158 m, Vacuum, 16.III.2014, El-Sonbati, S.; 1Å, same but Al-Dayer: 17°20.39'N, 043°07.86'E, Vacuum, 1.V.2014, Al Dhafer, H. & El-Sonbati, S.; 33, KSA: Bahah, Shada, Wadi Neera: 19°44.87'N, 041°20.01'E, 471 m, vacuum, 10.XII.2014, Al Dhafer, H., Fadl, H., Abdel-Dayem, S. & El Torky, A.; 2^Q, **Oman:** Samad Ashan Arrwdha: 22°53.33'N, 058°13.83'E, 20-30.X.2017, A. Al-Jahdami.

Distribution. Iran (Dlabola 1960b); Oman, Saudi Arabia (present study) (Figs 75, 76).

Ecology and biology. The abundance of this species varied phenologically between areas of the southwestern region of KSA. Peak abundance in Asir Province occurred in March, whereas in Jazan Province, the peak abundance occurred in January. Most specimens were collected by using light traps, but numerous specimens were also collected in Jazan Province from *Tamarix* spp. with a sweep net and by a portable vacuuming device. *Opsius richteri* comprised approximately 36% of the total number of specimens of this genus examined from KSA. This species was especially abundant at Wadi Qounonah, Asir Province, KSA (Figs 77–79).



Figures 23–37. Male genital structures of Opsius spp. 23–25. O. heydeni (Lethierry). 23. Aedeagus dorsal view; 24. Lateral view;
25. Style; 26–28. O. richteri Dlabola. 26. Aedeagus dorsal view, 27. Lateral view; 28. Style; 29–31. O. scutellaris (Lethierry).
29. Aedeagus dorsal view, 30. Lateral view; 31. Style; 32–34. O. versicolor (Distant). 32. Aedeagus dorsal view, 33. Lateral view;
34. Style; 35–37. O. wilsoni sp. nov. 35. Aedeagus dorsal view, 36. Lateral view; 37. Style.

Diagnosis. The aedeagus of *O. richteri* is similar to *O. scutellaris* with the aedeagal shaft branches diverging but can be distinguished by produced crown, aedeagal shafts and dorsal process distinctively curved or bent inward at base, and shaft branches two times as wide as basal process.

Opsius scutellaris (Lethierry)

Figs 9-12, 29-31, 44-46, 63, 64

Athysanus scutellaris Lethierry 1874: 449 Opsius scutellaris Lethierry 1874: 449; Lindberg 1954: 227 **Description.** In addition to generic characters, with the following characteristics.

Male genitalia. Pygofer slightly angled mid-posteriorly (Fig. 63); subgenital plate with gradually tapered apex (Fig. 44); connective Y-shaped (Fig. 46); apodemes narrow, extending to end of second abdominal segments, apodeme width three times as distance between each apodeme, posterior margin angled externally and tapered internally (Fig. 64); aedeagus with only a dorsal process, both distinctively curved inward at mid-length, aedeagal shafts with diverging branches, ratio of distance between two shafts at mid-length to tip length 5/11, curved inward



Figures 38–52. Male genital structures of *Opsius* spp. 38–40. *O. heydeni* (Lethierry). 38. Subgenital plate, 39. Valve; 40. Connective; 41–43. *O. richteri* Dlabola. 41. Subgenital plate, 42. Valve; 43. Connective; 44–46. *O. scutellaris* (Lethierry). 44. Subgenital plate, 45. Valve; 46. Connective; 47–49. *O. versicolor* (Distant). 47. Subgenital plate. 48. Valve; 49. Connective; 50–52. *O. wilsoni* sp. nov. 50. Subgenital plate, 51. Valve; 52. Connective.

at mid-length, longer that basal process, three times as wide as basal process, forming a hump or lamellate, basal process extending close to shaft branches, pointed; phallobase not inflated (Figs 29, 30).

Measurement. \bigcirc 2.8 mm; pygofer, 0.41 mm; valve, 0.26 mm; subgenital plate, 0.39 mm; style, 0.42 mm; connective, 0.43 mm; apodemes, 0.45 mm; aedeagus to process, 0.17 mm; aedeagus to shaft, 0.10 mm; distance at top of aedeagal shafts, 0.17 mm; distance at mid-length of aedeagal shafts, 0.08 mm.

Specimens examined. 23, KSA: Abha Province, Sad Abha: $18^{\circ}19.32$ 'N, $042^{\circ}31.00$ 'E, vacuum, 23.III.2014, El-Sonbati, S. A.

Distribution. Algeria, Canary Islands, China, Libya (Metcalf 1967); Saudi Arabia (present study) (Figs 75, 76).

Ecology and biology. Two males of *O. scutellaris* were collected at Sad Abha (dam of Abha) from weedy plants surrounding a large pool in Abha Al Jadidah Park located in the central part of the city. This species is considered uncommon, with only two specimens collected during extensive sampling not only in southwestern region of KSA but also in Abha Al Jadidah Park (Figs 77–79).

Diagnosis. Males of *O. scutellaris* can be distinguished from all members of the genus by subgenital apex with a lobe-like process; aedeagal shafts three times as wide as basal process, forming a hump or lamellate.

Opsius tigripes (Lethierry)

Athysanus tigripes Lethierry 1876a: 87; Lethierry 1876b:15 *Opsius tigripes* Vilbaste 1962: 140; Nast 1972: 325; Dlabola 1979: 131

Specimens examined. KSA. Wadi Al Ammariyah; Hofuf, 8.IV.–23.V.77. Büttiker, 15Ex. (examined but not available to be illustrated in present study)

Distribution. Afghanistan, Iran, Russia (Metcalf 1967); Saudi Arabia (Dlabola 1979) (Figs 75, 76).

Diagnosis. This species is similar to *O. heydeni* but the males can be distinguished by the aedeagal shafts and basal process slightly divergent throughout its length, with the aedeagal shafts being shorter than the basal process, and the basal process not straight and curved preapically.

Opsius versicolor (Distant)

Figs 13-18, 32-34, 47-49, 65-69

Cestius versicolor Distant 1908: 310 Opsius dissimilis Vilbaste 1961: 43 Hishimonus tamaricus Ishihara 1972: 84 Cestius sakroensis Ahmed and Sultana 1994: 126

Description. In addition to generic characters, with the following characteristics.

Male genitalia. Pygofer slightly angled posteriorly (Fig. 65); subgenital plates with stout apex (Fig. 47); connective Y-shaped (Fig. 49); apodemes tiny, not exceeding the first segment; apodeme width three times as distance between each apodeme, posterior margin gradually tapering, concave at preapical margin (Fig. 66); aedeagus with only a dorsal process, both straight or slightly curved inward preapically but not bent, aedeagal shafts with diverging branches, ratio of distance between two shafts at mid-length to tip length 5/11, straight, shorter than basal process, two times as wide as basal process, basal process extending narrower to each other, pointed; phallobase not inflated (Figs 32, 33).

Female genitalia. Female 7th sternite 2.5 times as broad at base as long medially, posterior margin with median lobelike projection with V-shaped notch in middle, posterolateral angles conically rounded (Fig. 67); first valvula convex; second valvula gradually tapered apically with rather small and serrate tooth on dorsal surface (Figs 68, 69).

Measurement. \bigcirc 3.3 mm; \bigcirc , 3.7 mm; pygofer, 0.65 mm; valve, 0.31 mm; subgenital plate, 0.46 mm; style, 0.31 mm; connective, 0.26 mm; apodemes, 0.10 mm; aedeagus to process, 0.26 mm; aedeagus to shaft, 0.17 mm; distance at top of aedeagal shafts, 0.17 mm; distance at mid-length of aedeagal shafts, 0.08 mm; female 7th sternite, 0.80 mm.

Specimens examined. $10 \oplus 9$, **KSA: Jazan**, Baish, Wadi Baish: $17^{\circ}22.46$ 'N, $042^{\circ}32.24$ 'E, Light trap, 30.I.2015, Mashry, H. & Iftekhar, R.; $1 \oplus 1$, same but AlAriydah, Jizan Dam: $17^{\circ}02.62$ 'N, $042^{\circ}98.36$ 'E, 187 m, Beating, 21.V.2012, Al Ansi, A.; $1 \oplus$, same but Wadi Jizan: $17^{\circ}01.28$ 'N, $042^{\circ}59.19$ 'E, 158 m, Sucking, 16.III.2014, El-Sonbati, S.; $1 \oplus$, same but Fifa, AlAbsia: $17^{\circ}15.83$ 'N, $043^{\circ}06.49$ 'E, 1770 m, 17.III.2014; $27 \oplus 118$, KSA: **Asir**,

Wadi Qounonah: 19°24.67'N, 041°36.39'E, 348 m, Light trap, 11.III.2012, El-Sonbati, S. & Al Dhafer, H.; 1^Q, same but Wadi Al Talalea: 19°02.90'N, 041°58.17'E, 242 m, Sweep net, 1.V.2012, Al Dhafer, H., Abdeldayem, S., Al Ansi, A. & Al Othman, A.; $2 \bigcirc 3 \circlearrowleft$, same but Wadi Namar: 24°34.04'N, 046°40.59'E, Sweep net, 29.II.2012, Al Ansi, A., Al Harbi, M. & Al Othman, A.; 1³, same but Wadi Targ: 19°37.39'N, 042°18.02'E, 1317 m, Light trap, 14.III.2012, Fad, H. & Setyaningrum, H.; 1♀1♂, same but Wadi Tourabah: 20°14.37'N, 041°15.23'E, 1757 m, Light trap, 9.III.2012, Al Dhafer, H., Fadl, H., Abdel-Dayem, S., El Torky, A. & Al Ansi, A.; $2 \bigcirc 1 \bigcirc$, same but Khamis Mushayt, Wadi Bisha: 18°20.02'N, 042°42.22'E, 1990 m, Sweep net, 27.IV.2011, Sharaf, M., Al Ansi, A. & Setyaningrum, H.; 2^Q2^A, same but Al-Hubail, Wadi Reem, 9.II.2016, Vacuum, 18°06.98'N, 042°13.94'E, 451 m, A. Ansi.; 22♀33♂, KSA: Bahah, Shada, Wadi Neera: 19°44.87'N, 041°20.01'E, 471 m, Vacuum, 10.XII.2014, Al Dhafer, H., Fadl, H., Abdel-Dayem, S., El Torky, A.; 1♀, KSA: Najran, Hubuna, Al Dhaiqah: 17°50.71'N, 044°15.83'E, 1228 m, Sweep net, 14.I.2013, AlAnsi, A., Rasool, I. & Khan, S.; 1 \bigcirc , KSA, **Muzahimiyah**, Al Khararah: 24°24.35'N, 046°14.67'E, Light trap, 17.IV.2012, Al Dhafer, H., Fadl, H., Abdel-Dayem, S., El Torky, A. & AlAnsi, A.; 1♀, KSA, Riyadh, Al Ammariyah: 24°40.00'N, 043°40.00'E, Beating, 22.II.2012, Al Drayhim, Y., Al Dhafer, H., El-gharbawy, A. & El-Sonbati, S.; 2943, Oman: Samad Ashan, Aswareeg, 1-10.X.2017, 22°49.50'N, 058°09.12'E, A. Al-Jahdhami; 13, same but, 9–10.VIII.2017; 1253, Muscat (Seeb), Botanic Garden, 5-8.XI.2017, Light trap, 23°33.59'N, 058°07.79'E, A. Al-Jahdhami.

Distribution. European Russia (Dlabola 1961), India, Indonesia (Metcalf 1967), Pakistan (Ahmed and Sultana 1994), Saudi Arabia (Dlabola 1979); Oman (present study) (Figs 75, 76).

Ecology and biology. *Opsius versicolor* was the most common species collected during this study comprising approximately 50% of the total number of specimens examined. Relative abundances varied, with numbers peaking in March in Asir Province, peak abundance in January in Jazan Province, and in November in Baha Province, KSA (Figs 77–79).

Diagnosis. Males of *O. versicolor* can be distinguished by tiny apodemes not exceeding the first segment, aedeagal shafts with diverging branches, and the basal process contiguous or coherent to each other. This species dimorphic, with the crown of males being slightly produced (Figs 13–16), and that of females parallel (Figs 17, 18).

Opsius wilsoni El-Sonbati, sp. nov.

http://zoobank.org/FEFF6893-1486-4728-9455-AABB9A0B5B94 Figs 19–22, 35–37, 50–52, 70–74

Description. In addition to generic characters, with the following characteristics.

Coloration. General coloration light yellow whitish, greenish brown, with black punctation on forewings (Figs 19–22). Face and vertex yellowish. Pronotum with



Figures 53–74. Male/Female genital structures of *Opsius* spp. **53–57.** *O. heydeni* (Lethierry). **53.** *∂*, Pygofer, **54.** *∂*, Apodeme; **55.** *♀*, 7th sternite; **56–57.** *♀*, Ovipositor. **58–62.** *O. richteri* Dlabola. **58.** *∂*, Pygofer, **59.** *∂*, Apodeme; **60.** *♀*, 7th sternite; **61, 62.** *♀*, Ovipositor. **63, 64.** *O. scutellaris* (Lethierry). **63.** *∂*, Pygofer, **64.** *∂*, Apodeme; **65–69.** *O. versicolor* (Distant). **65.** *∂*, Pygofer, **66.** *∂*, Apodeme; **67.** *♀*, 7th sternite; **68, 69.** *♀*, Ovipositor. **70–74.** *O. wilsoni* sp. nov. **70.** *∂*, Pygofer, **71.** *∂*, Apodeme; **72.** *♀*, 7th sternite; **73, 74.** *♀*, Ovipositor.

light yellow anterior margin, and with light green posterior margin. Scutellum light yellow whitish. Forewings greenish brown, with scattered black punctation, transparent at the outer edge, with brownish apical and subapical cells, with some dense brown stripes inside. Legs yellow with brown setal areolae, apices of tarsomeres and claws from brown to dark brown.

Head. Head slightly wider than pronotum. Crown parallel in length, slightly more than two times the width of compound eye, with tiny median groove, with round apex. Ocelli on crown posterad of anterior margin and close to eyes. Gena slightly incised with small projection. Antenna short, near upper corner of eye. Antennal ledge weakly carinate. Frontoclypeus anterodorsal part inflated, posteroventral part not inflated, shorter than wide, with fine erect seta on gena close to lateral frontal suture. Lateral frontal suture reaching ocellus, shorter than clypeogenal suture, toward middle of ocelli, ratio of frontoclypeal loral suture to clypellar loral suture more than ¹/₃. Lorum extended nearly to genal margin, wider than clypellus at base. Clypellar suture complete and arcuate. Clypellus, not inflated, expanded apically ovoid, not protruding the curve of gena, straight or convex apically.

Thorax. Pronotum wider than long, with convex anterior margin and concave posterior margin, short lateral margin, more than two times the length of vertex, about two times as long as scutellum. Scutellum wider than long.

Wings. Macropterous, forewings more than three times as long as wide, appendix restricted to anal margin, without reflexed costal veins, with A veins gently curved distally, A1 crossvein absent, A1–A2 crossvein absent, two closed anteapical cells, inner anteapical cell open. Hind wings not visible, submarginal vein complete.

Legs. Profemur and mesofemur inflated. Profemur row AM with AM1, profemur with two dorsoapical setae; intercalary row with eight fine scattered setae gradually reduced apically; AV row with numerous long setae. Protibia dorsal margin rounded, AD row with one macrosetae, PD row with four macrosetae, AV row with numerous macrosetae, PV row with 1-4 macrosetae. Mesofemur AV row with numerous setae, two dorsoapical seta, short and reduced. Metafemur setal formula 2+2+1, setae of penultimate pair set close to each other. Metatibia arched throughout its length, PD row with long and short macrosetae alternating or subequal in length, AD row with macrosetae and one smaller intercalary seta between each pair, AV row with numerous macrosetae and extending nearly to base, gradually increasing in size apically. Protarsomere and mesotarsomere I length shorter than tarsomeres II and III combined. Metatarsomere I length equal or slightly shorter to tarsomeres II and III combined.

Male genitalia. Pygofer slightly angled mid-posteriorly (Fig. 70); subgenital plates with gradually tapered apex (Fig. 50); connective linear (Fig. 52); apodemes narrow, extending to the apex of second abdomen segments, apo-



- + Opsius tigripes (Lethierry)
- Opsius versicolor (Distant)
- 🗙 Opsius wilsoni sp. n.

0 7501,500 3,000 4,500 6,000 Kilometers W E 75



Figures 75–79. 75, 76. Distribution of *Opsius* spp. **75.** World distribution (point indicates presence in the country). **76.** Local distribution; **77–79.** Habitats of *Opsius* spp. **77.** Locality: Muzahimiyah, Al Khararah: 24°24.35'N, 46°14.67'E; **78.** Locality: Abha, Sad Abha: 18°19.32'N, 42°31.00'E; **79.** Type locality: Jazan, Wadi Jazan: 17°01.275'N, 42°59.187'E.

Opsius heydeni (Lethierry)

Opsius pallasi (Lethierry)

Opsius scutellaris (Lethierry)

Opsius richteri Dlabola

deme width three times as distance between each apodeme, posterior margin a cute rounded externally and gradually tapered internally (Fig. 71); aedeagus with only dorsal process, both curved or bent inward at mid-length, aedeagal shafts with diverging branches, ratio of distance between two shafts at mid-length to tip length 1/3, bent inward at mid-length, as long as basal process, two times as wide as basal process, basal process extending narrow to shafts branches, pointed; phallobase not inflated (Figs 35, 36).

Female genitalia. Female 7th sternite 1.5 times as broad at base as long medially, posterior margin with median lobe-like projection with V-shaped notch in middle, posterolateral angles conically rounded, narrowed (Fig. 72); first valvula convex; second valvula gradually tapered apically with rather small and serrate tooth on dorsal surface (Figs 73, 74).

Measurement. $\stackrel{?}{\supset}$ 3.1 mm; $\stackrel{?}{\ominus}$, 3.4 mm; pygofer, 0.47 mm; valve, 0.25 mm; subgenital plate, 0.50 mm; style, 0.21 mm; connective, 0.26 mm; apodemes, 0.28 mm; aedeagus to process, 0.20 mm; aedeagus to shaft, 0.19 mm; distance at top of aedeagal shafts, 0.09 mm; distance at mid-length of aedeagal shafts, 0.03 mm; female 7th sternite, 0.81 mm.

Type specimens. *Holotype* 3, KSA: Jazan, Wadi Jazan: 17°05.58'N, 043°02.17'E, 158 m, vacuum, 16.III.2014, El-Sonbati, S. (KSMA). *Paratypes:* $7 \bigcirc 83$, same locality as Holotype; $1 \bigcirc$, KSA: Jazan, Fifa, Al Absia: 17°28.85'N, 043°14.30'E, VC, 20.III.2014, El-Sonbati, S. A.; 13, KSA: Najran, Hubuna, Wadi Hubuna: 17°55.40'N, 044°24.47'E, 1244, beating, 14.I.2013, Ansi, A.; Rasool, I.; Khan, S. (KSMA); $6 \bigcirc 33$, Asir, Abha, Al-Hubail, Wadi Reem, 9.II.2016, vacuum, 18°06.98'N,

042°13.94'E, 451 m, A. Ansi (NMWC). **Distribution.** Saudi Arabia (Jazan, Wadi Jazan; Jazan, Fifa, Al Absia, Najran, Hubuna, Wadi Hubuna) (present

study) (Figs 75, 76). Ecology and biology. Opsius wilsoni appeared to reach peak abundance in March. Most specimens were collected from Tamarix spp. (Figs 77–79) by using a vacuum device.

Diagnosis. Females and males of *O. wilsoni* can be recognized by a slightly incised gena with small projection. Additionally, males can be distinguished by aedeagal shafts with diverging branches at apex, ratio of distance between two shafts at mid-length to tip length 1/3, bent inward at mid-length.

Etymology. This species is named in honour of Dr Michael R. Wilson, Department of Natural Sciences, National Museum of Wales, Cardiff, Wales, United Kingdom.

Conclusions

Seven species of *Opsius* present in KSA were revised including including the description of a new species, and three new species records for KSA. A key of species based on males is presented that includes new characters for separation of KSA species. Our study also provides maps of the known geographical distribution of the genus and provides examples of typical habitats of the genus. Further study is needed to evaluate the variation in the species of the genus across their entire geographical range.

Acknowledgements

The authors are grateful to John Deeming (NMWC) for valuable suggestions, to Boris Kondratieff (Colorado State University) and James Zahniser (APHIS) for reading and improving the manuscript, to Dominique Zimmermann for her helpful editorial comments, and to Ali Al-Jahdhami (ONHM) for his assistance and loan of specimens. The authors would like to express their sincere appreciation to the Deanship of Scientific Research at King Saud University for funding their research group (no. RGP-1437–009).

References

- Ahmed M, Sultana Z (1994) Grassland leafhoppers (Cicadellidae: Homoptera) of Karachi, Pakistan. Records Zoological Survey of Pakistan 12: 125–133.
- de Bergevin E (1931) "Résultats Hemiptèrologiques." In Spedizione Scientifica all'Oasi di Cufra (Marzo-Luglio 1931). Annali del Museo civico di Storia Naturale di Genova. Genova 55: 422–430.
- Dietrich CH (2005) Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). Florida Entomologist 88: 502–517. https://doi.org/10.1653/0015-4040(2005)88[502:KTTFOC]2.0.CO;2
- Distant WL (1908) Rhynchota. IV. Homoptera and appendix (Pt.). The fauna of British India, including Ceylon and Burma. Taylor & Francis, London, XV+501 pp.
- Dlabola J (1960a) Einige neue Zikaden aus Dagestan und Zentralasien (Homoptera). Stuttgarter Beiträge zur Naturkunde aus dem Staatlichen Museum für Naturkunde in Stuttgart 40: 1–5.
- Dlabola J (1960b) Iranische Zikaden (Homoptera, Auchenorrhyncha): Ergebnisse der entomologischen Reisen Willi Richter, Stuttgart, im Iran 1954 und 1956—Nr. 31. Stuttgarter Beiträge zur Naturkunde aus dem Staatlichen Museum für Naturkunde in Stuttgart 41: 1–24.
- Dlabola J (1961) Die Zikaden von Zentralasien, Dagestan und Transkaukasien (Homopt. Auchenorrhyncha). Acta Entomologica Musei Nationalis Pragae 34: 241–358.
- Dlabola J (1979) Insects of Saudi Arabia. Homoptera. Fauna of Saudi Arabia 1: 115–139. https://doi.org/10.1007/978-1-349-03214-3 1
- Dlabola J (1980) Insects of Saudi Arabia. Homoptera: Auchenorrhyncha (Part 2). Fauna of Saudi Arabia 2: 74–94.
- Dlabola J (1981) Ergebnisse der Tschechoslowakisch-Iranischen entomologischen Expeditionen nach Iran (1970 und 1973). Acta Entomologica Musei Nationalis Pragae 40: 127–311.
- El-Sonbati SA, Wilson MR, Al Dhafer HM (2015) A new species of the leafhopper genus *Naevus* Knight, 1970 (Hemiptera: Cicadellidae: Deltocephalinae: Opsiini), from Saudi Arabia. Zootaxa 4059: 393–400. https://doi.org/10.11646/zootaxa.4059.2.10
- El-Sonbati SA, Wilson MR, Al Dhafer HM (2016) *Paraorosius*, a new genus of leafhopper (Hemiptera: Cicadellidae: Deltocephalinae:

Opsiini), with description of a new species from the Middle East. Zootaxa 4150: 581–590. https://doi.org/10.11646/zootaxa.4150.5.5

- El-Sonbati SA, Wilson MR, Al Dhafer HM (2017) A new leafhopper genus with two new species related to *Masiripius* Dlabola, 1981 (Hemiptera, Deltocephalinae, Cicadellidae, Opsiini). European Journal of Taxonomy 308: 1–24. https://doi.org/10.5852/ejt.2017.308
- El-Sonbati SA, Wilson MR, Al Dhafer HM (2018) Contribution to the knowledge of selected genera of the tribe Opsiini (Hemiptera: Cicadellidae: Deltocephalinae) from the Kingdom of Saudi Arabia. Acta Entomologica Musei Nationalis Pragae 58(1): 257–266. https://doi.org/10.2478/aemnp-2018-0023
- El-Sonbati SA, Wilson MR, Al Dhafer HM (2019) Revision of the leafhopper genus *Orosius* Distant, 1918 (Hemiptera: Cicadellidae: Deltocephalinae: Opsiini) in the Arabian Peninsula with the description of a new species. Zootaxa 4565(1): 37–48. https://doi. org/10.11646/zootaxa.4565.1.2
- Fieber FX (1866) Neue Gattungen und Arten in Homoptern (Cicadina Bur.). Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wien. Wien 16: 497–516. https://doi. org/10.5962/bhl.title.9291
- Guba I, Glennie K (1998) Geology and geomorphology. In: Ghazanfar SA, Fisher M (Eds) Vegetation of the Arabian Peninsula. Springer, Dordrecht, 39–62. https://doi.org/10.1007/978-94-017-3637-4_3
- Ishihara T (1972) A valid genus, *Hishimonus* Ishihara, 1953 (Hemiptera, Euscelidae). Transactions of the Shikoku Entomological Society 11(3): 84.

Khatri I, Webb MD (2010) The Deltocephalinae leafhoppers of Pakistan (Hemiptera, Cicadellidae). Zootaxa 2365: 1–47. https://doi. org/10.11646/zootaxa.2365.1.1

- Lethierry LF (1874) Hémiptères nouveaux. Petites Nouvelles Entomologiques. Paris 1: 449.
- Lethierry LF (1876a) Homoptères nouveaux d'Europe et des contrées voisines. Annales de la Société Entomologique de Belgique 19: lxxvi–lxxxviii.
- Lethierry LF (1876b) Homopterès nouveaux d'Europe et des contrés voisines. Compte Rendu des Séances de la Société Entomologique de Belgique 19: 5–17.
- Lethierry LF, Puton A (1876) Faunule des hémiptères de Biskra. Annales de la Société Entomologique de France (Serie 5) 6: 19–56.
- Lindberg H (1936) Die Cicadinen der Kanarischen Inseln. Commentationes Biologicae. Societas Scientiarum Fennica. Helsingfors 4(9): 1–19.
- Lindberg H (1954) Hemiptera Insularum Canariensium. Systematik, Ökologie und Verbreitung der Kanarischen Heteropteren und Cicadinen. Commentationes Biologicae. Societas Scientiarum Fennica 14(1): 1–304.
- Lindberg H (1958) Hemiptera Insularum Caboverdensium. Systematik, Okologie und Kapverdischen Inseln. Ergebnisse der Zoologischen Expedition von Professor Hakan Lindberg nach den Kapverde-In-

seln im Winter 1953–1954, Nr. 22. Commentationes Biologicae Societas Scientiarum Fennica 19(1): 1–246.

- Metcalf ZP (1967) General Catalogue of the Homoptera. Fascicle VI: Cicadelloidea. Part 10: Euscelidae. Section I. United States Department of Agriculture, Agriculture Research Service, Washington, DC, v + 1077 pp.
- Nast J (1972) Palaearctic Auchenorrhyncha (Homoptera). An annotated check list. Polish Scientific Publishers, Warszawa, 550 pp.
- Newete SW, Allem SM, Venter N, Byrne MJ (2019) *Tamarix* efficiency in salt excretion and physiological tolerance to salt-induced stress in South Africa. International Journal of Phytoremediation 22(1): 3–9. https://doi.org/10.1080/15226514.2019.1633997
- Oman PW, Knight WJ, Nielson MW (1990) Leafhoppers (Cicadellidae): A bibliography, generic check-list and index to the world literature 1956–1985.
- Puton A (1875) Homoptera. Am. Serv. (Gulaerostria. Zett. Fieb.) Sect. I. Auchenorhyncha. Dumer. (Cicadina. Burm.). Catalogue des Hémipterès (Hétéroptères, Cicadines et Psyllides) d'Europe et du Bassin de la Méditerranée 2e ed. Deyrolle, Paris, 165 pp.
- Siemion GM, Stevens LE (2015) Interactions among *Tamarix* (Tamaricaceae), *Opsius stactogalus* (Cicadellidae), and litter fungi limit riparian plant establishment. Advances in Entomology 3(2): 65–81. https://doi.org/10.4236/ae.2015.32008
- Vilbaste J (1961) New species of cicadellids (Homoptera: Jassidae). Uzbekskii Biologicheskii Zhurnal 1: 42–50.
- Vilbaste J (1962) Uber die Zikadenfauna des östlichen Teiles des Kaspischen Tieflandes. Eesti NSV Tead. Academia J.L.S.A., Tallinn 55: 129–151.
- Virla EG, Logarzo GA, Paradell SL (2010) Occurrence of the tamarix leafhopper, *Opsius stactogalus* Fieber (Hemiptera: Cicadellidae), in Argentina. Journal of Insect Science 10(1): 23. https://doi. org/10.1673/031.010.2301
- von Kéler SV (1955) Entomologisches Wörterbuch mit besonderer Berücksichtigung der morphologischen Terminologie. Akademie Verlag, Berlin, 679 pp.
- Wagner W (1942) Beitrag zur Kenntnis der italienischen Zikaden. Bollettino del Laboratorio di Zoologia Generale e Agraria della R. Scuuola Superiore d'agricoltura in Portici 32: 118–124.
- Wiesenborn WD (2004) Mouth parts and alimentary canal of Opsius stactogalus Fieber (Homoptera: Cicadellidae). Journal of the Kansas Entomological Society 77(2): 152–155. https://doi. org/10.2317/0307.28.1
- Zahniser JN, Dietrich CH (2013) A review of the tribes of Deltocephalinae (Hemiptera: Auchenorrhyncha: Cicadellidae). European Journal of Taxonomy 45: 1–211. https://doi.org/10.5852/ejt.2013.45
- Zahniser JN (2019) An online interactive key and searchable database of Deltocephalinae (Hemiptera: Cicadellidae). http://zahniser.speciesfile.org [Accessed on: 2019-7-7]

<u> PENSOFT</u>.



Biology of two European *Tenthredo* species (Hymenoptera, Tenthredinidae) feeding on *Gentiana*

Andrew Liston¹, Ewald Altenhofer², Romana Netzberger³, Marko Prous^{1,4}

1 Senckenberg Deutsches Entomologisches Institut, Eberswalder St. 90, 15374 Müncheberg, Germany

2 Etzen 39, 3920 Groß Gerungs, Austria

3 Innerzaun 26/2, 3321 Kollmitzberg, Austria

4 Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia

http://zoobank.org/24D3ACCC-AD2B-4726-9E01-908549F3E54A

Corresponding author: Andrew Liston (aliston@senckenberg.de)

Academic editor: Ralph Peters • Received 30 December 2019 • Accepted 6 February 2020 • Published 21 February 2020

Abstract

Very few sawflies using Gentianaceae as larval host plants have been recorded. We identified larvae collected in Austria on *Gentiana* asclepiadea L. as *Tenthredo atra* Linnaeus, 1758 and *T. propinqua* Klug, 1817. If its current taxonomic circumscription as a single species is accepted, *T. atra* is a highly polyphagous species, whereas *T. propinqua* may be more specialised: *Gentiana asclepiadea* is its first recorded host. We sequenced plant DNA from the head of one *T. propinqua* larva, which confirmed that it had been feeding on this plant. This is the first recorded use of *G. asclepiadea* by sawfly larvae. Larvae are illustrated, and identification characters are described.

Key Words

Gentianaceae, host plants, larvae, sawflies, Symphyta, Tenthredinoidea

Introduction

The study of the immature stages of sawflies, including the identification of their larval hosts, has a long tradition in Europe, reaching back to the pioneering studies of Réaumur (1740). Despite many advances since then, we still know little or nothing about the biology of some taxa. Here, we fill one of these gaps by documenting the host plant association of two *Tenthredo* species with a member of the Gentianaceae, a plant family which has hitherto seldom been mentioned as a host of sawflies.

Recently, DNA sequencing has proved itself as a potent tool for the identification of sawfly larvae (e.g. Shinohara et al. 2017; Prous et al. 2019). In this study we used DNA sequences to identify one of the sawfly species. Compared to the traditional method of rearing an adult from a larva and determining the adult using morphological characters, sequencing can provide an identification result much more quickly, and the risk is avoided of all individuals dying before they reach maturity, in which case no identification will be obtained. We also demonstrate that DNA sequencing can be used to identify or confirm the host of a larva, using DNA extracted from the larva. This is especially useful for larvae that were collected, for example by sweeping, without any clear indication of what they were feeding on, and might also help to identify the hosts of species of Tenthredininae which do not feed on the plant species in which eggs are laid, as reported by Chevin (2009) for some *Macrophya* species.

Methods

Nearly fully grown larvae of two *Tenthredo* species were beaten from, or detected visually on *Gentiana* asclepiadea L. in the Gesäuse National Park, Styria, Austria, by E. Altenhofer and R. Netzberger in 2016 and 2019. Some larvae were kept by EA for rearing, and

Copyright Andrew Liston et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. others were preserved in 95% ethanol. Identification of Tenthredo atra Linnaeus, 1758 is based on the morphology of adults and larvae. Tenthredo propinqua Klug, 1817 was identified by genetic sequences obtained from a larva. Total DNA was extracted from the head of one T. propingua larva (DEI-GISHym12639), and one mitochondrial (1087 bp of CO1) and two nuclear gene fragments (1654 bp of NaK and 2543 bp of POL2) were sequenced (methodology as in Prous et al. 2019). To test which host plant the larva had been feeding on, we used the same larval extract to amplify a plastid region between trnL 5' exon and trnF using primers c and f (Taberlet et al. 1991). The region, which turned out to be 816 bp, contains two variable introns and the trnL 3' exon and was sequenced with primers c, d, e, and f (Taberlet et al. 1991). The sequences have been deposited in the GenBank (NCBI) database (accession numbers MN856146-MN856149).

Material examined

The abbreviation SDEI refers to the insect collection of the Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany.

Tenthredo atra Linnaeus, 1758

Austria: Styria: Gesäuse, Kroisalm, 47.60N 14.63E, 900 m, 26.08.2016, 3 females reared from larvae on *Gentiana asclepiadea* (emerged May 2017), specimens were overlooked after emergence, and are in very poor condition, i.e. fragmented, with diverse parts gummed on one card (DEI-GISHym12664), and 1 larva, leg. E. Altenhofer (SDEI). Gesäuse, E Admont, 47.58N 14.62E, 11.09.2019, 10 larvae on *Gentiana asclepiadea*, leg. E. Altenhofer (SDEI). The last of these larvae entered the ground to overwinter on 21.09.2019. Gesäuse, Hartelsgraben, 47.59N 14.73E, 23.08.2019, larva on *Gentiana asclepiadea*, photographic record by R. Netzberger (Fig. 1).

Tenthredo propinqua Klug, 1817

Larvae:

Austria: Styria: Gesäuse (E Admont), between Gstatterboden and Hochscheibenalm, 47.58N 14.62E, 600– 1150 m, 15.09.2019, 10 larvae on *Gentiana asclepiadea*, leg. E. Altenhofer (2 larvae in SDEI [DEI-GISHym12639, 12640], others retained by EA for rearing).

Imagines:

Ukraine: 1 male (DEIGISHym20102), Jablunitsa, Berkut, 48.72N 24.37E, 840 m, 08.07.2004, leg. E. Heibo (SDEI). 1 male (DEIGISHym20103), Jablunitsa, Berkut, 48.72N 24.37E, 840 m, 06.07.2004, leg. E. Heibo (SDEI). 1 male (DEIGISHym20104), Jasinja, Tatariv, 48.37N 24.56E, 710 m, 03.07.2004, leg. E. Heibo (SDEI). 1 female (DEIGISHym20105), Jablunitsa, Berkut, 48.72N 24.37E, 840 m, 06.07.2004, leg. E. Heibo (SDEI). Austria: 1 female (DEIGISHym17738), Carinthia, Eisenkappel 10km E, St Margarethen, 46.46N 14.66E, 28.06.1993, leg. L. Behne (SDEI).

Tenthredo scrophulariae Linnaeus, 1758

The larvae illustrated in Figs 6, 7 were photographed by Henri Savina in France, Ariège, Aulus-les-Bains, 42.80N 1.33E, respectively on 08.09.2007 and 30.09.2007. Host: *Scrophularia* sp.

Results

Tenthredo atra

Figs 1, 2

Notes. Tenthredo atra has already been associated by various authors with larval hosts in many higher plant taxa. Taeger et al. (1998), in a summary of these records, mentioned the families Brassicaceae, Caprifoliaceae, Lamiaceae, Plantaginaceae, and Solanaceae. There are also records of larvae of T. atra feeding on Asteraceae (Pschorn-Walcher and Altenhofer 2006), Betulaceae and Salicaceae (Loth 1913), Ranunculaceae (Conde 1934), Rosaceae (Kangas 1985), and Urticaceae (Pschorn-Walcher and Altenhofer 2000). It is not clear whether records from Menvanthes trifoliata (Menvanthaceae) and Sedum telephium (Crassulaceae), which are sometimes named as hosts of T. atra (e.g. Taeger et al. 1998), really refer to this species, or respectively to the closely related T. moniliata Klug, 1817 and T. ignobilis Klug, 1817. Taeger et al. (1998) mentioned some additional plant taxa on which oviposition by T. atra has been observed but which have not been proved to be hosts of the larvae. Our identification of the larvae from Gentiana as T. atra accepts the premise that the name refers to only one, highly polyphagous species. However, a wide morphological variability, most obvious in the colour pattern of T. atra imagines, might indicate that more than one species are currently grouped under this name.

The larvae from *Gentiana asclepiadea* (Figs 1, 2) are in general appearance not distinguishable from larvae of T. atra from other hosts, nor from the larvae of the related T. moniliata on Menyanthes trifoliata (Conde 1934; Liston personal observations). Lorenz and Kraus (1957) did not examine larvae of T. atra, and their description is based on those of Cameron (1882) and Carpentier (1888). Lorenz and Kraus (1957) did not mention the faint, oblique, darker dorso-lateral stripes shared by the larvae from Gentiana, the larva described by Cameron (1882; as T. dispar Klug, 1817 from Succisa pratensis), and larvae of T. moniliata examined by Liston. Note also that Carpentier's (1888) description, as T. dispar, is of larvae from Menyanthes trifoliata, and may therefore refer to T. moniliata, but he did not mention any body markings. On the other hand, the larva of Tenthredo ignobilis, another species in the complex with T. atra,



Figures 1, 2. *Tenthredo atra* larvae, nearly full-grown, on *Gentiana asclepiadea* (photographed respectively on 23.08.2019, 11.09.2019). Photos: R. Netzberger (1), E. Altenhofer (2).

possibly differs from *T. atra* in lacking the oblique body markings (Liston 2015: fig. 9).

Larvae of the later instars feed mainly on the leaves; they feed from the edge, leaving irregular holes. Inflorescences are also sometimes consumed, at least under rearing conditions (Fig. 2). The largest full-grown larvae are similar in size to those of *T. propinqua*, i.e. somewhat over 20 mm long.

Tenthredo propinqua Figs 3–5

Notes. A mitochondrial CO1 sequence from one larva (DEI-GISHym12639) corresponded closely (maximum divergence 0.5%) with sequences from *T. propinqua* imagines (DEI-GISHym20102, DEI-GISHym20103, DEI-GISHym20104, DEI-GISHym20105, DEI-



Figures 3–7. Larvae of *Tenthredo propinqua* and *scrophulariae*. 3–5. *Tenthredo propinqua*, from *Gentiana asclepiadea*. Arrows indicate some of the black dorso-median markings, which on the abdomen occupy the width of a single annulet; 3. Preserved in ethanol (wax dissolved); 4. Alive, with wax coating (photographed on 11.09.2019); 5. Head, preserved in ethanol. 6, 7. *Tenthredo scrophulariae* larvae, on *Scrophularia* species. Arrows indicate some of the black dorso-median markings, which on the abdomen extend across two annulets at least in part; 6. Half-grown (photographed on 08.09.2007); 7. Nearly full-grown (photographed on 30.09.2007). Photos: A. Liston (3, 5), E. Altenhofer (4), H. Savina (6, 7).

GISHym17738). Nuclear sequences (NaK and POL2) are available only for the specimen sequenced here (DEI-GISHym12639). The sequenced plastid trnL-trnF region (816 bp) from the larval DNA extract confirmed *Gentiana* as the host. The closest (99–100% similarity) according to NCBI BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) were four species of *Gentiana*, among them *G. asclepiadea*. A shorter *G. asclepiadea* sequence in GenBank (accession AB453085, 387 bp) was identical to our sequence, while a longer one (AJ580515) differed by three substitutions and one deletion over the length of 781 bp (because of apparently numerous sequencing errors at the 3' end of AJ580515, 21 bp of that sequence were excluded from the comparison).

Gentiana asclepiadea is the first recorded host plant of the hitherto unknown larva of *T. propinqua*, which is a close relative of *T. scrophulariae* Linnaeus, 1758. These species have long been known to strongly resemble each other in the morphology of their imagines, but they are distinguishable using some colour characters (Enslin 1912). Their larvae are also closely similar in general appearance (see the description of a *T. scrophulariae* larva by Lorenz and Kraus 1957 and below). However, *T. scrophulariae* has a very different host plant spectrum, which consists mainly of *Scrophularia* and *Verbascum* species, but sometimes *Buddleja* species (Muche 1962), all of which belong to the Scrophulariaceae.

Differences in the pattern of black markings may enable T. propingua larvae to be distinguished from T. scrophulariae, but a larger number of T. propinqua larvae should be checked, to confirm that the differences are consistent. In T. propingua, each of the medio-dorsal black spots on the abdominal segments occupies only the width of single annulet (Figs 3, 4), whereas in T. scrophulariae, these spots occupy parts or the whole width of two annulets (Figs 6, 7). The position of the corresponding spots on the thorax is, however, similar in both species. At least in the later instars of T. scrophulariae larvae, the position of these markings is thought to be stable: compare Fig. 6 (half-grown) with Fig. 7 (nearly full-grown). After each moult, the integument of the larvae of both species temporarily lacks the covering of white wax and has a greenish ground colour. The head colour pattern of T. propingua (Fig. 5) is the same as described by Lorenz and Kraus (1957) for T. scrophulariae. In practice, the identity of their host plant should be sufficient to distinguish larvae of these species.

The feeding habits of *Tenthredo propinqua* larvae are similar to those of *T. atra*, i.e. irregularly shaped parts of the leaf-blade are consumed from the edge. But, unlike for *T. atra*, we did not observe feeding on the inflorescences by *T. propinqua*. The largest full-grown larvae are 22–25mm long, which is about the same as given by Lorenz and Kraus (1957) for *T. scrophulariae*.

Discussion

As far as we are aware, neither *Gentiana* nor any other member of the Gentianaceae has previously been recorded as a larval host of a sawfly, except by Wang et al. (2015), who studied in China the effect of florivory by larvae on *Halenia elliptica* D. Don; they referred the larvae to as an undescribed species of Tenthredinidae. Otherwise, the only reported interaction between a sawfly species and a species of Gentianaceae involves visits to the inflorescences of *Frasera speciosa* Douglas ex Griseb. by the Nearctic *Tenthredo erythromera* Provancher, 1885 (Norment 1988).

Tenthredo propinqua is a rather rarely collected species (Ritzau 1998), whose known distribution comprises south-eastern Europe, Turkey, and the Transcaucasus (Lacourt 1999). Although the eastern part of the range of Gentiana asclepiadea is more or less congruent with that of T. propingua, the sawfly has not yet been recorded further west than Berchtesgaden (Bavaria, Germany), although the plant is widespread in Switzerland and occurs as far west as northern Spain (Zajac and Pindel 2011). Tenthredo propingua has been considered to be to some extent endangered or even locally extinct, at least in the Alps of eastern Bavaria on the north-western edge of its range (Ritzau 1998; Liston et al. 2012). In the future, we should be able to more effectively assess its distribution and conservation status by searching for its larvae.

Approximately 400 species of *Gentiana* occur worldwide in Eurasia, North Africa, the Americas, and eastern Australia, but South-East Asia is a hotspot of diversity of this genus, with 248 species known from China alone, whereas only 27–29 species occur in Europe (Ho and Pringle 1995; Mel'nyk et al. 2014). Because China also possesses a very rich fauna of *Tenthredo* species (Wei et al. 2006), it is possible that *Gentiana* is more widely used there as a host plant by these sawflies than it is in Europe.

Acknowledgements

The Museum für Naturkunde, Berlin, generously paid for open access publication of this work. Henri Savina (Toulouse, France) kindly permitted us to reproduce his images of larvae of *Tenthredo scrophulariae*. Erik Heibo (Lierskogen, Norway) provided tissue samples of *T. propinqua*. Dustin Kulanek and Katja Kramp (SDEI, Müncheberg) did some of the lab work. Akihiko Shinohara and Spencer Monckton reviewed the manuscript and suggested many worthwhile improvements.

References

- Cameron P (1882) A Monograph of the British Phytophagous Hymenoptera. (*Tenthredo, Sirex* and *Cynips*, Linné.). Volume 1. The Ray Society, London, 1–340. [21 pls] https://doi.org/10.5962/bhl. title.59527
- Carpentier L (1888) Notes sur quelques larves de tenthrédides. Mémoires de la Societé Linnéenne du Nord de la France 7: 254–286.
- Chevin H (2009) Biologie comparée des espèces francaises du genre Macrophya (Hymenoptera, Symphyta, Tenthredinidae). Bulletin des Naturalistes des Yvelines 36: 44–50.
- Conde O (1934) Ostbaltische Tenthredinoidea, II. Teil. Korrespondenzblatt des Naturforscher-Vereins zu Riga 61: 168–198.
- Enslin E (1912) Die Tenthredinoidea Mitteleuropas. Deutsche Entomologische Zeitschrift [1912](Beiheft 1): 1–98. https://doi.org/10.1002/ mmnd.48019120209
- Ho T, Pringle JS (1995) Gentianaceae: Gentiana Linnaeus. In: Wu Z, Raven PH (Eds) Flora of China, Volume 16 – Gentianaceae through Boraginaceae. Science Press and Missouri Botanical Garden Press, Beijing and St. Louis, 15–93.
- Kangas JK (1985) Pälkäneen Sahapistiäisfauna 1953–1983. Pälkäne-Seuran Julkaisuja 5: 1–113.
- Lacourt J (1999) Répertoire des Tenthredinidae ouest-paléarctiques (Hymenoptera, Symphyta). Mémoires de la Société Entomologique de France 1–432.
- Liston AD (2015) New records and host plants of Symphyta (Hymenoptera) for Germany, Berlin and Brandenburg. Contributions to Entomology. Beiträge zur Entomologie 65(2): 383–391. https://www. contributions-to-entomology.org/article/view/1890/188
- Liston AD, Jansen E, Blank SM, Kraus M, Taeger A (2012) Rote Liste und Gesamtartenliste der Pflanzenwespen (Hymenoptera: Symphyta) Deutschlands. Stand März 2011. In: Binot-Hafke M, Balzer S, Becker N, Gruttke H, Haupt H, Hofbauer N, Ludwig G, Strauch M (Eds) Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutsch-

lands. Wirbellose Tiere Teil 1. Naturschutz und Biologische Vielfalt, Bonn-Bad Godesberg 70 (3): 489–556.

- Lorenz H, Kraus M (1957) Die Larvalsystematik der Blattwespen (Tenthredinoidea und Megalodontoidea). Abhandlungen zur Larvalsystematik der Insekten 1: 1–389.
- Loth N (1913) Verzeichnis der im Gebiete des rheinischen Schiefergebirges und in einem Teile der niederrheinischen Tiefebene vorkommenden Tenthrediniden. Berliner entomologische Zeitschrift 58: 46–95.
- Mel'nyk V, Drobyk NM, Twardovska MO, Kunakh V (2014) Karyology of European species of genus *Gentiana* L. In: Rybczynski JJ, Davey MR, Mikula A (Eds) The Gentianaceae- Volume 1: Characterization and Ecology. Springer, Berlin and Heidelberg, 219–230. https://doi. org/10.1007/978-3-642-54010-3_7
- Muche WH (1962) Neue Wirtspflanze f
 ür Allantus scrophulariae L. Entomologische Nachrichten 6(2): 24.
- Norment CJ (1988) The effect of nectar-thieving ants on the reproductive success of *Frasera speciosa* (Gentianaceae). American Midland Naturalist 120(2): 331–336. https://doi.org/10.2307/2426005
- Prous M, Liston A, Kramp K, Savina H, Vårdal H, Taeger A (2019) The West Palaearctic genera of Nematinae (Hymenoptera, Tenthredinidae). ZooKeys 875: 63–127. https://doi.org/10.3897/zookeys.875.35748
- Pschorn-Walcher H, Altenhofer E (2000) Langjährige Larvenaufsammlungen und Zuchten von Pflanzenwespen (Hymenoptera, Symphyta) in Mitteleuropa. Linzer biologische Beiträge 32(1): 273–327.
- Pschorn-Walcher H, Altenhofer E (2006) Neuere Larvenaufsammlungen und Zuchten von mitteleuropäischen Pflanzenwespen (Hymenoptera, Symphyta). Linzer biologische Beiträge 38(2): 1609–1636.
- Réaumur RAF de (1740) Troisieme Mémoire. Et le premier sur les Mouches à quatre aîles. Des fausses Chenilles, & des Mouches à scies, dans lesquelles elles se transforment. In: Réaumur RAF de 1740: Mémoires pour servir à l'Histoire des Insectes. Tome Cinquiéme.

Suite de l'Histoire des Mouches à deux aîles, & l'Histoire de plusieurs Mouches à quatre aîles, sçavoir, des Mouches à scies, des Cigales, & des Abeilles. Imprimerie Royale, Paris, 87–144.

- Ritzau C (1998) Tenthredo propinqua Klug, 1817 neu für Deutschland (Hymenoptera: Tenthredinidae). In: Taeger A, Blank SM (Eds) Pflanzenwespen Deutschlands (Hymenoptera, Symphyta). Kommentierte Bestandsaufnahme. Goecke & Evers, Keltern, 43–44.
- Shinohara A, Hara H, Kramp K, Blank SM, Kameda Y (2017) Bird droppings on chestnut leaves or sawfly larvae: DNA barcodes verify the occurrence of the archaic *Megaxyela togashii* (Hymenoptera, Xyelidae) in Hokkaido, Japan. Zootaxa 4221(2): 220–232. https:// doi.org/10.11646/zootaxa.4221.2.6
- Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. Plant Molecular Biology 17: 1105–1109. https://doi.org/10.1007/ BF00037152
- Taeger A, Altenhofer E, Blank SM, Jansen E, Kraus M, Pschorn-Walcher H, Ritzau C (1998) Kommentare zur Biologie, Verbreitung und Gefährdung der Pflanzenwespen Deutschlands (Hymenoptera, Symphyta). In: Taeger A, Blank SM (Eds) Pflanzenwespen Deutschlands (Hymenoptera, Symphyta). Kommentierte Bestandsaufnahme. Goecke & Evers, Keltern, 49–135.
- Wang L, Meng L, Luo J (2015) Florivory Modulates the Seed Number-Seed Weight Relationship in *Halenia elliptica* (Gentianaceae). The Scientific World Journal 2015: 1–7. https://doi. org/10.1155/2015/610735
- Wei M, Nie H, Taeger A (2006) Sawflies (Hymenoptera: Symphyta) of China - Checklist and Review of Research. In: Blank SM, Schmidt S, Taeger A (Eds) Recent Sawfly Research: Synthesis and Prospects. Goecke & Evers, Keltern, 505–574.
- Zajac A, Pindel A (2011) Review of the Willow Gentian, Gentiana asclepiadea L. Biodiversity 12(3): 181–185. https://doi.org/10.1080/1 4888386.2011.628247

PENSOFT.



Molecular taxonomy of *Tomares* hairstreaks (Lepidoptera, Lycaenidae, Theclinae)

Vazrick Nazari¹, Wolfgang ten Hagen²

1 P.O. Box 45063, Ottawa, Ontario K2M 2YI Canada

2 Frühlingstrasse 1, 63853 Mömlingen, Germany

http://zoobank.org/827AA17E-345F-4D28-9659-7BE18130125C

Corresponding author: Vazrick Nazari (nvazrick@yahoo.com)

Academic editor: Harald Letsch • Received 18 January 2020 • Accepted 20 March 2020 • Published 5 May 2020

Abstract

Tomares hairstreaks comprise about 10 species distributed from Europe and North Africa to Central Asia. The taxonomy of the genus is hampered by the absence of diagnostic characters by which specimens can be unambiguously assigned to species. Our investigation of morphology and DNA barcode variations within and between *Tomares* species shows that while well-defined species (*T. ballus, T. mauritanicus, T. callimachus, T. desinens* and *T. fedtschenkoi*) diverge, poorly characterized taxa (*T. nogelii, T. nesimachus, T. dobrogensis, T. romanovi* and *T. telemachus*) show very little to no differentiation in mtDNA. We reinstate *Tomares callimachus* spp. *hafis* (Kollar, 1849) as a valid subspecies (**stat. rev.**) and propose taxa *telemachus* Zhdanko, 2000 and *uighurica* Koçak, Seven & Kemal, 2000 as synonyms of *T. romanovi* and *T. nogelii nogelii respectively* (**syn. nov.**). We relegate *Polyommatus epiphania* Boisduval, 1848, recently revived as a valid subspecies of *T. callimachus*, back to synonymy under the latter, and reconsider the status of *T. nogelii dobrogensis* (Caradja, 1895) in the light of new molecular data. We use a nuclear gene (EF-1α) in addition to COI barcodes to reconstruct the phylogeny of the group.

Key Words

biogeography, butterflies, DNA, hybridization, introgression, phylogenetics

Introduction

Over the last decade, lycaenid butterflies have been a popular model group in studies of hybridization (Mallet et al. 2011; Gillespie et al. 2013; Nice et al. 2013; Sakamoto and Yago 2017), sympatric and cryptic speciation (Dincă et al. 2011; Vodă et al. 2015; Lukhtanov et al. 2015; Busby et al. 2017; Bereczki et al. 2018), population genomics (Gompert et al. 2014; Vanden Broeck et al. 2017; Chaturvedi et al. 2018), chromosome evolution (Lukhtanov and Dantchenko 2017), ecological specialization (Downey and Nice 2013; Schär et al. 2018) and conservation genetics (Sielezniew et al. 2012; Frye and Robbins 2015; Takeuchi et al. 2015; Koubínová et al. 2017; Roitman et al. 2017; Matthews et al. 2018). Part of this popularity maybe due to the fact that lycaenids have the highest rate of protein-coding sequence evolution among butterflies (Pellissier et al. 2017). Nevertheless, lycaenid taxonomy is still riddled with cases of uncertainty. Ranking is often disputed in geologically young species-complexes with limited phenotypic or genetic differentiation, or where geographical clines, hybridization, and sympatric or cryptic speciation are involved.

The ~10 species in Palaearctic hairstreak genus *Tomares* Rambur 1840 (*sensu* Weidenhoffer and Bozano 2007) present such a case. These butterflies are characterized by having 11 veins on the forewings (10, 11 or 12 in other Theclinae Swainson 1831), tailless hindwings with vestigial tornal lobe, bright red-orange patches on otherwise dark brown upperside of both wings, and tibiae with large projections at the tarsal end. These characteristics have granted them a tribe of their own (Tomarini Eliot 1973). Despite being generally rare, all *Tomares* species show individual and local variability in adult size as well

as ground color intensity and the shade and size of the orange patches on their wings, which can sometimes be completely absent. Some Tomares are better characterized than others: Tomares fedtschenkoi is a large, phenotypically distinct species with a disjunct distribution in Central Asia (Tuzov et al. 2000; Weidenhoffer and Bozano 2007). Tomares ballus, a myrmecophilous species ranging from France to North Africa, and T. mauritanicus, a variable butterfly with an almost continuous distribution along the Atlas Mountains, are also easily distinguishable (Tennent 1996; Tolman and Lewington 1997; Tarrier and Delacre 2008). The remaining species share a common range from southeastern Europe to Jordan (Larsen 1974; Benyamini 1990) and Central Asia (Lukhtanov and Lukhtanov 1994; Toropov and Zhdanko 2009) and present several cases of poorly understood taxonomy.

Among these, the closely related T. callimachus and T. desinens are both distinguished by the absence of orange coloration within the transverse bands on the underside of the hind wings (UNH). They both fly in sympatry in Azerbaijan and Iran (Nekrutenko and Effendi 1980; Nazari 2003). Despite some geographic variability among disjunct populations, recognition of subspecies in T. callimachus has been discouraged (Hesselbarth et al. 1995; van Oorschot and Wagener 2000). Tomares desinens was described in 1980 from a series collected in the semi-arid zone of Talysh mountains in Azerbaijan, and was later found also in northern Iran (Nazari 2003) and southeastern Turkey (Kemal and Koçak 2005). Beside being the smallest species, T. desinens is also characterised by chequered fringes as well as complete development of UNH elements without any trace of green scales.

The eastern species *T. romanovi*, often readily identifiable by its striking bluish-green UNH and the reduction or absence of maculae, is found from southeastern Turkey to the Kopet Dagh Mountains where it is sympatric with *telemachus*, a poorly described taxon based on undulated wing margins, light grey UNH and alleged differences in female genitalia, all variable characters interchangeable with the sympatric *T. romanovi*. Specimens with reduced green scales and prominent maculae on their UNH, approaching that of *T. nogelii*, occur also in Caucasus and southeastern Turkey.

The most difficult problem however concerns the taxonomic identity of the remaining three taxa, *T. nogelii*, *T. nesimachus* and *T. dobrogensis*. The issue has been addressed extensively in the past (Larsen 1974; Hesselbarth and Schurian 1984; Hesselbarth et al. 1995; Koçak 2000; van Oorschot and Wagener 2000). In summary, lack of unique external morphological characters, the nearly identical male genitalia, presence of local and clinal variation, and co-occurrence of distinct yet similar phenotypes in sympatry and synchrony, particularly in Turkey, presents serious challenges in interpretation of species or definition of subspecies in this group. Two distinct phenotypes exist within *T. nogelii*, connected by a bewildering array of intermediates (van Oorschot and Wagener 2000; Weidenhoffer and Bozano 2007). The often smaller *T. nesimachus* is known from Anatolia to Jordan, and is considered endangered in Israel (Pe'er and Settele 2008). The often larger *dobrogensis*, presumed extinct in its type locality in Romania until recently (Dincă et al. 2009; Rákosy and Craioveanu 2015) but common in disjunct populations in Ukraine, Crimea and xerothermic localities north of the Crimean peninsula (Nekrutenko and Tshikolovets 2005), was elevated to species due to its presumed "nearly sympatric" occurrence with the smaller *T. nogelii* in Turkey (Koçak 2000), creating an odd distribution pattern that is unique among butterflies in the region (Hesselbarth et al. 1995).

The documented variation and overlap of species characters and ranges between the taxa in the T. nogelii complex continues to be a serious problem in their interpretation. In their comprehensive investigation, van Oorschot and Wagener (2000) found no single character that could be used to distinguish these taxa, and advocated use of various character combinations in conjunction with ecological characters (such as larval hosts) to achieve species identification. Perhaps out of desperation, Koçak (2000) suggested the rank of 'semi-species' for nogelii, nesimachus and dobrogensis under the 'superspecies' T. nogelii. The need for a genetic analysis has been expressed before (van Oorschot and Wagener 2000). We tested the usefulness of mtDNA COI barcodes in combination with ecological and morphological characters to reassess the taxonomy proposed by van Oorschot and Wagener (2000) and Weidenhoffer and Bozano (2007), and reconstructed a phylogeny for Tomares using an additional nuclear gene (EF-1 α) in conjunction with COI barcode data.

Materials and methods

Taxon sampling

A total of 274 specimens representing all species and many subspecies of Tomares were sampled, of which 240 produced usable barcode sequences (Suppl. material 1: SI1). In addition, 15 public barcode records from BOLD and two GenBank sequences of Tomares from previous studies (KT286572, KF647240) were included in our dataset. Two other Genbank records (FN601323, KJ020235) were excluded due to suspicion of contamination. Sister-group relationships in Theclini is not yet fully resolved; however, following Espeland et al. (2018) we included Genbank COI and EF-1a sequences for one member of Theclini (Artopoetes metamuta, GU372569, GU372660) and one member of Arhopalini (Semanga superba, KT286525, KT286218) as putative outgroups. Fresh material could not be found for a few populations of Tomares, including the rare T. ballus cyrenaica known from Libya and Egypt, although our specimens from Tunisia (DNAwthTomares 025, 026 and 125) seem to be related. The voucher data are publicly available through the BOLD dataset "DS-TOMARES", accessible at https:// doi.org/10.5883/DS-TOMARES.

Molecular techniques

Two dry legs from each adult specimen were detached and stored in individual vials. The extraction of total genomic DNA, amplification and sequencing were performed in the Centre for Biodiversity Genomics (Guelph, Ontario, Canada) using previously described protocols (Hajibabaei et al. 2005). Initially, full-length mtDNA barcode sequences (658 bp) were obtained for nearly all specimens, and based on results from sequence similarity (neighbour-joining) analyses and the quality of DNA, a subset was selected for additional gene sequencing. Failed samples were targeted for smaller overlapping fragments of COI (132 bp) using mini-barcode primers and protocols described previously (Meusnier et al. 2008). Elongation factor 1 alpha (EF-1a) sequences were also obtained for all 10 species using primers and protocols described previously (Brower and DeSalle 1994; Aubert et al. 1999). This nuclear marker was chosen due to its relative ease of amplification and its proven usefulness in genusand subfamily-level phylogenetic studies in Lepidoptera (e.g. see Nazari et al. 2007; Todisco et al. 2018). Amplified DNA from all specimens was sequenced in both directions for each gene, and final sequencing products were run on an ABI 3730XL DNA analyzer (Life Technologies, Foster City, CA). Complementary strands were assembled into contigs and edited manually, and primers were removed using SEQUENCHER 4.5 (Gene Codes Corporation, Ann Arbor, MI). Sequences were aligned using CLUSTALX 2.0 (Thompson et al. 1997), evaluated by eye and converted to Nexus using SE-AL 2.0a11 (Rambault 2002). New sequences were deposited in Gen-Bank, and accession numbers are given in Suppl. material 1: SI1. COI barcode sequences are also available publicly through the BOLD dataset "DS-TOMARES", accessible at https://doi.org/10.5883/DS-TOMARES.

Morphological characters

The widespread mtDNA haplotype sharing observed among five species (*T. nogelii*, *T. nesimachus*, *T. dobrogensis*, *T. romanovi*, *T. telemachus*) did not help in resolving the long standing problem of species identities in this complex. To remedy this, we examined morphological characters and re-evaluated the taxonomic status and geographical boundaries of the available names under this complex specifically looking for cases of sympatry and synchrony. The problem of correct identification of specimens in this group however makes past records in the literature difficult to verify.

Dissections of male and female specimens of *Tomares* were carried out by WtH. Some of the dissected specimens were also included in the molecular analysis. Male and female genitalia were prepared using standard protocols and fixed in Euparal glycerin. Male genitalia were photographed in dorsal and ventral view. In a few cases, the aedeagus was damaged proximally. Female

genitalia preparations included the last two tergites, but components often had to be fixed and photographed separately in dorsal view. Photographs were taken under a standardized condition and digitally processed. Females of *T. telemachus* and *T. desinens* were not dissected due to lack of sufficient material (Suppl. material 2: SI2). To find additional diagnostic characters, male androconial patches, antennae, and fringes of upperside and underside of the wings in the *T. nogelii* species-group, as well as *T. callimachus* from various localities, were examined and photographed under microscope (Suppl. material 3: SI3).

Sequence data analysis

Neighbour-joining (NJ) trees for barcode data were constructed initially using the QUICKTREE algorithm (Howe et al. 2002) and under the Kimura two-parameter (K2P) model (Kimura 1980). Additional NJ and Maximum Parsimony (MP) analyses was conducted in PAUP* 4.0a164 (Swofford 2003); Maximum Likelihood (ML) trees were generated using PHYML online (Guindon and Gascuel 2003) under AIC criterion and 100 bootstrap replicates (Suppl. material 4: SI4). The best-fit model selected by PHYML for the combined dataset (GTR + G + I) was further corroborated by IQ-TREE (Nguyen et al. 2015), and parameters from this model were used to conduct a Bayesian analysis in MRBAYES 3.2.6 (Ronquist et al. 2011). The MCMC analysis was allowed to run for 10,000,000 generations until stationary was reached. Convergence of parameters after the exclusion of the burnin phase was tested using TRACER 1.7.1 (Rambaut et al. 2018). The haplotype diagram was constructed in TCS 1.21 (Clement et al. 2000), with a 95% confidence limit for parsimony. Shorter barcode fragments or those with ambiguous bases were excluded from haplotype analyses. Trees were edited using FIGTREE 1.4.4 (Rambault 2018).

Results

Morphology

Genitalia of both sexes in all *Tomares* species differed in size in accordance with the specimen wingspan. Female genitalia were relatively uniform, with triangular papillae anales, sclerotized ductus bursae and doctus seminalis, and round and membranous corpus bursae with no signa (Suppl. material 2: SI2). The spine on the proximal part of the valva in male genitalia showed consistent variation: it was reduced or absent in *T. mauritanicus* and *T. ballus*, small and projecting backward in *T. fedtschenkoi*, and small and projecting forward in *T. desinens* and *T. callimachus callimachus*. In the southern population of *T. callimachus*, the spine was needle-shaped and proportionally longer than the northern populations. The remaining five species (the *nogelii*-complex) showed very similar male genitalia with a distinct, forward-looking and needle-shaped spine, with

Syrian *nesimachus* having proportionally the shortest spine in this group (Fig. 1). The male androconial patch on the UPF in *Tomares* species was larger in *dobrogensis* and *nogelii* and corresponded with the specimen size, but otherwise it was not very useful in discriminating between the "difficult" taxa (Suppl. material 3: SI3). A summary of variable morphological and ecological characters in the *nogelii*-complex is presented in Table 2.

Molecules

Despite a wide geographic coverage, various populations of *T. ballus*, *T. mauritanicus* and *T. fedtschenkoi* formed well-supported clusters with small internal variation. We observed a gap in DNA barcodes $(1.00 \pm 0.24\%)$, as well as EF-1 α sequences, between the "northern" (Kazakhstan, Ukraine, Russia and N. Azerbaijan) and "southern" (S. Azerbaijan, Armenia, Iran and Turkey) populations of *T. callimachus*. The disjunct Kazakh population of *callimachus* showed identical mtDNA haplotypes with specimens from Ukraine and southern Russia. Further subdivisions were evident within the southern cluster (Fig. 2). Minor variation observed in the male genitalia of *T. callimachus* (e.g. in the length of spines on proximal part of valvae; not shown) appeared to be independent of geographical origin and did not correspond to the N-S split in DNA barcodes.

While average K2P distances between five *Tomares* taxa (*ballus, mauritanicus, callimachus, desinens* and *fedtschenkoi*) ranged between 1.6–3.0% (Table 1), the taxa nogelii, nesimachus, dobrogensis, romanovi and *telemachus* formed a large unresolved cluster with very little to no differentiation but with a high internal diversity ($0.36 \pm 1.38\%$). The haplotype network analysis in TCS identified 30 haplotypes in this group, six of which were shared between two or three species (Fig. 3). The haplotype-sharing appeared both in sympatry and allopatry, but geographically constrained, unique haplotypes with one another except *romanovi* and *dobrogensis*, and *telemachus* only shared haplotypes with *romanovi*. To



Figure 1. Right valvae in male genitalia of *Tomares* species. 1. *T. mauritanicus* GP76 (Morocco); 2. *T. ballus* GP77 (Morocco); 3. *T. fedtschenkoi* GP78 (Tajikstan); 4. *T. desinens* GP86 (Qazvin, Iran); 5. *T. callimachus callimachus* GP75 (Crimea); 6. *T. callimachus hafis* GP86 (Zanjan, Iran); 7. *T. nesimachus* GP84 (Damascus, Syria); 8. *T. "telemachus"* GP79 (Turkmenistan); 9. *T. romanovi* GP74 (Lorestan, Iran); 10. *T. nogelii nogelii* GP88 (Nevshehir, Turkey); 11. *T. nogelii nogelii* GP85 (Sivas, Turkey); 12. *T. nogelii dobrogensis* GP83 (Ukraine). All dissections and images by WtH.

Table 1. Average K2P distances and standard deviation of COI barcodes between Tomares taxa.

	ballus	mauritanicus	callimachus	desinens	fedtschenkoi	nogelii	nesimachus	dobrogensis	romanovi	telemachus
ballus	0.3 ± 0.2									
mauritanicus	1.6 ± 0.2	0.2 ± 0.2								
callimachus	3.0 ± 0.3	3.0 ± 0.2	0.6 ± 0.4							
desinens	2.5 ± 0.2	2.5 ± 0.1	2.4 ± 0.2	0.2 ± 0.2						
fedtschenkoi	2.4 ± 0.2	3.0 ± 0.2	2.5 ± 0.3	2.1 ± 0.2	0.2 ± 0.2					
nogelii	2.2 ± 0.2	2.2 ± 0.2	2.3 ± 0.2	1.6 ± 0.1	2.4 ± 0.2	0.2 ± 0.2				
nesimachus	2.2 ± 0.3	2.1 ± 0.2	2.3 ± 0.2	1.6 ± 0.2	2.3 ± 0.2	0.3 ± 0.3	0.3 ± 0.3			
dobrogensis	2.3 ± 0.3	2.2 ± 0.2	2.3 ± 0.3	1.7 ± 0.2	2.4 ± 0.3	0.4 ± 0.2	0.4 ± 0.3	0.5 ± 0.3		
romanovi	2.1 ± 0.3	2.0 ± 0.2	2.2 ± 0.2	1.5 ± 0.2	2.3 ± 0.2	0.4 ± 0.1	0.3 ± 0.2	0.5 ± 0.2	0.3 ± 0.2	
telemachus	2.3 ± 0.3	2.2 ± 0.2	2.3 ± 0.2	1.6 ± 0.1	2.4 ± 0.2	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1

23



Figure 2. Neighbour-Joining tree of 271 barcode sequences of Tomares. Values are bootstrap of 100 replicates for supported nodes.

better understand the extent of haplotype variation within this group, we separated the records and re-evaluated the haplotype network based on geographical localities and morphological identifications. Two main haplogroups were observed, one of which consisted exclusively of *nogelii*, *nesimachus* and *dobrogensis* from central and eastern Turkey together with a single *nesimachus* specimen from Israel (Fig. 3). We found 10 sites with multiple haplotypes in southern Turkey (Konya, Niğde, Adana), Israel (Dalyya), Syria, Azerbaijan, Turkmenistan (KopetDagh) and Ukraine (Fig. 4), although records from these sites were never in synchrony.

Our phylogenetic reconstruction of combined sequence data strongly supports monophyly of *Tomares* and five species within the genus (*ballus, mauritanicus, fedtchenkoi, callimachus* and *desinens*). However, throughout all analyses, the taxa *nogelii, nesimachus, romanovi, dobrogensis* and *telemachus* formed a well-supported clade, within which they were paraphyletic with respect to each other (Fig. 5).

Character	nogelii, dobrogensis	nesimachus	romanovi, telemachus
collection dates	25 April–30 May	5 April–31 May	15 April–31 May
elevation (m)	85–2075	250-2000	600–1300
habitat	hygric habitats	xeric rocky habitats with sparse	usually xeric rocky habitats with
		vegetation	sparse vegetation; rarely other
zoogeographic zone	Pontomediterranean – Armenian	Syrian – Palaeoeremic	Iranian – Caspian
larval host plant (primary, secondary)	Astragalus, Asteracantha	Astracantha, Astragalus	Astragalus
orange patch on UPF	absent in 40% of specimens	always present	always present
dark patch at the tip of UPF	continuous along costal and	nearly triangular	continuous along costal and outer
	outer margins		margins
submarginal black spots on UPF	connected, forming an	variable; usually a series of disjunct	connected, forming an undulated or
	undulated dark band	spots, sometimes connected to form	serrated dark band
		a deeply serrated band	
marginal black border on UPF	always wide, equally or wider	always narrow	always wide, equally or wider than
	than costal border		costal border
orange patch on UPH	reduced or absent in nearly 30%	always present, wide, nearly	always present, variable in size and
	of specimens, if present always	rectangular basally, with both sides	shape
	narrow and nearly rectangular	of the angle more or less equal in	
		length	
UNH pattern (see Suppl. material	usually gray-brown with	usually gray-brown with prominent	usually uniform bluish-green with
3: SI3)	prominent maculae	maculae	no maculae; varies in peripheral
			populations
needle-shape spine in male genitalia	long	short	long
(see Fig. 1)			

 Table 2. Summary of characters that show variation among taxa in the nogelii complex.



Figure 3. TCS Haplotype Network of the *nogelii* complex. Colors indicate morphological identifications (red = *nogelii*, blue = *do-brogensis*, orange = *nesimachus*, green = *romanovi*, yellow = *telemachus*). The most common haplotype (large circle) comprises central and eastern Turkish individuals of *nogelii*, '*nesimachus*' and '*dobrogensis*', as well as a single *nesimachus* from Israel.



Figure 4. Distribution of taxa in the *nogelii* complex. Shapes represent morphological identifications ($\Box = nogelii$, $\Delta = nesimachus$, $\circ = romanovi$), colors represent COI barcode haplotypes (red = *nogelii* haplotypes, orange = *nesimachus* haplotypes, green = *romanovi* haplotypes). Sites with shared or more than one haplotypes are circled. Records in gray are concatenated from literature. Approximate taxon boundaries are inferred from represented haplotypes. For haplotype network, see Figure 3.



Figure 5. Bayesian phylogeny of selected *Tomares* sequences based on combined data (COI + EF-1α). Values above branches are bootstrap support obtained under Parsimony and Likelihood criteria for each node, and values below branches are Bayesian posterior probabilities. Images: 1) *ballus* wth013 Morocco, 2) *ballus* wth055 Spain, 3) *mauritanicus* wth017 Morocco, 4) *fedtchenkoi* wth020 Kyrgyzstan, 5) *callimachus* callimachus wth051 Azerbaijan, 6) *callimachus hafis* wth053 Iran, 7) *desinens* wth042 Iran, 8) *dobrogensis* wth080 Crimea, 9) *nogelii* zma153 Turkey, 10) *nesimachus* wth065 Syria, 11) *romanovi obscura* zma161 Turkey, 12) *romanovi cachetinus* zma146 Azerbaijan, 13) *romanovi romanovi* wth010 Armenia, 14) *telemachus* wth005 Turkmenistan.

Discussion

No fossils of Tomares are known, and the only fossil attributable to Theclinae is a geologically very young larva (Sohn et al. 2012). The most recent common ancestor (MRCA) of Tomarini and Theclini + Arhopalini seems to have split in Late Eocene around 34 million years ago, giving rise to Deudorigini and Eumaeini later in Oligocene (Espeland et al. 2018). Our phylogenitic reconstruction for the genus shows that the first split within ancestral Tomares occurred between the MRCA of (ballus + T. mauritanicus) + fedtchenkoi and the MRCA of the remaining species. The low inter-species divergence in DNA barcodes (1.6-3%) suggest that Tomares, much like Agrodiaetus, is a geologically young genus that probably arose in Pleistocene (Vila et al. 2010). Pleistocene dispersal between Africa and Europe has been suggested in a wide range of plants and animals, including butterflies (Leestmans 2005; Schmitt et al. 2006; Weingartner et al. 2006; Nazari et al. 2007, 2009; Nazari and Sperling 2008; ten Hagen and Miller 2010; Dincă et al. 2011; Vodă et al. 2016). The maculated UNH pattern in Tomares appears to be a plesiomorphic character substituted several times by a carpet of uniform green scales. This trait likely has some survival value: Species with green UNH (e.g. romanovi) feel safe and camouflaged resting on large green leaves even in bright sunshine, while species with maculated and brown UNH (e.g. nesimachus) normally hide by sitting on the ground with their wings closed and are easily frightened (WtH personal observation).

While morphology and DNA barcodes unequivocally demonstrate separate species status for T. ballus, T. mauritanicus and T. fedtchenkoi, they do not support recognition of subspecies within them. Separating populations into subspecies in the highly variable T. mauritanicus has been dismissed before (Tennent 1996). Lack of genetic differentiation or consistent morphological characters to discriminate between North African (e.g. ssp. cyrenica Turati, 1924) and European populations of T. ballus suggest a recent range expansion or vicariance event. For T. desinens, we found the subspecific diagnostic characters suggested by Weidenhoffer and Bozano (2007) inefficient as we observed character gradients and intermediate states between populations from eastern Albors Mountains to Talysh and western Iran. Therefore we do not recognize subspecies boundaries within these four species.

The split in the range of *T. callimachus*, supported by both COI and EF-1 α genes, suggests a long period of lack of genetic exchange between the northern and the southern populations. The male genitalia in southern populations show a distinctly narrow and needle-shaped spine that is very different from the northern group (Fig. 1). Other subtle differences between these two groups exist: northern populations generally fly in low elevations (sea level to 1400 m), have duller UNH, fringes that are not (or are barely) chequered, and a smoothly-indented inner edge of the black marginal band on the UPF, while the southern populations fly at higher elevations (400– 2600 m), show higher contrast in UNH pattern, distinctly chequered fringes, and an often deeply serrated inner edge of the UPF black marginal band. A separate taxonomic status, at least at subspecies level, is thus warranted. The type locality of T. callimachus is "Helenendorf" (previously Khanlar, now Goygol, Azerbaijan), a border area between the two populations and approximately 50 km from the locality of our specimen wth051, which is part of the northern group. Although it is impossible to ascertain the exact locality in the vicinity of Helenendorf where the type series were collected, the lectotype (high quality photos examined courtesy of V. Tshikolovets) shows some characteristics of the northern group (dull UNS, barely chequered fringes, and a weakly-serrated inner edge of the UPF marginal band). Zolotuhin and Anikin (2017) interpreted the illegible lectotype label as "calmuuc", referring to the city of Kalmukov in the Uralsk district, Kazakhstan. We reject this interpretation as the label seems to simply read "calimac[us]"; however, even if this interpretation is correct, the lectotype unambiguously belongs to the northern group. We therefore regard the northern populations as ssp. callimachus (Eversmann 1848), distributed from Ukraine to Central Asia and northern Azerbaijan (Greater Caucasus Mountains). We disagree with Zolotuhin and Anikin (2017) in recognizing the Georgian population as a distinct subspecies (ssp. *epiphania*, type locality: Odessa; = *callim*achus stat. rev.). This taxon, first mentioned by Boisduval (1848) in comparison to T. ballus and subsequently described by Herrich-Schäffer ([1850]), clearly refers to the nominal T. callimachus. The type material of epiphania is lost, and this taxon has been in synonymy with T. callimachus for at least 120 years (Staudinger and Rebel 1901). The oldest available name for the southern population is hafis Kollar, 1849, described from "Farsistan" (= Shiraz, southern Iran; type in NHMW, Vienna), and currently in synonymy with T. callimachus (Hesselbarth et al. 1995). The original description of hafis matches well with our examined material from the southern cluster. Therefore, the name T. callimachus ssp. hafis (stat. rev.) is here revived to represent the southern subspecies, distributed in Lesser Caucasus, Armenia, southern and southeastern Turkey, northeastern Iraq, and western, southwestern, northern and northeastern Iran to the Kopet Dagh range. The polyphagous larvae of ssp. callimachus feeds on several species of Astragalus, Hedysarum and Onobrychis (Weidenhoffer and Vanek 1977; Tuzov et al. 2000; Stradomsky and Fomina 2013; Bury and Savchuk 2015), but no confirmed records exist for the southern populations. If the two subspecies are later discovered in sympatry, the status of *hafis* should be revised to a distinct species. We could not examine specimens from the Pakistani Baluchistan recently described as ssp. huertasae (Tshikolovets and Pagès 2016); however, considering the striking morphology of this population and absence of Tomares in the large gap between Zagros mountains and Pakistan, this taxon may represent a distinct species.

The remaining five taxa (nogelii, nesimachus, dobrogensis, romanovi and telemachus) form a clade of closely-related haplotypes with no apparent distinction between taxa. The concordance between mitochondrial COI and nuclear EF-1a genes rules out selective sweeps caused by endosymbiotic bacteria (Toews and Brelsford 2012). Tomares romanovi has been generally excluded from this complex or only referred to for its curious similarities with nogelii in genitalia and pattern on the underside of the forewing (UNF). Indeed, romanovi is often easily distinguishable by its uniform bluish-green UNH and complete lack of maculae; however, peripheral populations within the range of romanovi (e.g. those from the Kopet Dagh range, Georgia, Azerbaijan and southeastern Turkey) often demonstrate a reduction or absence of these bluish-green scales and presence of maculae on the UNH, approaching some forms of nogelii. The range of romanovi is to the east of nogelii, and they are parapatric in eastern Turkey (Van and Agri; van Oorschot and Wagener 2000), and although no sympatric records are known, we observed shared haplotypes between romanovi and nogelii from Agri and Erzincan. Several 'subspecies' described from the boundary of these two species (e.g. T. nogelii obscura, T. nogelii cesa, T. romanovi cachetinus) demonstrate such intermediate states in their morphology. We suggest that these may represent hybrid specimens between romanovi and nogelii in eastern Turkey and the Caucasus. The range of this hybrid zone, as far as evident from our data, extends probably from Azerbaijan in the east to Elaziğ in the west (Fig. 4). The taxon telemachus, described from Karachaudan (Turkmenistan; type in ZISP, Saint Petersburg) based on minor differences with the sympatric romanovi, appears to be part of a larger range of variation within the heterogeneous romanovi populations in the Kopet Dagh range. With the exception of the examined telemachus paratypes, we could not conclusively assign identities to specimens originating from this region due to the intermediate or overlapping character states. Considering also the identical male and female genitalia and shared COI haplotypes, we synonymize telemachus with romanovi (syn. nov.)

While Oberthür's original (1893) description and illustration of nesimachus from "Akbès" (Hatay, southern Turkey) matched very well with our examined material from southern Turkey and the Levant, the central and eastern Turkish specimens generally matched better with T. nogelii. We did not detect presence of any of the 'nesimachus' haplotypes among central and eastern Turkish populations, where various 'ecotypes' of nogelii all share a different haplotype. We did not find character combinations proposed by van Oorschot and Wagener (2000) accurate or useful in separating individuals of nogelii and nesimachus. In our opinion, nesimachus-like phenotypes reported as far north as Çankiri and Gümüşhane (van Oorschot and Wagener 2000) are not true nesimachus. The diagnostic characters of the genuine nesimachus include: *a*) a nearly triangular dark patch at the tip of UPF; b) orange patch on UPH nearly rectangular basally, with

both sides of the angle more or less equal in length; c) marginal black line on UPF always narrow; d) considerable variation in submarginal black spots on UPF; sometimes reduced, sometimes complete and connected with marginal line, but the marginal line remains narrow; e) no specimens with darkened or reduced orange patch of UPF are known. All reports of nesimachus and nogelii in central and eastern Turkey, particularly those in sympatry and synchrony, should thus be regarded with skepticism. The nesimachus from Syria have a proportionally shorter needle-shape spine in male genitalia (Fig. 1). Our data show that nogelii and nesimachus overlap only along a narrow range in southern Turkey and the Levant, the exact boundaries of which is yet to be determined. We observed increased haplotype diversity in Adana and Konya and shared haplotypes in Niğde, Mersin and Dalia (Israel), although the two taxa were never synchronous at these localities. Populations of nogelii from Mersin and Adana belong to a different haplogroup that seems to be limited in range to the Taurus Mountains and is shared in Niğde with the common haplotype from central and eastern Turkey as well as with the southern nesimachus (Fig. 4), and potentially represent hybrid populations between nogelii and nesimachus. Our nesimachus specimens from Syria (Damascus and As-Suwayda), collected in sympatry and synchrony, show multiple haplotypes, one of which is shared with a specimen from Jordan. Lebanese populations of nesimachus and nogelii are also not sympatric (nogelii flies in western slopes and near the coast, nesimachus in Antilebanon and eastern slopes) (Larsen 1974) and can be easily told apart. Only nesimachus extends as far south as Jordan (Larsen and Nakamura 1983). Adult flight period is correlated with the flowering time of their larval host: nesimachus adults in general appear 2-4 weeks earlier than those of nogelii, fly in xeric rocky habitats with sparse vegetation, and their larvae only feed on yellow-flowered Astracantha, whereas nogelii adults emerge later, usually prefer hygric habitats, and their larvae feed on Astragalus (Hesselbarth et al. 1995; van Oorschot and Wagener 2000) (Fig. 6). We consider all available evidence to conclude that nesimachus is a Levantine species that hybridizes with its northern sister-species T. nogelii along a contact zone that extends from southern Turkey to the Levant (Fig. 4). The name aurantiaca may refer to hybrid populations from Gaziantep, but an examination of the type series (in ZMHB, Berlin) is pending. In southern Turkey, nesimachus and romanovi are parapatric but show identical haplotypes across a wide geographic range including, remarkably, between Iran and Jordan (Fig. 3). Two old specimens from Mardin (Hesselbarth et al. 1995: pl. 92, figs 41, 54; ITZA, Amsterdam) show nesimachus-like development of maculae as well as a romanovi-like green suffusion on the UNH, suggesting hybridization between the two taxa.

All other records of *nogelii*, *nesimachus* and *dobrogensis* from central and eastern Turkey represent various populations of *T. nogelii* ssp. *nogelii* with different larval hosts that share a common, widespread haplotype across



Figure 6. Collection dates vs. elevation in nogelii (white), nesimachus (black) and romanovi (gray).

central to northeastern Turkey (Fig. 4). Small, early-flying nogelii feed on smaller Astracantha or Astragalus, while larger, late-flying nogelii feed on the large Astragalus ponticus. The forewing length of specimens from Cappadocia and adjacent areas may be twice that of other specimens, but no other consistent differences exist. The taxon uighurica Kocak, Seven & Kemal, 2000 (type in CESA, Ankara) was described from Ankara based on these large specimens occurring in June "almost" sympatrically with worn specimens of nogelii in April and early June (Koçak 2000). A correlation between adult wingspan and larval host has been demonstrated before (Hesselbarth et al. 1995; van Oorschot and Wagener 2000). All Tomares larvae feed exclusively hiding in flower buds, flowers and young seeds inside the umbel (Weidenhoffer and Vanek 1977, WtH personal observation). Large spherical flower stands of Astragalus ponticus likely provide more nutrients than the smaller Astracantha, contributing to development of larger adults. Here we consider uighurica an infra-subspecific name representing an ecotype of nogelii (syn. nov.). Individuals from central Turkey attributed to dobrogensis examined in our study also did not show any significant phenotypic or molecular differences from nogelii collected elsewhere in Anatolia and shared haplotypes with them, while the populations from Ukraine, Crimea and Romania were distinct, showed several unique haplotypes, and were recorded exclusively feeding on Astragalus ponticus. We, therefore, recognize ssp. *dobrogensis* representing the isolated populations of *T. nogelli* in Romania and north of the Black Sea, and conclude that it does not occur in Turkey.

Conclusion

Hybridization is not rare in butterflies, and any slight overlap in morphology, behaviour and ecology are likely to allow it to occur (Descimon et al. 1989; Descimon and Mallet 2009). Comprehensive investigations into pre-zygotic isolating mechanisms, post-zygotic hybridization barriers and hybrid viability are required before it can be conclusively demonstrated whether the 'intermediate' specimens from the periphery of species ranges, or different ecotypes co-occurring syntopically in Turkey, are hybrids or reflect natural variation within a single species. Lack of differences in genitalia, overlap in geographic ranges, presence of intermediate phenotypes, low divergence between taxa and widespread haplotype sharing point to either conspecificity of nogelii, nesimachus and romanovi, or presence of extensive introgression between these closely related taxa. On the other hand, accrued and consistent differences in host plant usage, habitat types, elevation, behavior, flight time, and certain wing pattern elements (e.g. the green UNH in romanovi) support continued recognition of these taxa as young sister species, in the process of lineage sorting, that co-occur, and occasionally interbreed,

in contact zones at the periphery of their ranges. The three taxa occupy different zoogeographic zones (*nogelii*: Pontomediterranean – Armenian; *nesimachus*: Syrian – Palaeo-eremic, *romanovi*: Iranian – Caspian) (Uvarov 1921; Larsen 1974; Por 1975; Schintlmeister 2008). We prefer to maintain these taxa as separate species for now until genome-wide analyses and new data on karyotypic diversity and symbiosis with ants shed more light on the evolution of these fascinating butterflies.

Revised classification of *Tomares* species

For additional synonymy, see Hesselbarth et al. (1995) and Weidenhoffer and Bozano (2010).

Tomares ballus (Fabricius, 1787)

Distribution. Southwest France to southern Spain and Portugal, Gibraltar, Morocco, Algeria, north Libya, south Tunisia and north Egypt.

Larval host. Lotus hispidus, Boujeania hispida (?), Anthyllis vulneraria, A. cyticoides, Heliatheum sp. and Medicago sp. in Spain (Korb 1924; Higgins and Riley 1970; Muñoz Sariot 2011); Anthyllis tetraphylla, Erophaca boetica, and Medicago cf. turbinata in Morocco (Tennent 1996).

Tomares mauritanicus (Lucas, 1849)

Distribution. Algeria and Morocco.

Larval host. Hedysarum pallidum, Hippocrepis multisiliquosa, H. minor, Astragalus epiglottis, and A. pentaglottis (Higgins and Riley 1970, Tennent 1996).

Tomares callimachus (Eversmann, 1848) ssp. *callimachus* (Eversmann, 1848)

= Polyommatus epiphania Boisduval, 1848 stat. rev.

Distribution. From Ukraine to Central Asia and N Azerbaijan.

Larval host. Recorded on a number of Astragalus species from Alatau Mountains and NW Kazakhstan to South Russia, Crimea and Georgia: Astragalus leptostachys, A. macropterus, A. physodes, A. suprapilosus, A. utriger and A. vulpinus, as well as Hedysarum candidum in Crimea and Onobrychis radiate in Georgia (Weidenhoffer and Vanek 1977; Zhdanko 1997; Tuzov et al. 2000; Stradomsky and Fomina 2013; Bury and Savchuk 2015).

ssp. hafis (Kollar, 1849) stat. rev.

Distribution. Lesser Caucasus, Armenia, south and southeast Turkey, north Iraq, west, southwest, north and northeast Iran to Kopet Dagh.

Larval host. Not recorded. The record of Astragalus physodes from "Kulp" (Diyarbakir, Turkey) by Korb (1924) is erroneous as the plant does not occur in Turkey (Hesselbarth et al. 1995).

ssp. huertasae Tshikilovets & Pagès, 2016

Distribution. Pakistan: Baluchistan. Larval host. Not recorded.

Tomares desinens Nekrutenko & Effendi, 1980

Distribution. Southeast Azerbaijan, east Turkey (Van), north and northwest Iran. Larval host. Not recorded.

Larval nost. Not recorded.

Tomares fedtschenkoi (Erschoff, 1874)

Distribution. South Turkmenistan, Uzbekistan, Kyrgyzstan, south Kazakhstan and Tajikistan. Records from Afghanistan and Pakistan are questionable (Tshikolovets and Pagès 2016; Tshikolovets et al. 2018).

Larval host. *Astragalus chlorodontus* and *Astragalus agameticus* (Zhdanko 1997).

Tomares nogelii (Herrich-Schäffer, [1851]) ssp. *nogelii* (Herrich-Schäffer, [1851])

=uighurica Koçak, Seven and Kemal in Koçak, 2000 syn. nov.

Distribution. Northeast to central Anatolia, and south to the Levant.

Larval host. Asteracantha spp. (early fliers); Astragalus ponticus and A. micropterus (late fliers) in Turkey (Hesselbarth et al. 1995).

ssp. dobrogensis (Caradja, 1895)

Distribution. Romania, Crimea, Ukraine. Does not occur in Turkey.

Larval host. Astragalus ponticus in Ukraine and Romania (Tuzov et al. 2000; Bury and Savchuk 2015; Rákosy and Craioveanu 2015).

Tomares nesimachus (Oberthür, 1893)

Distribution. Southern Turkey (Mersin, Adana, Hatay to Mardin) to Lebanon, Israel and Jordan.

Larval host. Astracantha spp. (Oorschot and Wagner 2000); Astragalus macrocarpus in Israel and Jordan (Larsen and Nakamura 1983); A. densifolius in Mersin, Turkey (Leestmans et al. 1986).

Tomares romanovi (Christoph, 1882)

= Tomares telemachus Zhdanko *in* Tuzov et al. 2000 syn. nov.

Distribution. East Turkey, Georgia, Armenia, Azerbaijan, Iran, and Kopet Dagh range in Turkmenistan.

Larval host. Astragalus finitimus in Kopet Dagh and in Armenia (Yerevan)(Weidenhoffer and Vanek 1977; Hesselbarth et al. 1995; Tuzov et al. 2000); *Astragalus schachrudensis* in Kopet Dagh, Azerbaijan (Ordubad) and Armenia (Ockschaberd) (Christoph 1882; Korb 1924; Zhdanko 1997).

Acknowledgements

We thank Harry van Oorschot † (Amsterdam, the Netherlands), Andree Salk (Berlin, Germany), Sergej Churkin (Moscow, Russia), Vadim Tshikolovets (Kiev, Ukraine), Giancristoforo Bozano (Milano, Italy), Tomasso Racheli (Rome, Italy), Valentin Tikhonov (Pyatigorsk, Russia), Gerardo Lamas (Lima, Peru), and Martin Lödl (Natural History Museum Vienna, Austria) for providing specimens, and Mihai Stănescu, Mario Ramos González and Harald Letsch for their reviews and helpful comments. This research was supported through funding to the Canadian Barcode of Life Network from Genome Canada (through the Ontario Genomics Institute), NSERC and other sponsors listed at http://www. bolnet.ca. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

- Aubert J, Legal L, Descimon H, Michel F (1999) Molecular phylogeny of swallowtail butterflies of the tribe Papilionini (Papilionidae, Lepidoptera). Molecular Phylogenetics and Evolution 12: 156–167. https://doi.org/10.1006/mpev.1998.0605
- Benyamini D (1990) A field guide to the butterflies of Israel. Jerusalem (Keter Publishing House), 234 pp.
- Bereczki J, Pecsenye K, Varga Z, Tartally A, Tóth JP (2018) Maculinea rebeli (Hirschke)–a phantom or reality? Novel contribution to a long-standing debate over the taxonomic status of an enigmatic Lycaenidae butterfly. Systematic Entomology 43: 166–182. hhttps:// doi.org/10.1111/syen.12259
- Boisduval JP (1848) On communique la note suivante de M. le Docteur Boisduval relative aux lépidoptères recueillis par M. Kindermann aux environs d'Odessa et au pied du Caucase. Annales de la Société Entomologique de France 2(6): XXVIII–XXX.
- Brower AVZ, De Salle R (1994) Practical and theoretical considerations for choice of a DNA sequence region in insect molecular systematics, with a short review of published studies using nuclear gene regions. Annals of the Entomological Society of America 87: 702–716. https://doi.org/10.1093/aesa/87.6.702
- Bury J, Savchuk V (2015) New data on the biology of ten lycaenid butterflies (Lepidoptera: Lycaenidae) of the genera *Tomares* Rambur, 1840, *Pseudophilotes* Beuret, 1958, *Polyommatus* Latreille, 1804, and *Plebejus* Kluk, 1780 from the Crimea and their attending ants (Hymenoptera: Formicidae). Acta Entomologica Silesiana 23: 1–16.
- Busby RC, Faynel C, Moser A, Robbins RK (2017) Sympatric diversification in the Upper Amazon: a revision of the Eumaeine genus *Paraspiculatus* (Lepidoptera: Lycaenidae). Smithsonian Contributions to Zoology 649: 1–66. https://doi.org/10.5479/si.1943-6696.649
- Caradja A (1895) Verzeichniss der bisher beobachteten Schmetterlinge. Deutsche entomologische Zeitschrift Iris 8: 10–102.

- Chaturvedi S, Lucas LK, Nice CC, Fordyce JA, Forister ML, Gompert Z (2018) The predictability of genomic changes underlying a recent host shift in Melissa blue butterflies. Molecular Ecology 27: 2651–2666. https://doi.org/10.1111/mec.14578
- Christoph H (1882) Einige neue Lepidoptera aus Russisch-Armenien. Horae Societatis Entomologicae Rossicae 17: 104–122.
- Clement M, Posada D, Crandall KA (2000) TCS: a computer program to estimate gene genealogies. Molecular Ecology 9: 1657–1660. https://doi.org/10.1046/j.1365-294x.2000.01020.x
- Descimon H, Genty F, Vesco JP (1989) Natural hybridization between Parnassius apolla (L) and Parnassius phoebus (F) in southern alps (Lepidoptera, Papilionidae). Annales de la Societe Entomologique de France 25: 209–234.
- Descimon H, Mallet J (2009) Bad species. In: Settele J, Shreeve TG, Konvicka M, Dyck VH (Eds) Ecology of Butterflies in Europe. Cambridge University Press, Cambridge, 219–249.
- Dincă V, Cuvelier S, Székely L, Vila R (2009) New data on the Rhopalocera (Lepidoptera) of Dobrogea (south-eastern Romania). Phegea 37: 1–21.
- Dincă V, Dapporto L, Vila R (2011) A combined genetic-morphometric analysis unravels the complex biogeographical history of *Polyom-matus icarus* and *Polyommatus celina* Common Blue butterflies. Molecular Ecology 20: 3921–3935. https://doi.org/10.1111/j.1365-294X.2011.05223.x
- Downey MH, Nice CC (2013) A role for both ecology and geography as mechanisms of genetic differentiation in specialized butterflies. Evolutionary Ecology 27: 565–578. https://doi.org/10.1007/s10682-012-9626-7
- Eliot JN (1973) The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bulletin of the British Museum of Natural History (Entomology) 28: 371–505. https://doi.org/10.5962/ bhl.part.11171
- Espeland M, Breinholt J, Willmott KR, Warren AD, Vila R, Toussaint EFA, Maunsell SC, Aduse-Poku K, Talavera G, Eastwood R, Jarzyna MA, Guralnick R, Lohman DJ, Pierce NE, Kawahara AY (2018) A comprehensive and dated phylogenomic analysis of butterflies. Current Biology 28: 770–778. https://doi.org/10.1016/j. cub.2018.01.061
- Eversmann EF (1848) Beschreibung einiger neuer falter Russlands. Bulletin de la Société impériale des naturalistes de Moscou 21: 205–232.
- Fabricius JC (1787) Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus. Tom II. Hafniae, Impensis C. G. Proft, 382 pp. https://doi.org/10.5962/bhl.title.36471
- Frye JA, Robbins RK (2015) Is the globally rare frosted elfin butterfly (Lycaenidae) two genetically distinct host plant races in Maryland? DNA evidence from cast larval skins provides an answer. Journal of Insect Conservation 19: 607–615. https://doi.org/10.1007/s10841-015-9783-4
- Gillespie M, Wratten SD, Cruickshank R, Wiseman BH, Gibbs GW (2013) Incongruence between morphological and molecular markers in the butterfly genus *Zizina* (Lepidoptera: Lycaenidae) in New Zealand. Systematic Entomology 38: 151–163. https://doi. org/10.1111/j.1365-3113.2012.00659.x
- Gompert Z, Lucas LK, Buerkle CA, Forister ML, Fordyce JA, Nice CC (2014) Admixture and the organization of genetic diversity in a butterfly species complex revealed through common and rare genetic variants. Molecular Ecology 23: 4555–4573. https://doi. org/10.1111/mec.12811

Graves P (1918) Some new forms of Lycaenidae from Egypt. The Entomologist 51: 97–98.

- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Systematic Biology 52: 696–704. https://doi.org/10.1080/10635150390235520
- Hajibabaei M, Dewaard JR, Ivanova NV, Ratnasingham S, Dooh RT, Kirk SL, Mackie PM, Hebert PDN (2005) Critical factors for assembling a high volume of DNA barcodes. Philosophical Transactions of the Royal Society, B Biological Sciences 360: 1959–1967. https:// doi.org/10.1098/rstb.2005.1727
- Herrich-Schäffer GAW ([1843–1856]) Systematische Bearbeitung der Schmetterlinge von Europa, zugleich als Text, Revision und Supplement zu Jakob Hübner's Sammlung europäischer Schmetterlinge. G. J. Manz, Regensburg. 6 volumes. https://doi.org/10.5962/bhl.title.67734
- Hesselbarth G, Schurian KG (1984) Beitrag zur Taxonomie, Verbreitung und Biologie von *Tomares nogelii* (Herrich-Schäffer, [1851]) in der Türkei (Lepidoptera, Lycaenidae). Entomofauna 5: 243–250.
- Hesselbarth G, van Oorschot H, Wagener S (1995) Die Tagfalter der Türkei unter Berücksichtigung der angrenzenden Länder. Selbstverlag Sigbert Wagener, Bocholt. 3 volumes, 1354 pp.
- Higgins LG, Riley ND (1970) Field guide to the butterflies of Britain and Europe. Collins, London, 380 pp.
- Howe K, Bateman A, Durbin R (2002) QuickTree: building huge neighbour-joining trees of protein sequences. Bioinformatics 18: 1546– 1547. https://doi.org/10.1093/bioinformatics/18.11.1546
- Kemal M, Koçak AÖ (2005) Annotated Checklist of the Lepidoptera of Çatak Valley (Van Province, Turkey). Priamus 11: 29–58.
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120. https://doi. org/10.1007/BF01731581
- Koçak AÖ (2000) Enkhere vilayitidiki kepineklirining sinonumik tizimliği (Lepidoptera). Center for Entomological Studies Ankara, Miscellanous Papers 67/69: 1–22. [in Uighur language]
- Kollar V, Redtenbacher L (1849) Ueber den Charakter der Insecten-Fauna von Südpersien. Denkschriften der Kaiserlichen Akademie der Wissenschaften 1: 42–53.
- Korb SK, Yakovlev RV (1998) Zwei neue Unterarten der Tagfalter aus dem Palaaektischen Faunengebiet. Lambillionea 98: 140–141.
- Korb M (1924) Ueber die von mir beobachteten paläarktischen Lepidopteren [Vorkommen, Lebensweise u. s. w.]. Mitteilungen der Münchner Entomologischen Gesellschaft 14: 18–24.
- Koubínová D, Dincã V, Dapporto L, Vodă R, Suchan T, Vila R, Alvarez N (2017) Genomics of extreme ecological specialists: multiple convergent evolution but no genetic divergence between ecotypes of *Maculinea alcon* butterflies. Scientific Reports 7(13752): 1–10. https://doi.org/10.1038/s41598-017-12938-8
- Larsen TB (1974) The butterflies of Lebanon. Beirut, Lebanon (National Council for Scientific Research), 255 pp.
- Larsen TB, Nakamura I (1983) The Butterflies of East Jordan. Entomologist's Gazette 34: 135–208.
- Leestmans R, Mottet P, Verhulst J, Carbonell F (1986) Contributions a la connaissance de la faune printanière des lépidoptères du Sud de l'Asie Mineure (Insecta, Lepidoptera). Linneana Beligica 10: 334–381.
- Leestmans R (2005) Considération biogéographiques concernant les *Elphinstonia* "jaunes" du Sud-Ouest méditerranéen (Lepidoptera: Pieridae, Anthocharini). Linneana Belgica 20: 93–96.
- Lucas H (1849) Exploration Scientifique de l'Algerie pendant les Annees 1840, 1841, 1842. Histoire naturelle des animaux arti-

- Lukhtanov VA, Lukhtanov A (1994) Die Tagfalter Nordwestasiens (Lepidoptera, Diurna). Herbipoliana 3: 1–440.
- Lukhtanov VA, Dantchenko AV, Vishnevskaya MS, Saifitdinova AF (2015) Detecting cryptic species in sympatry and allopatry: analysis of hidden diversity in *Polyommatus (Agrodiaetus)* butterflies (Lepidoptera: Lycaenidae). Biological Journal of the Linnean Society 116: 468–485. https://doi.org/10.1111/bij.12596
- Lukhtanov VA, Dantchenko AV (2017) A new butterfly species from south Russia revealed through chromosomal and molecular analysis of the *Polyommatus (Agrodiaetus) damonides* complex (Lepidoptera, Lycaenidae). Comparative Cytogenetics 11: 769–795. https:// doi.org/10.3897/compcytogen.v11i4.20072
- Mallet J, Wynne IR, Thomas CD (2011) Hybridisation and climate change: brown argus butterflies in Britain (*Polyommatus* subgenus *Aricia*). Insect Conservation and Diversity 4: 192–199. https://doi. org/10.1111/j.1752-4598.2010.00122.x
- Matthews DL, Miller JY, Warren AD, Toomey JK, Portell RW, Lott TA, Grishin NV (2018) Are Miami blues in Cuba? A review of the genus *Cyclargus* Nabokov (Lepidoptera: Lycaenidae) with implications for conservation management. Insecta Mundi 0676: 1–38.
- Meusnier I, Singer GAC, Landry JF, Hickey DA, Hebert PND, Hajibabaei M (2008) A universal DNA mini-barcode for biodiversity analysis. BMC Genomics 9: 1–4. https://doi.org/10.1186/1471-2164-9-214
- Muñoz Sariot MG (2011) Biologia Y ecologia de los Licènidos Espanñoles. Granada, Muñoz Sariot, 383 pp.
- Nazari V (2003) Butterflies of Iran. Department of Environment, Dayere Sabz Publications, Tehran, 568 pp.
- Nazari V, Zakharov EV, Sperling FAH (2007) Phylogeny, historical biogeography, and taxonomic ranking of Parnassiinae (Lepidoptera, Papilionidae) based on morphology and seven genes. Molecular Phylogenetics and Evolution 42: 131–156. https://doi.org/10.1016/j. ympev.2006.06.022
- Nazari V, ten Hagen W, Bozano GC (2009) Molecular systematics and phylogeny of the 'Marbled Whites' (Lepidoptera: Nymphalidae, Satyrinae, *Melanargia* Meigen). Systematic Entomology 35: 132–147. https://doi.org/10.1111/j.1365-3113.2009.00493.x
- Nekrutenko YP, Effendi RM (1980) A new species of *Tomares* from Talysh Mountains. Nota Lepidopterologica 3: 69–72.
- Nekrutenko YP, Tshikolovets V (2005) The Butterflies of Ukraine. Rayevsky Scientific Publishers, Kiev, 231 pp.
- Nice CC, Gompert Z, Fordyce JA, Forister ML, Lucas LK, Buerkle CA (2013) Hybrid speciation and independent evolution in lineages of Alpine butterflies. Evolution 67-4: 1055–1068. https://doi. org/10.1111/evo.12019
- Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300
- Oberthür C (1893) Descriptions d'Insectes nouveaux ou peu connus. II. Lépidoptères d'Asie. Études d'entomologie 18: VIII–49. https://doi. org/10.5962/bhl.title.9398
- Pe'er G, Settele J (2008) The rare Butterfly *Tomares nesimachus* (Lycaenidae) as a bioindicator for pollination services and ecosystem functioning in Northern Israel. Israel Journal of Ecology and Evolution 54: 111–136. https://doi.org/10.1560/IJEE.54.1.111
- Pellissier L, Kostikova A, Litsios G, Salamin N, Alvarez N (2017) High rate of protein coding sequence evolution and species diversifica-

tion in the Lycaenids. Frontiers in Ecology and Evolution 5: 1–90. https://doi.org/10.3389/fevo.2017.00090

- Por FD (1975) An outline of the zoogeography of the Levant. Zoological Scripta 4: 5–20. https://doi.org/10.1111/j.1463-6409.1975. tb00713.x
- Rákosy L, Craioveanu C (2015) Redescovering *Tomares nogelii do-brogensis* Caradja, 1895 in Romania. Entomologica Romanica 19: 13–16.
- Rambault A (2002) Sequence Alignment Editor, version 2.0. http://tree. bio.ed.ac.uk/software/seal/ [Accessed March 2019]
- Rambault A (2018) Figtree v1. 4.4. Computer program and documentation distributed by the author. http://github.com/rambaut/figtree [Accessed March 2019]
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904. https://doi.org/10.1093/sysbio/ syy032
- Roitman M, Gardner MG, New TR, Nguyen TTT, Roycroft EJ, Sunnucks P, Yen AL, Harrisson KA (2017) Assessing the scope for genetic rescue of an endangered butterfly: the case of the Eltham copper. Insect Conservation and Diversity 10: 399–414. https://doi. org/10.1111/icad.12235
- Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi. org/10.1093/sysbio/sys029
- Sakamoto Y, Yago M (2017) Potential for interspecific hybridization between Zizina emelina and Zizina otis (Lepidoptera: Lycaenidae). Journal of Insect Conservation 21: 509–515. https://doi.org/10.1007/ s10841-017-9991-1
- Schär S, Eastwood R, Arnaldi KG, Talavera G, Kaliszewska ZA, Boyle JH, Espeland M, Nash DR, Vila R, Pierce NE (2018) Ecological specialization is associated with genetic structure in the ant-associated butterfly family Lycaenidae. Proceedings of the Royal Society B 285: 20181158. https://doi.org/10.1098/rspb.2018.1158
- Schintlmeister A (2008) Palaearctic Macrolepidoptera Vol. 1: Notodontidae. Apollo Books, Stenstrup, 482 pp. https://doi.org/10.1002/ mmnd.200900017
- Schmitt T, Habel JC, Zimmermann M, Müller P (2006) Genetic differentiation of the marble white butterfly, *Melanargia galathea*, accounts for glacial distribution patterns and postglacial range expansion in Southeastern Europe. Molecular Ecology 15: 1889–1901. https://doi.org/10.1111/j.1365-294X.2006.02900.x
- Sielezniew M, Rutkowski R, Ponikwicka-Tyszko D, Ratkiewicz M, Dziekańska I, Švitra G (2012) Differences in genetic variability between two ecotypes of the endangered myrmecophilous butterfly *Phengaris* (= *Maculinea*) *alcon*-the setting of conservation priorities. Insect Conservation and Diversity 5: 223–236. https://doi. org/10.1111/j.1752-4598.2011.00163.x
- Sohn JC, Labandeira C, Davis D, Mitter C (2012) An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. Zootaxa 3286: 1–132. https://doi.org/10.11646/zootaxa.3286.1.1
- Staudinger O, Rebel H (1901) Catalog der Lepidopteren des palaearctischen Faunengebietes. I. Theil: Famil. Papilionidae-Hepialidae. R Friedländer and Sohn, Berlin, 411 pp. https://doi.org/10.5962/bhl. title.120482

- Stradomsky BV, Fomina EA (2013) The developmental stages of some blue butterflies (Lepidoptera: Lycaenidae) of Russian South. Part V. Caucasian Entomological Bulletin 9: 299–302. [in Russian] https:// doi.org/10.23885/1814-3326-2013-9-2-299-302
- Swainson W (1831) Zoological illustrations, or, original figures and descriptions of new, rare, or interesting animals, selected chiefly from the classes of ornithology, entomology, and conchology, and arranged according to their apparent affinities (2nd series, vol. II). Baldwin and Cradock, London, 91 pp. https://doi.org/10.5962/bhl.title.42278
- Swofford DL (2003) PAUP: A computer program for phylogenetic inference using maximum parsimony. Journal of General Physiology 102: 9A.
- Takeuchi T, Takahashi J, Kiyoshi T, Nomura T, Tsubaki Y (2015) Genetic differentiation in the endangered myrmecophilous butterfly *Niphanda fusca*: a comparison of natural and secondary habitats. Conservation Genetics 16: 979–986. https://doi.org/10.1007/ s10592-015-0717-1
- Tarrier MR, Delacre J (2008) Les papillons de jour du Maroc. Publication Scientifiques du Museum, Paris, 480 pp.
- ten Hagen W, Miller MA (2010) Molekulargenetische Untersuchungen der paläarktischen Arten des Genus *Callophrys* Billberg, 1820 mit Hilfe von mtDNA-COI-Barcodes und taxonomische Überlegungen (Lepidoptera: Lycaenidae). Nachrichten des Entomologischen Vereins Apollo, N.F. 30: 177–197.
- Tennent WJ (1996) The butterflies of Morocco, Algeria and Tunisia. Gem Publishing Company, Wallingford, 252 pp.
- Thompson JD, Gibson TJ, Plewniak F, Jeanmougin F, Higgins DG (1997) The CLUSTALX Windows inference: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acid Research 25: 4876–4882. ttps://doi.org/10.1093/ nar/25.24.4876
- Todisco V, Grill A, Fiedler K, Gottsberger B, Dincă V, Vodă R, Lukhtanov V, Letsch H (2018) Molecular phylogeny of the Palaearctic butterfly genus *Pseudophilotes* (Lepidoptera: Lycaenidae) with focus on the Sardinian endemic *P. barbagiae*. BMC Zoology 3: 1–4. https://doi.org/10.1186/s40850-018-0032-7
- Tolman T, Lewington R (1997) Butterflies of Britain and Europe. Harper Collins, London, 320 pp.
- Toropov SA, Zhdanko AB (2009) The butterflies (Lepidoptera, Papilionoidea) of Dzunghar, Tien Shan, Alai and eastern Pamirs. Bd.
 2: Danaidae, Nymphalidae, Libytheidae, Riodinidae, Lycaenidae. Selbstverlag, Bishkek, 377 pp. [13 pl. Addendum]
- Toews DPL, Brelsford A (2012) The biogeography of mitochondrial and nuclear discordance in animals. Molecular Ecology 21: 3907–3930. https://doi.org/10.1111/j.1365-294X.2012.05664.x
- Tshikolovets VV (2000) The butterflies of Uzbekistan. Konvoj, Kiev and Brno, 400 pp. [49 pls.]
- Tshikolovets VV, Pagès J (2016) The butterflies of Pakistan. Tshikolovets Publications, Pardubice, 317 pp.
- Tshikolovets VV, Pliushch I, Pak O, Skrylnik Y (2018) The butterflies of Afghanistan. Tshikolovets Publications, Pardubice, 262 pp.
- Tuzov VK, Gorbunov OG, Dantcheneko AV [Eds] (2000) Guide to the butterflies of Russia and adjacent territories (Lepidoptera, Rhopalocera) (Vol. 2). Pensoft, Sofia and Moskow, 580 pp.
- Uvarov BP (1921) The geographical distribution of orthopterous insects in the Caucasus and Western Asia. Proceedings of the Zoological Society of London 1921: 447–472. https://doi. org/10.1111/j.1096-3642.1921.tb03273.x
- van Oorschot H, Wagener S (2000) Zu *Tomares* in der Türkei. Ergänzungen und Korrekturen zu Hesselbarth, van Oorschot and Wagener, 1995: die Tagfalter der Türkei. 3 (Lepidoptera). Phegea 28: 87–117.
- Vanden Broeck A, Maes D, Kelager A, Wynhoff I, WallisDeVries MF, Nash DR, Oostermeijer JGB, Van Dyck H, Mergeay J (2017) Gene flow and effective population sizes of the butterfly *Maculinea alcon* in a highly fragmented, anthropogenic landscape. Biological Conservation 209: 89–97. https://doi.org/10.1016/j.biocon.2017.02.001
- Vila R, Lukhtanov VA, Talavera G, Gil-T F, Pierce NE (2010) How common are dot-like distributions? Taxonomical oversplitting in western European Agrodiaetus (Lepidoptera: Lycaenidae) revealed by chromosomal and molecular markers. Biological Journal of the Linnean Society 101: 130–154. https://doi.org/10.1111/j.1095-8312.2010.01481.x
- Vodă R, Dapporto L, Dincă V, Vila R (2015) Why do cryptic species tend not to co-occur? A case study on two cryptic pairs of butterflies. PLoS ONE 10(2): e0117802. https://doi.org/10.1371/journal. pone.0117802
- Vodă R, Dapporto L, Dincă V, Shreeve TG, Khaldi M, Barech G, Rebbas K, Sammut P, Scalercio S, Hebert PDN, Vila R (2016) Historical and contemporary factors generate unique butterfly communities on islands. Scientific Reports 6(28828): 1–11. https://doi.org/10.1038/ srep28828
- Weidenhoffer Z, Bozano GC (2007) Guide to the butterflies of the Palaeartic region, Lycaenidae part III. Omnes Artes, Milano, 97 pp.
- Weidenhoffer Z, Vanek J (1977) Beitrag zur Biologie von Tomares romanovi und Tomares callimachus (Lep.: Lycaenidae). Entomologische Zeitschrift 87: 131–134.
- Weingartner E, Wahlberg N, Nylin S (2006) Speciation in *Pararge* (Satyrinae: Nymphalidae) butterflies-North Africa is the source of ancestral populations of all *Pararge* species. Systematic Entomology 31: 621–632. https://doi.org/10.1111/j.1365-3113.2006.00333.x
- Zhdanko A (1997) A new blue butterfly species of the genus *Callophrys* (Lepidoptera, Lycaenidae) from the Kopet Dagh. Selevinia, Almaty 1996/1997: 21–22. [in Russian]
- Zolotuhin VV, Anikin VV (2017) In: Anikin VV, Sachkov SA, Zolotuhin VV (2017) "Fauna lepidopterologica Volgo-Uralensis": from P. Pallas to present day. Proceedings of the Museum Witt Munich 7: 1–696.

Supplementary material 1

SI 1. Material examined and Genbank accessions.

Authors: Vazrick Nazari, Wolfgang ten Hagen Data type: Microsoft Excel Spreadsheet

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

Link: https://doi.org/10.3897/dez.67.50252.suppl1

Supplementary material 2

SI 2. Male and female genitalia dissections of *Tomares* species.

Authors: Vazrick Nazari, Wolfgang ten Hagen Data type: pdf document

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

Link: https://doi.org/10.3897/dez.67.50252.suppl2

Supplementary material 3

SI 3. Androconia, forewing upperside and hindwing underside in select *Tomares* species.

Authors: Vazrick Nazari, Wolfgang ten Hagen Data type: pdf document

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

Link: https://doi.org/10.3897/dez.67.50252.suppl3

Supplementary material 4

SI 4. Phylogenetic trees resulting from Maximum Parsimony (MP, PAUP) and Maximum Likelihood (ML, PHYML) analyses of COI, EF-1a and Combined datasets with bootstrap support values.

Authors: Vazrick Nazari, Wolfgang ten Hagen Data type: pdf document

- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons. org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: https://doi.org/10.3897/dez.67.50252.suppl4

PENSOFT.



A review of *Himalcercyon* stat. nov., with description of a new species from the Chinese Himalaya and an updated key to Asian genera of Megasternini (Coleoptera, Hydrophilidae)

Fenglong Jia¹, Zulong Liang¹, Martin Fikáček^{2,3}

- 2 Department of Entomology, National Museum, Cirkusová 1740, CZ-193 00 Praha 9, Czech Republic
- 3 Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic

http://zoobank.org/56BB973D-BE4E-47AE-BC98-C1F1151C41C4

Corresponding author: Martin Fikáček (mfikacek@gmail.com)

Academic editor: James Liebherr • Received 12 January 2020 • Accepted 11 March 2020 • Published 11 May 2020

Abstract

Himalcercyon Hebauer, 2002 **stat. nov.** is elevated to genus rank based on the unique form of its mesoventral elevation. The genus is reviewed, redescribed, and illustrated in detail. Two species are recognized: *Himalcercyon mirus* (Hebauer, 2002) **comb. nov.** from Nepal and *H. franzi* **sp. nov.** from Chinese Himalaya (Xizang Autonomous Region). Both species are illustrated and diagnosed. An updated key to the Asian genera of the tribe Megasternini (Coleoptera, Hydrophilidae, Sphaeridiinae) is provided, along with the SEM micrographs of ventral morphology of these genera. New replacement name *Oreosternum* **nom. nov.** is proposed for *Oreocyon* Hebauer, 2002 which is preoccupied by *Oreocyon* Marsh, 1872 (Mammalia, Oxyenidae) and *Oreocyon* Krumbiegel, 1949 (Mammalia, Canidae).

Key Words

Asia, morphology, new replacement name, new species, new status, Oriental Region, Sphaeridiinae, taxonomy, Xizang, China

Introduction

Megasternini is the largest clade of terrestrial water scavenger beetles, containing approximately 580 described species currently classified in 52 genera (Jia et al. 2011, 2019; Ryndevich 2011; Short and Fikáček 2011; Fikáček et al. 2012a, 2013, 2015b; Fikáček and Rocchi 2013; Makhan 2013; Deler-Hernández et al. 2014; Arriaga-Varela et al. 2017, 2018a, b; Ryndevich and Prokin 2017; Ryndevich et al. 2017; Shatrovskiy 2017; Szczepański et al. 2018). Since the 1980s, 20 new genera of Megasternini have been described from the Afrotropical, Australian, Oriental, and Neotropical regions by Hansen (1989, 1990, 1999a), Hebauer (2002a, 2003), Fikáček et al. (2013), and Arriaga-Varela et al. (2018a). Nearly half of the described megasternine species are classified in the

genus Cercyon. This led d'Orchymont (1942), Smetana (1978), and Hebauer (2002a, 2003) to divide Cercyon into numerous subgenera, 11 of which are currently considered valid (Hansen 1999b; Short and Hebauer 2006). However, most of these only contain one to a few species, and the majority of Cercyon species are still members of the nominotypical subgenus Cercyon s. str. A phylogeny of the Hydrophilidae based on molecular data from six genes (Short and Fikáček 2013), which included only four Cercyon species, indicated that Cercyon is very likely a polyphyletic genus. Moreover, preliminary studies have revealed that even some of the small subgenera are not monophyletic (e.g., Arriaga-Varela et al. 2018a). Additional studies are therefore necessary to establish a natural classification of the group and allow for reliable identification of genera and species.

¹ Institute of Entomology, Life Science School, Sun Yat-sen University, Guangzhou, 510275, Guangdong, China

The mountains on the southern margin of the Qinghai-Xizang (Tibetan) Plateau are known for their highly diverse and endemic faunas (e.g., Huang et al. 2007; Deng et al. 2020), of which terrestrial Hydrophilidae are a component. More than 80 species of terrestrial hydrophilid beetles have been reported from Nepal and Bhutan (Hansen 1999b; Hebauer 2002a, b), most of which are until now only known from the Himalayas. Recently, some of the species originally described from the Himalayas have also been recorded from the mountains in the Chinese provinces of Yunnan and Sichuan (e.g., Cercyon divisius Hebauer, 2002: Ryndevich et al. 2017), indicating that the mountain systems on southern and south-eastern margin of Qinghai-Xizang are interconnected, thus forming the so-called Sino-Himalayan subregion (for details see Proches and Ramdhani 2012). Other species originally known from the Himalayas are widespread at high elevations on the Qinghai-Xizang Plateau (C. berlovi Shatrovskiy, 1999: Jia et al. 2011) and seem to be plateau endemics that reach lower altitudes at the margins of their range, which seems uncommon for endemics of the plateau (see, e.g., Angus et al. 2016).

Recently, we received a small sample of terrestrial hydrophilids from Motuo County, Xizang Autonomous Region, China, a region in the Himalayas at the southern margin of the Qinghai-Xizang Plateau. In contrast to the more northern regions of the Xizang Autonomous Region, Motuo County includes middle to low elevations and is affected by monsoon rains; it is, therefore, warmer and more humid than the main plateau areas. The material contained a species of the Megasternini which is unique in the morphology of its mesoventral plate. We originally considered it to be an undescribed genus, but a detailed survey of megasternine taxa described from the Himalaya region revealed that Cercyon mirus Hebauer, 2002 from Nepal, which was assigned to the monotypic subgenus Himalcercyon Hebauer, 2002 in the original description (Hebauer 2002a), shares the unusual mesoventral morphology with our specimens. Hence, we here redescribe Himalcercyon and elevate this subgenus to the rank of genus based on its unique ventral morphology; we (re)describe and illustrate both species. We also provide an updated key to the Asian genera of the Megasternini.

Material and methods

We examined the type series of *Cercyon mirus* and the small series (10 specimens) of the new species from Motuo County. Male genitalia of the holotypes of both species were examined and photographed in the original position (i.e. with the median lobe inserted in the tegmen). Due to the very limited material available, separation of the median lobe is not always easy and sometimes results in partial damage of some parts of the aedeagus.

Genitalia were photographed in glycerol. The aedeagus of the holotype of C. mirus was subsequently embedded in a drop of alcohol-soluble Euparal resin on a piece of glass glued to a small piece of cardboard attached below the respective specimen. Habitus photographs were taken using a Canon D-550 digital camera with attached Canon MP-E65mm f/2.8 1-5 macro lens. Genitalia were photographed using a Canon D1100 digital camera attached to an Olympus BX41 compound microscope (C. mirus) or using an Olympus SZX7 stereomicroscope (new species); combined, focus-stacked images were made with Helicon Focus (Helicon Soft Ltd, Ukraine) software. Scanning electron micrographs of C. mirus and of the Asian genera of the Megasternini were taken using a Hitachi S-3700N environmental electron microscope at the Department of Paleontology, National Museum in Prague; SEMs of the new species were taken using a Phenom Prox scanning electron microscope in the Biological Museum of the Sun Yat-sen University. Images were combined into figures using Adobe Photoshop CS6. All original images, including additional views not presented in this paper, are included in the dataset submitted to the Zenodo archive (https://zenodo.org/ under https:// doi.org/10.5281/zenodo.3693743. SEMs of the megasternine genera for the identification key are mostly based on specimens deposited in NMPC, except for rare genera (Kahanga, Gillisius) for which holotypes were examined.

Examined specimens are deposited in the following collections:

- NMPC National Museum, Praha, Czech Republic (M. Fikáček);
- **SMNS** Staatliches Museum für Naturkunde, Stuttgart, Germany (W. Schawaller);
- SYSU Biological Museum, Sun Yat-sen University, China (F.-L. Jia).

Taxonomy

Himalcercyon Hebauer, 2002, stat. nov. Figures 1–4

Cercyon (Himalcercyon) Hebauer, 2002: 39.

Type species. Cercyon (Himalcercyon) mirus Hebauer, 2002.

Diagnosis. Dorsal surface pubescent; anterior margin of clypeus rounded; frontoclypeal suture not forming transverse ridge between eyes; eyes small, separated $5-6\times$ the width of one eye; prosternum strongly carinate medially, without ridge demarcating median portion from lateral portions (Figs 2D, 3B); antennal grooves distinct, well demarcated laterally, not reaching lateral margins of prothorax (Figs 2D, 3B); mesoventrite bearing hydrofuge pubescence; mesoventral elevation arrowhead-shaped, widely attaching metaventral process



Figure 1. Habitus and genital morphology of *Himalcercyon* species. A–D. *H. mirus* (A, B. Paratypes; C, D. Holotype). E–H. *H. franzi* sp. nov. (E, F. Paratypes; G, H. Holotype). A, E. Dorsal view; B, F. Lateral view; C, G. Aedeagus in dorsal view; D, H. Sternite IX in dorsal view.

(Figs 2F, 3C), cavities for reception of procoxae ending far anterior to mesocoxae (Figs 2F, 3C); metaventrite with a pentagonal posteromedian glabrous area weakly projecting anteriorly between mesocoxae; femoral lines absent; anterolateral transverse arcuate ridge absent (Fig. 2E); each elytron with 10 striae (Figs 1A, B, E, F, 3H); first abdominal ventrite carinate throughout (Fig. 2A); last abdominal ventrite with a glabrous apical area (Fig. 2A); median lobe deeply inserted into phallobase (Fig. 1C, G); median portion of sternite IX tongue-shaped (Fig. 1D, H).

Redescription. Body broadly oval and moderately convex; body outline not interrupted between pronotum and elytra.



Figure 2. Morphology of *Himalcercyon mirus* (Hebauer, 2002). A. Complete ventral view. B. Mentum. C. Prosternal carina in ventrolateral view. D. Prosternum and hypomeron. E. Meso- and metaventrite. F. Details of mesoventral plate.

Head. Excised in front of eyes laterally, antennal base exposed. Labrum concealed under clypeus, not exposed dorsally. Clypeus not deflexed, truncate anteriorly, without anterolateral extensions; anterior margin narrowly beaded. Frontoclypeal suture obsolete, only visible as impunctate bar. Frons with even surface. Eyes rather small, rounded, projected laterally; interocular

distance ca $5-6\times$ the width of one eye in dorsal view. Dorsal punctation of head consisting of punctures each bearing a long seta. Maxillary palpus slightly longer than half of width of head, with ventral sucking disc in male; palpomere 2 strongly swollen, longer than palpomere 3; palpomere 4 symmetrical, slightly shorter than palpomere 2, but longer than palpomere 3. Men-



Figure 3. Morphology of *Himalcercyon franzi* sp. nov. A. Mentum. B. Prosternum and hypomeron. C. Mesoventral elevation. D. Antenna. E. Mesotarsus, ventral view. F. Median portion of metaventrite. G. Elytral punctation. H. Elytral apex.

tum ca $2.1-2.4\times$ as wide as long, trapezoidal, anterior margin not emarginate medially (Figs 2B, 3A). Labial palpomere 3 slightly longer and as broad as palpomere 2, symmetrical. Gula well developed throughout, wide posteriorly, moderately narrowed anteriorly. Antennae with nine antennomeres, ca $0.7\times$ width of head; scape a little longer than antennomeres 2-6 combined; club compact, pubescent, ca $2 \times$ as long as wide (Fig. 3D), slightly longer than scape.

Prothorax. Pronotum relatively short and transverse, widest at base; surface smooth, punctation consisting of setiferous punctures, all punctures of the same size and shape; transverse series of punctures along posterior margin absent. Prosternum well developed, slightly tec-

tiform, strongly carinate medially, without elevated median portion or ridge demarcating median portion from lateral parts (Figs 2D, 3C); antennal grooves distinct, well demarcated, arcuate laterally, not reaching lateral margins of prothorax (Figs 2D, 3B). Prosternal process reaching midpoint of procoxae, not bifurcate apically (Fig. 2D).

Mesothorax. Mesoventrite fused to mesepisterna, bearing hydrofuge pubescence; median portion abruptly raised in posterior half to form arrowhead-shaped elevation (Figs 2E, F, 3C), its surface pubescent; cavities for reception of procoxae ended well before mesocoxae (Figs 2E, F, 3C). Each elytron with 10 punctate striae (Figs 1A, B, E, F, 3H), striae sharply impressed. Interval punctation consisting of setiferous punctures (Fig. 3G). Scutellar shield small, triangular.

Metathorax. Metaventrite moderately raised medially, forming a bare pentagonal area weakly projected anteriorly between mesocoxae (Figs 2E, 3F); lateral portions with coarse punctures, bearing fine hydrofuge pubescence (Fig. 2E). Anterolateral ridge absent; femoral lines absent (Fig. 2E). Metepisterna subparallel, ca $6.5 \times$ as long as wide. Hind wings well developed, ca $2.4 \times$ as long as wide; r-m-crossvein rising from base of radial cell; cubital spur rising from apex of M-Cu loop; m-crossvein vestigial; basal cell elongate, wedge cell absent; anal lobe weakly developed.

Legs. Coxae partly with hydrofuge pubescence, mesocoxae moderately separated (Fig. 2A). Femora with tibial grooves demarcated by ventral and dorsal ridges; ventral face of pro- and mesofemora glabrous, metafemora with fine microsculpture consisting of transverse lines. Tibiae weakly, gradually widened from base to apices, with fine and sparse lateral spines. Tarsi with five tarsomeres, with dense and short setae ventrally. Meso- and metatarsi with tarsomere 1 ca $2\times$ as long as tarsomere 2 (Fig. 3E), tarsomere 5 slightly shorter than tarsomere 1; claws small and moderately curved (Fig. 3E).

Abdomen with five ventrites covered by fine hydrofuge pubescence; ventrite 1 $2\times$ as long as ventrite 2, strongly carinate throughout (Fig. 2A); posterior margin of ventrite 5 simply rounded, with an apical glabrous area. Aedeagus (Fig. 1C, G) of the *Cercyon* type, i.e. with median lobe reaching deeply into phallobase in natural position; parameres ca $2\times$ as long as phallobase, with transversely bent apices; phallobase with asymmetrical basis (manubrium). Median part of sternite IX not reduced, forming a broad tongue-shaped structure (Fig. 1D, H).

Discussion. Hebauer (2002a) proposed Himalcercyon as a subgenus of Cercyon, mentioning that it corresponds to Cercyon in all characters except for the shape of the mesoventral plate. The form of the mesoventral elevation is one of most important generic characters in the Megasternini, and clearly differentiates both Himalcercyon species from all other members of the genus Cercyon. Both species of Himalcercyon are very similar to each other in all important characters and in the general form of male genitalia, indicating that they are likely closely related. Moreover, both species occur in the Himalayas. All of this supports Himalcercyon as a monophyletic clade that differs from Cercyon, as well as other megasternine genera, in the character currently considered as crucial at the generic level. For this reason, we elevate Himalcercyon to genus rank. See Diagnosis for the characters distinguishing Himalcercyon from other megasternine genera, and the identification key for a comparison of *Himalcercyon* with other Asian Megasternini.

Key to species of Himalcercyon

- Body broadly oval, elytra combined 1.1× longer than wide (Fig. 1A). Prosternum widely carinate medially (Fig. 2C, D). Antennal groove weakly arcuate laterally (Fig. 2D). Mesoventral elevation wider, ca 1.5× as long as wide (Fig. 2E, F). Apex of the median lobe narrowly rounded, median lobe about as long as parameres and phallobase combined (Fig. 1C) *H. mirus* (Hebauer, 2002)

Himalcercyon franzi sp. nov.

http://zoobank.org/AF02DECB-FD93-4C0F-BAC8-13498287A831 Figures 1E-H, 3, 4

Type locality. China, Xizang Autonomous Region, Motuo County, track from Dayandong to Hanmi, 2200–2400 m a.s.l. [GPS ca 29.4283N, 95.0498E].

Material examined. Holotype: CHINA ● 1 ♂; Xizang, Motuo County, Dayandong-Hanmi; 2200–2400 m a.s.l.; 13 Aug 2005, Tang Liang leg.; SYSU [verbatim label data: "CHINA, Xizang, Motuo Coun., Dayandong-Hanmi, alt. 2200–2400 m, 13.viii.2005, TANG Liang leg."].

Paratypes: CHINA • 9; same data as for holotype;
SYSU • 4; Xizang, Motuo County, Nage-Dayandong;
2900–3300 m a.s.l.; 12 Aug 2005; Tang Liang lgt.; SYSU
1; Xizang, Motuo County, Nage-Dayandong; 2900–3300 m a.s.l.; 12 Aug 2005; Tang Liang lgt.; NMPC.

Description. *Form and color.* Body size 2.5–2.8 mm (2.6 mm in holotype), body width 1.5–1.7 mm (1.55 mm



Figure 4. Known distribution of *Himalcercyon*: **Circles.** *H. mirus* (Hebauer); **Square.** *H. franzi* sp. nov. Color shading of the map indicated altitude: green = lowest, brown = highest.

in holotype), widest at anterior third of elytra, arcuately narrowing posteriad (Fig. 1E). Dorsum dark brown; head of some specimens with paler clypeus; pronotal lateral margins yellow brown; elytral apices and posterior half of lateral elytral margins slightly paler; epipleuron reddish brown; antenna, maxillary and labial palpi reddish brown; legs reddish brown, with darker femora.

Head. Clypeus with moderately dense fine setiferous punctures, smooth between punctures. Frons with punctures coarser and somewhat denser than those on clypeus, smooth between punctures. Mentum 2× wider than long, rugose, with dense coarse punctures (Fig. 3A), slightly concave anteriorly. Antenna with pedicel ca 0.2× as long as scape, pedicel ca. as long as antennomeres 3 and 4 combined, cupule small (Fig. 3D).

Thorax. Pronotum with punctation similar to that on frons, interstices without microsculpture; lateral marginal bead shortly overlapping to anterior margin but not to posterior margin, stopping at posterior angle. Scutellar shield smooth, with three to five punctures. Elytral striae sharply impressed (Figs 1E-F), striae 6, 8, and 9 not reaching base; intervals with much finer and sparser punctures than on pronotum, each interval puncture bearing a fine short seta (Fig. 3G), interstices between punctures smooth. Epipleuron with bare outer and pubescent inner portion delimited from each other by a fine ridge, inner pubescent part narrower than the outer part, reaching the level of posterior part of metaventrite. Mesoventral elevation arrowhead-shaped, ca 2.0× longer than wide, densely pubescent (Fig. 3C). Metaventrite with large median elevation, finely and sparsely punctate (Fig. 3F), interstices without microsculpture; lateral portions microsculptured with sparse coarse punctures and dense pubescence. Legs with trochanters densely pubescent, femora with sparse and moderately coarse punctures, interstice between punctures with fine microsculpture consisting of transverse lines.

Male genitalia. Middle lobe of abdominal sternite IX wide, shorter than lateral struts (Fig. 1H). Aedeagus (Fig. 1G) with median lobe ca $0.8 \times$ as long as tegmen; paramere ca $1.5 \times$ as long as phallobase. Paramere gradu-

ally narrowed from base to apex, truncate apically, widened inwards to form a process with a few setae. Median lobe broader than paramere, gradually narrowing in apical third, apex pointed, gonopore subapical.

Etymology. The species is named after Dr Franz Hebauer, a German taxonomist of the Hydrophiloidea who recognized and described *Himalcercyon* as a subgenus of *Cercyon*.

Distribution. Only known from the type locality in the eastern Himalaya (Motuo county, Xizang Autonomous Region, China) (Fig. 4).

Himalcercyon mirus (Hebauer, 2002), stat. nov. Figures 1A–D, 2, 4

Cercyon (Himalcercyon) mirus Hebauer 2002: 39.

Type locality. Nepal, Kathmandu district, Sheopuri Mt., 2100–2300 m a.s.l. [GPS ca 27.816672N, 85.400000E].

Material examined. Holotype: NEPAL ● 1 ♂; Kathmandu Distr. Sheopuri Mt.; 2100–2300 m a.s.l.; 25 Jun 1988; W. Schawaller leg.; SMNS.

Paratypes: NEPAL • 2 $\bigcirc \bigcirc$; same data as for holotype; SMNS • 1 \bigcirc ; same data as for holotype; NMPC • 1 \bigcirc ; Annapurna, Telbrung Danda; 2600–2800 m a.s.l.; 13 Jun 1997; Schmidt leg.; SMNS.

Redescription. *Form and color.* Body size 3.1–3.5 mm (3.4 mm in holotype), body width 2.0–2.1 mm (2.0 mm in holotype), widest at anterior third of elytra, weakly narrowing posteriad (Fig. 1A). Dorsum pitchybrown to black; head with paler clypeus; pronotal margins brown; elytral apices and posterior half of lateral elytral margins brownish; epipleuron pitchy brown laterally, reddish mesally; antenna, maxillary and labial palpi brown to reddish brown; legs reddish brown, with darker femora.

Head. Clypeus with moderately dense fine setiferous semicircular punctures, smooth between punctures. Frons with punctures of the same size and density as those on clypeus, smooth between punctures. Mentum $1.4 \times$ wider than long, rugose, with dense punctures (Fig. 2B), slightly concave anteriorly. Antenna with pedicel ca $0.2 \times$ as long as scape, pedicel ca. as long as antennomeres 3 and 4 combined, cupule small.

Thorax. Pronotum with punctation similar to that on frons, interstices without microsculpture; lateral marginal bead shortly overlapping to anterior margin but not to posterior margin, stopping at posterior angle. Scutellar shield smooth, with five to seven punctures. Elytral striae sharply impressed (Fig. 1A), striae 6, 8, and 9 not reaching base; intervals with finer and sparser punctures than on pronotum, each puncture bearing a fine short seta, interstices between punctures smooth. Epipleuron with bare outer and pubescent inner portion delimited from each other by a fine ridge, inner pubescent part narrower than the outer part, reaching the level of posterior



Figure 5. Ventral view of thorax of eastern Palaearctic and Oriental genera of the Megasternini. A. Cryptopleurum ferrugineum. B. Megasternum concinnum. C. Pacrillum manchuricum. D. Pachysternum nigrovittatum. E. Peltocercyon coomani. F. Armostus schenklingi.

part of metaventrite (Fig. 1A). Mesoventral elevation arrowhead-shaped, ca 1.5×1000 fm wide, sparsely pubescent (Fig. 2F). Metaventrite with large median elevation, finely and sparsely punctate (Fig. 2E), interstices without microsculpture; lateral portions microsculptured, with sparse coarse punctures and dense pubescence. Legs with trochanters densely pubescent, femora with sparse and moderately coarse punctures, interstice between punctures with fine microsculpture consisting of transverse lines. *Male genitalia.* Middle lobe of abdominal sternite IX narrow, shorter than lateral struts (Fig. 1D). Aedeagus (Fig. 1C) with median lobe ca as long as tegmen; paramere ca $1.5 \times$ as long as phallobase. Paramere gradually narrowed from base to apex, obliquely truncate apically, widened inwards to form a process with a few setae. Median lobe ca as wide as paramere, gradually narrowing in apical third, apex narrowly rounded, gonopore subapical.

Distribution. Known from two localities in central Nepal (Fig. 4).



Figure 6. Ventral view of thorax of eastern Palaearctic and Oriental genera of the Megasternini. A. Morastus gracilipalpis. B. Oosternum sp. (O. soricoides group). C. Emmidolium excavatum. D. Chimaerocyon shimadai. E. Paroosternum sp. F. Oreosternum frigidum.

Key to Eastern Palaearctic and Oriental genera of the Megasternini

The following key is mainly based in the ventral characters, namely the form of prosternum and meso- and metaventrite, which are illustrated in Figures 5–8. The concept of some of the genera will likely be modified in the future; the key reflects the current status. The key includes all genera occurring east of Iran, the Black Sea, and the Ural Mountains. (i.e. it does not cover the Near East and the Arabian Peninsula); eastwards it includes all regions west of New Guinea. See Table 1 for the number of described species and references to the most important keys or taxonomic treatments for each genus. Remarks and numbers of species only refer to those from the Eastern Palaeartic and Oriental Regions.

1	Antennal grooves larg	e, reaching to the la	ateral margin of hypomeron (Fig	g. 5A, B,	D)	2
---	-----------------------	-----------------------	---------------------------------	-----------	----	---

2	Metaventrite with complete femoral lines reaching from posteriomesal portion to anterolateral corner (Fig. 5A, D) 3 Metaventrite without complete femoral lines, at most with short vestiges anterolaterally. (Fig. 5B, C)
3 -	Mesoventral plate wider than long. Prosternum with wide plate without median carina (Fig. 5A). Mentum with sharply pointed anterolateral corners (Fig. 8D)
4	distinct median carina (Fig. 5D). Mentum with bluntly rounded anterolateral corners Pachysternum Motschulsky Median portion of prosternum roof-like, high (Fig. 5C). Mesoventral plate longer than wide. Metaventrite without any
	traces of femoral lines (Fig. 5C). Anterior tibia without anterolateral excision
-	than long. Metaventrite with vestiges of femoral lines in anterolateral corners (Fig. 5B). Anterior tibia anterolaterally with emargination
5	Metaventrite with postcoxal ridge widely diverging from posterior margin of coxal cavity and forming an arcuate ridge reaching lateral margin of metaventrite (Figs 5F, F, 6A, B)
_	Metaventrite with postcoval ridge parallel to posterior margin of coval cavity or pearly so, reaching anterolateral corner
_	of metaventrite and not forming any arcuate ridge (Figs 6C–F, 7, 8A–C)
6	Metaventrite with complete temoral lines crossing the arcuate postcoxal ridge and X-shape in form (Fig. 5E). Mesoventral
	elevation narrowly elongate or narrow but widely contacting metaventritePeltocercyon d'Orchymont
_	Metaventrite without X-shaped structure, femoral lines absent or short, not crossing with arcuate postcoxal ridge (Figs 5F, 6A, B)
7	Mesoventral plate widely contacting metaventrite (Fig. 6A, B). Median portion of prosternum at least weakly delimited from lateral portions
_	Mesoventral plate separated from metaventrite by a wide deep gap (Fig. 5F). Median portion of prosternum simply carinate not delimited from lateral portions
8	Metaventrite with deen triangular impression along its lateral margin (Fig. 64)
_	Metaventrite without such impression (Fig. 6R)
9	Median portion of prosternum highly elevated and/or delimited from lateral portions by sharp ridges (Figs 6C_F 7A_D) 10
_	Median portion of prosternum finely carinate not delimited from lateral portions (Figs 7F, F, 8A, B)
10	Pronotum with deep longitudinal grooves (Fig. 8E). Bare portion of metaventrite very wide (Fig. 6C). Tiny beatles: length
10	ca 1.2 mm
-	Surface of pronotum without distinct longitudinal depressions. Bare portion of metaventrite confined to medial part
	only. Tiny to moderately large beetles
11	Median portion of prosternum in form of very small triangular, very highly elevated projection. Antennal grooves absent
	(Fig. 6D). Abdomen with apical emargination Chimaerocyon Fikaček, Maruyama, Vondraček & Short
-	Median portion of prosternum never so tiny and not so highly elevated. Antennal grooves present, even though some-
10	times rather small. Abdomen never with apical emargination
12	Prosternal elevation with lateral margins deeply excised (Fig. 6E, F)
-	Prosternal elevation with lateral margins or ridges straight (Fig. /A–D)
13	Paroosternum Scott
_	Large species, ca 3.0 mm. Metaventrite without femoral lines (Fig. 6F). Antennal grooves absent Oreosternum nom. nov.
14	Elytral series deeply impressed with the impressions contiguous to anterior margin of each elytron (Fig. 8F, G). Mesoven- tral elevation longer than wide, rhomboid to suboval (Fig. 7A, B)
-	Elytral series not impressed or impressions of elytral striae series not reaching anterior margin of each elytron. Mesoven-
15	Pronotum highly bulged in lateral view, not forming a continuous curve with elvtra. Anterior margin of prosternal eleva-
	tion strongly projecting anteriad (Fig. 7A). Mesoventral elevation subrhomboid
_	Pronotum not highly bulged in lateral view, forming a continuous curve with elvtra. Anterior margin of prosternal eleva-
	tion straight (Fig. 7B). Mesoventral elevation suboval
16	Grooves for reception of procoxae ending far before the anterior margin of mesocoxal cavities (Fig. 8C). Mesoventral
	plate elongate
_	Grooves for reception of proxocae reaching nearly the mesocoxal cavities (Fig. 7C, D). Mesoventral elevation approxi-
17	Indulty as while as iong
τ/	meeting mesally and forming a short median longitudinal ridge. Metatibiae densely pubescent ventrally (Fig. 8H). Large
	species: 2.5–3.3 mm
-	Mesoventral elevation more less pentagonal, without any marginal rim (Fig. 7D). Postcoxal ridges mesally bending pos- teriad, remaining separate, forming two short median longitudinal ridges (in one species largely obsolete). Metatibie without dense ventral pubescence. Medium sized to tiny species: 2.0–2.9 mm

* the type species, G. madurensis d'Orchymont, 1925, keys out here.

18 -	Abdominal ventrite 1 without median carina. Mesoventral elevation narrowly laminar (Fig. 7E) Cycreon d'Orchymont Abdominal ventrite 1 carinate medially. Mesoventral elevation in form of a lamina or an elongate plate
19	Ventral face of meso- and metatibiae with dense, long pubescence. Ventral morphology similar to Figure 7F Pilocnema Hansen
-	Ventral face of meso- and metatibiae never densely pubescent, at most with sparse short setae. Ventral morphology similar to Figures 2, 3, and 8A, B
20	Mesoventral elevation laminar or forming an oval elongate plate; posterior part of the plate rounded or acute (as in Fig. 8A, B)
-	Mesoventral elevation elongate, but sharply cut off posteriorly, contacting metaventrite more or less in a straight line (as in Figs 2F, 8C)
21	Median portion of prosternum with a pair of transverse ridges partly delimiting prosternal process (Fig. 8A) Pseudocercyon d'Orchymont
- 22	Median portion of prosternum without such ridges, only simply carinate (Fig. 8B)
- 23 -	Mesoventral elevation elongate oval (as in Fig. 8C); if small lateral lobes are present, they are below the plate

* the status of *Gillisius* and Asian *Pelosoma* is unclear.



Figure 7. Ventral view of thorax of eastern Palaearctic and Oriental Megasternini. A. *Bolbonotum* sp. B. *Kahanga inconspicua*, holotype. C. *Australocyon* sp. (*A. pilocnemoides* group). D. *Nipponocercyon shibatai*. E. *Cycreon floricola*. F. *Pilocnema* sp.



Figure 8. Ventral view of thorax and additional diagnostic characters of eastern Palaearctic and Oriental genera of the Megasternini. A-C. Ventral view: A. *Pseudocercyon andrewesi*. B. *Cercyon* sp. C. *Gillisius madurensis*, holotype. D-H. Other characters: D. *Cryptopleurum coomani*, mentum. E. *Emmidolium excavatum*, pronotum. F. *Bolbonotum* sp., base of elytra. G. *Kahanga inconspic-ua*, holotype, base of elytra. H. *Australocyon* sp. (A. *pilocnemoides* group), hind femur.

New replacement name

Oreosternum nom. nov.

= Oreocyon Hebauer 2002a: 35 (not Marsh 1872: 406, not Krumbiegel 1949: 591).

Type species. Oreocyon frigidus Hebauer, 2002 (= Oreosternum frigidum comb. nov.)

Comments. While preparing the key, we noticed that the genus name *Oreocyon* is preoccupied by two older names: *Oreocyon* Marsh, 1872 (a fossil oxyaenid mammal, today a synonym of *Patriofelis* Leidy, 1872)

and *Oreocyon* Krumbiegel, 1949 (a genus of Canidae described based on fur remains, later renamed to *Dasycyon* Krumbiegel, 1953 due to homonymy and today considered as a synonym of *Canis* Linnaeus, 1758). To avoid the homonymy, we are here proposing a new replacement name *Oreosternum* nom. nov. for *Oreocyon* Hebauer, 2002. The new name combines the prefix *oreo*- referring to mountains as used in the original name, and the core *sternum*, referring to the expected close relationship of this genus to *Paroosternum* Scott, 1913 exhibited by the prosternal morphology (see the key above). The new name is gender neutral.

Table 1	List of Eastern	Palaearctic and	Oriental	general	of the l	Megasternini,	, with num	ber of	described	species an	id ref	erences	to
the mos	st important keys	or taxonomic tr	eatments										

Genus	Described species	Keys or original descriptions
Armostus	11	d'Orchymont 1942; Hebauer 2002a; Hoshina and Satô 2006
Australocyon	7	Hansen 2003; Fikáček et al. 2012
Bolbonotum	3	Hansen 1999a
Cercyon 148 Shatrovskiy 1992; Hansen 199		Shatrovskiy 1992; Hansen 1999b; Short and Hebauer 2006; Hoshina 2008; Jia et al.
		2011; 2019; Ryndevich et al. 2017; 2019; Ryndevich and Prokin 2017
Chimaerocyon	2	Fikáček et al. 2013
Cryptopleurum	7	d'Orchymont 1926; Jia and Zhang 2017
Cycreon	4 + 1 ssp.	Arriaga-Varela et al. 2018b
Emmidolium	1	Fikáček 2007
Gillisius	2	d'Orchymont 1925a; 1926
Himalcercyon	2	this paper
Kahanga	1	Hansen 1999a
Megasternum	4	Shatrovskiy 1989; Fikáček et al. 2012; Ryndevich 2017
Morastus	1	d'Orchymont; 1926
Nipponocercyon	3	Hoshina and Fikáček 2010; Fikáček et al. 2012; 2015a
Oosternum	9	Hebauer 2002a; Hoshina and Satô 2004b; 2005
Oreosternum	1	Hebauer 2002
Pachysternum	11	Fikáček et al. 2012
Pacrillum	5	Hoshina and Satô 2004a; Fikáček and Hebauer 2005; Shatrovskiy 1989 as Agnaeformia
Paroosternum	5	Hebauer 2006
Pelosoma	2	d'Orchymont 1925b; 1932
Peltocercyon	4	d'Orchymont 1925a; Hoshina 2016; 2018
Pilocnema	1	Hansen 2003
Pseudocercyon	1	d'Orchymont 1926

Discussion

The genus-level systematics of the tribe Megasternini are currently based on the traditionally understood genera, defined by characters of the prosternum and meso- and metaventrite, i.e. structures which are morphologically very diverse within the clade. Following this approach, it is possible to define small and morphologically rather uniform genera for roughly half of the known species. On the other hand, the remaining half of megasternine species (i.e. ca 270 species) is assigned to the genus Cercvon Leach, 1817 as they are rather uniform in ventral characters. Eleven subgenera are defined inside of Cercyon to facilitate the identification of species, some of which seem to truly group related species (e.g., Arcocercyon Hebauer, 2003, Paracycreon d'Orchymont, 1942), but others very likely grouping unrelated species sharing a single derived character (e.g., Acycreon d'Orchymont, 1942; see Arriaga-Varela et al. 2018b). Preliminary molecular analyses (Short and Fikáček 2013, Arriaga-Varela unpubl. data) clearly indicate that Cercyon as currently circumscribed is a polyphyletic genus which needs to be reclassified in the future. To facilitate future analyses, it is necessary to reexamine Cercyon species and define groups of morphologically similar and likely closely related species. Selected representatives of these groups should later be included in the phylogenetic analysis. To that end, this paper recognizes *Himalcercyon* as such a group. The phylogenetic position of this clade needs to be tested in future analyses.

Acknowledgements

We thank Dr Li-zhen Li, Dr Liang Tang, Mr Jia-yao Hu, Mr Xiao-bin Song (all Shanghai Normal University, China) for their kind help during the visit of the senior author and for the donation of type specimens to us. We are obliged to Max Barclay Christine Taylor (Natural History Museum, London, UK) and Pol Limbourg (Institute Royal des Sciences Naturelles, Brussels, Belgium) for allowing us to examine holotypes of Kahanga inconspicua and Gillisius madurensis whose SEMs we used in the key. We are indebted to B. Clarkson (Instituto Oswaldo Cruz - Fiocruz, Rio de Janeiro, Brazil), S.K. Ryndevich (Baranovichy State College, Baranovichy), A.E.Z. Short (University of Kansas, Lawrence, USA) and J.K. Liebherr (Cornell University, Ithaca, USA) for their comments and corrections of the early draft of this paper. This study was supported by National Natural Science Foundation of China (31772494) to F.-L. Jia and by the Ministry of Culture of the Czech Republic (DKRVO 2019-2023/5.I.b, National Museum, 00023272) to M. Fikáček.

References

Angus RB, Jia F-L, Chen Z-N, Zhang Y, Vondráček D, Fikáček M (2016) Taxonomy, larval morphology and cytogenetics of *Lihelophorus*, the Tibetan endemic subgenus of *Helophorus* (Coleoptera: Hydrophiloidea). Acta Entomologica Musei Natioalis Pragae 56 (1): 109–148.

- Arriaga-Varela E, Seidel M, Deler-Hernández A, Senderov V, Fikáček M (2017) A review of the *Cercyon* Leach (Coleoptera, Hydrophilidae, Sphaeridiinae) of the Greater Antilles. ZooKeys 681: 39–93. https://doi.org/10.3897/zookeys.681.12522
- Arriaga-Varela E, Seidel M, Fikáček M (2018a) A new genus of coprophagous water scavenger beetle from Africa (Coleoptera, Hydrophilidae, Sphaeridiinae, Megasternini) with a discussion on the *Cercyon* subgenus *Acycreon*. African Invertebrates 59 (1): 1–23. https:// doi.org/10.3897/AfrInvertebr.59.14621
- Arriaga-Varela E, Wong SY, Kirejtshuk A, Fikáček M (2018b) Review of the flower-inhabiting water scavenger beetle genus *Cycreon* (Coleoptera, Hydrophilidae), with descriptions of new species and comments on its biology. Deutsche Entomologische Zeitschrift 65: 99–115. https://doi.org/10.3897/dez.65.26261
- Deler-Hernández A, Cala-Riquelme F, Fikáček M (2014) A review of the genus *Oosternum* Sharp of the West Indies (Coleoptera: Hydrophilidae: Sphaeridiinae). Deutsche Entomologische Zeitschrift 61(1): 43–63. https://doi.org/10.3897/dez.61.7566
- Deng T, Wu FX, Zhou ZK, Su T (2020) Tibetan Plateau: an evolutionary junction for the history of modern biodiversity. Science China Earth Sciences 63: 172–787. https://doi.org/10.1007/s11430-019-9507-5
- d'Orchymont A (1925a) Contribution à l'étude des hydrophilides III. Bulletin et Annales de la Société Entomologique de Belgique 65: 261–295.
- d'Orchymont A (1925b) Contribution à l'étude des hydrophilides IV. Bulletin et Annales de la Société Entomologique de Belgique 65: 298–305.
- d'Orchymont A (1926) Contribution à l'étude des hydrophilides VI. Bulletin et Annales de la Société Entomologique de Belgique 66: 201–248.
- d'Orchymont A (1932) Zur Kenntnis der Kolbenwasserkäfer (Palpicornia) von Sumatra, Java und Bali. Archiv für Hydrobiologie, Supplement Band XI (Tropische Binnengewässer II): 623–714. [pls XIV–XVII]
- d'Orchymont A (1937) Contribution à l'étude des Palpicornia IX. Bulletin et Annales de la Société Entomologique de Belgique 77: 213–255.
- d'Orchymont A (1942) Palpicornia (Coleoptera). Notes diverses et espèces nouvelles. III. Bulletin du Musée Royal d'Histoire Naturelle de Belgique 18(26): 1–20.
- Fikáček M (2007) Emmidolium excavatum Orchymont (Coleoptera: Hydrophilidae: Sphaeridiinae) confirmed in Africa and the Arabian Peninsula. Acta Entomologica Musei Nationalis Pragae 47: 117–122.
- Fikáček M, Hebauer F (2005) A new aberrant species of the genus Pacrillum from Nepal (Hydrophilidae: Sphaeridiinae: Megasternini). Acta Entomologica Musei Nationalis Pragae 45: 59–64.
- Fikáček M, Rocchi S (2013) Cercyon hungaricus, a new junior subjective synonym of C. bononiensis (Coleoptera: Hydrophilidae). Zootaxa 3616(1): 95–98. https://doi.org/10.11646/zootaxa.3616.1.8
- Fikáček M, Jia F-L, Prokin A (2012a) A review of the Asian species of the genus *Pachysternum* (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3219(1): 1–53. https://doi.org/10.11646/zootaxa.3219.1.1
- Fikáček M, Ryndevich S, Jia F (2012b) An aberrant species of Nipponocercyon from Sichuan, China (Coleoptera, Hydrophilidae, Sphaeridiinae). ZooKeys 214: 13–27. https://doi.org/10.3897/zookeys.214.3437
- Fikáček M, Maruyama M, Vondráček D, Short AEZ (2013) Chimaerocyon gen. nov., a morphologically aberrant myrmecophilous genus of water scavenger beetle (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3716(2): 277–288. https://doi.org/10.11646/zootaxa.3716.2.8
- Fikáček M, Angus RB, Gentili E, Jia F, Minoshima, YN, Prokin A, Przewozny M, Ryndevich SK (2015a) Helophoridae, Hydrochidae, Hydrophilidae. In: Löbl I, Löbl D (Eds) Catalogue of Palaearctic Coleoptera (Vol. 2). Brill, Leiden/Boston, 25–76.

- Fikáček M, Jia F-L, Ryndevich S (2015b) A new aberrant species of *Nipponocercyon* from the mountains of southeastern China (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3904(4): 572–580. https://doi.org/10.11646/zootaxa.3904.4.6
- Hansen M (1989) New genera of Sphaeridiinae (Coleoptera: Hydrophilidae). Entomologica Scandinavica 20: 251–262. https://doi. org/10.1163/187631289X00320
- Hansen M (1990) Australian Sphaeridiinae (Coleoptera: Hydrophilidae): a taxonomic outline with descriptions of new genera and species. Invertebrate Taxonomy 4: 317–395. https://doi.org/10.1071/IT9900317
- Hansen M (1991) The hydrophiloid beetles. Phylogeny, classification and a revision of the genera (Coleoptera: Hydrophiloidea). Biologiske Skrifter 40: 1–367.
- Hansen M (1999a) Fifteen new genera of Hydrophilidae (Coleoptera), with remarks on the generic classification of the family. Entomologica Scandinavica 30: 121–172. https://doi. org/10.1163/187631200X00228
- Hansen M (1999b) Hydrophiloidea (s.str.) (Coleoptera). World catalogue of insects Volume 2: Hydrophiloidea (Coleoptera). Apollo Books, Stenstrup, 416 pp.
- Hansen M (2003) Discovery of Australocyon Hansen and Pilocnema Hansen (Coleoptera, Hydrophilidae) outside the Australian region. In: Cuccodoro G, Leschen RAB (Eds) Systematics of Coleoptera: papers celebrating the retirement of Ivan Löbl. Memoirs of Entomology International Associate Publisher 17: 53–84.
- Hebauer F (2002a) Hydrophilidae of northern India and southern Himalaya (Coleoptera: Hydrophilidae). Acta Coleopterologica 18(1): 3–72.
- Hebauer F (2002b) New Hydrophilidae of the Old World (Coleoptera: Hydrophilidae). Acta Coleopterologica 18(3): 3–24.
- Hebauer F (2003) Review of the Malgassic Cercyon, with description of new species and a new genus (Coleoptera: Hydrophilidae). Acta Coleopterologica 19(2): 5–26.
- Hebauer F (2006) Revision of the genus *Paroosternum* Scott, 1913 (Coleoptera: Hydrophilidae: Sphaeridiinae). Acta Coleopterologica 22(2): 38–58.
- Hoshina H (2008) A new species of the genus *Cercyon* (Coleoptera: Hydrophilidae) from Fukui Pref., Japan. Memoirs of the Research and Education Center for Regional Environment, University of Fukui 15: 1–7.
- Hoshina H (2016) Taxonomic report of the genus *Peltocercyon* (Coleoptera: Hydrophilidae: Sphaeridiinae). Japanese Journal of Systematic Entomology 22(1): 131–133.
- Hoshina H (2018) Discovery of second Japanese species of the genus *Peltocercyon* (Coleoptera: Hydrophilidae: Sphaeridinae) with description of a new species. Japanese Journal of Systematic Entomology 24(2): 293–295.
- Hoshina H, Fikáček M (2010) Morphological study and taxonomic revision of the genus *Nipponocercyon* (Coleoptera: Hydrophilidae: Sphaeridiinae). Acta Entomologica Musei Nationalis Pragae 50: 117–130.
- Hoshina H, Satô M (2004a) First record of the genus *Pacrillum* (Coleoptera: Hydrophilidae) from Japan, with a redescription of *P. manchuricum*. The Entomological Review of Japan 59: 233–239.
- Hoshina H, Satô M (2004b) Two new species of the genus *Oosternum* (Coleoptera: Hydrophilidae) from Japan. Memoirs of the Research and Education Center for Regional Environment, University of Fukui 11: 9–15.
- Hoshina H, Satô M (2005) Taxonomic notes of the genus *Oosternum* (Coleoptera: Hydrophilidae) from Japan. Memoirs of the Research

and Education Center for Regional Environment Fukui University 12: 1–9.

- Hoshina H, Satô M (2006) A taxonomic study of the genus Armostus (Coleoptera: Hydrophilidae) from Japan. The Coleopterists Bulletin 60: 95–104. https://doi.org/10.1649/840.1
- Huang XL, Lei FM, Qiao GX (2007) Areas of endemism and patterns of diversity for aphids of the Qinghai-Tibetan Plateau and the Himalayas. Journal of Biogeography 35: 230–240. https://doi.org/10.1111/ j.1365-2699.2007.01776.x
- Jia F-L, Fikáček M, Ryndevich SK (2011) Taxonomic notes on Chinsese *Cercyon*: description of a new species, new synonyms, and additional faunistic records (Coleoptera: Hydrophilidae: Sphaeridiinae). Zootaxa 3090: 41–56. https://doi.org/10.11646/zootaxa.3090.1.3
- Jia F-L, Zhang R-J (2017) A review of the genus *Cryptopleurum* from China (Coleoptera: Hydrophilidae). Acta Entomologica Musei Nationalis Pragae 57(2): 577–592. https://doi.org/10.1515/aemnp-2017-0090
- Jia F, Liang Z, Ryndevich SK, Fikáček M (2019) Two new species and additional faunistic records of *Cercyon* Leach, 1817 from China (Coleoptera: Hydrophilidae). Zootaxa 4565: 501–514. https://doi. org/10.11646/zootaxa.4565.4.4
- Krumbiegel I (1949) Der Andenwolf: ein neuentdecktes Grosstier. Umschau in Wissenschaft und Technik 49: 590–591.
- Makhan D (2013) Sacosternum amrishi sp. nov. the first species of the genus from Suriname (Hydrophilidae: Sphaeridiinae: Megasternini). Calodema 254: 1–4.
- Marsh OC (1872) Note on a new genus of carnivores from the Tertiary of Wyoming. American Journal of Science and Art (Series 3) 4(19–24): 1–406. https://doi.org/10.2475/ajs.s3-4.21.202
- Procheş Ş, Ramdhani S (2012) The world's zoogeographical regions confirmed by cross-taxon analyses. BioScience 62(3): 260–270. https://doi.org/10.1525/bio.2012.62.3.7
- Ryndevich SK (2011) New data on Holarctic and Oriental Spercheidae and Hydrophiloidae (Coleoptera: Hydrophiloidea). Euroasian Entomological Journal 10(3): 337–340.
- Ryndevich SK (2017) New faunistic records of hydrophilid beetles (Coleoptera: Hydrophiloidea: Hydrophilidae) from Eurasia. BarSU Herald. Series of Biological Sciences (General Biology), Agricultural Sciences (Agronomy) 5: 65–70.
- Ryndevich SK, Jia F-L, Fikáček M (2017) A review of the Asian species of the *Cercyon unipunctatus* group (Coleoptera: Hydrophilidae: Sphaeridiinae). Acta Entomologica Musei Nationalis Pragae 57(2): 535–576. https://doi.org/10.1515/aemnp-2017-0089

- Ryndevich SK, Prokin AA (2017) Two new species of *Cercyon (Clinoc-ercyon)* from Russian Far East (Coleoptera: Hydrophilidae). Zoo-taxa 4300(1): 125–134. https://doi.org/10.11646/zootaxa.4300.1.7
- Ryndevich SK, Hoshina H, Prokin AA (2019) Review of species of the genus *Cercyon* of Russia and adjacent regions. VI. Subgenus *Cercyon*, the *C. shinanensis* group (Coleoptera: Hydrophilidae). Zoosystematica Rossica 28(2): 258–266. https://doi.org/10.31610/ zsr/2019.28.2.258
- Shatrovskiy AG (1989) 12. Sem. Hydrophilidae Vodolyubi. [12. Fam. Hydrophilidae – Water scavenger beetles]. In: Ler PA (Ed.) Opredelitel' Nasekomykh Dal' Nego Vostoka SSSR v Shesti Tomakh. Tom 3. Zhestkokrylye, ili zhuky. Chast 1. [Keys to the insects of the Far East of the USSR in six volumes (Vol. 3). Coleoptera or beetles. Part 1]. Nauka, Leningrad, 264–293. [in Russian]
- Shatrovskiy AG (1992) New and little known Hydrophiloidea (Coleoptera) from Southern Primorye territory and adjacent regions. Entomological Review 71(2): 359–371.
- Shatrovskiy AG (1999) New species of asian hydriphilids of genus *Cercyon* Leach (Coleoptera: Hydrophilidae) collected on expeditions of great Russian travelers. Izvestiyu Kharkovskogo entomologicheskogo obshchestva 7(1): 5–7.
- Shatrovskiy AG (2017) A new species of *Cycreon* d'Orchymont, 1919 from Singapore (Coleoptera: Hydrophilidae: Megasternini). Zootaxa 4317(3): 588–592. https://doi.org/10.11646/zootaxa.4317.3.11
- Short AEZ, Fikáček M (2011) World catalogue of the Hydrophiloidea (Coleoptera): additions and corrections II (2006–2010). Acta Entomologica Musei Nationalis Pragae 51(1): 83–122.
- Short AEZ, Fikáček M (2013) Molecular phylogeny, evolution and classification of the Hydrophilidae (Coleoptera). Systematic Entomology 38: 723–752. https://doi.org/10.1111/syen.12024
- Short AEZ, Hebauer F (2006) World catalogue of the Hydrophiloidea – additions and corrections, 1 (1999–2005). Koleopterologische Rundschau 76: 315–359.
- Smetana A (1978) Revision of the subfamily Sphaeridiinae of America north of Mexico (Coleoptera: Hydrophilidae). Memoirs of the Entomological Society of Canada 105: 1–292. https://doi.org/10.4039/ entm110105fv
- Szczepański WT, Vondráček D, Seidel M, Wardhaugh C, Fikáček M (2018) High diversity of *Cetiocyon* beetles (Coleoptera: Hydrophilidae) along an elevational gradient on Mt. Wilhelm, New Guinea, with new records from the Bird's Head Peninsula. Arthropod Systematics and Phylogeny 76: 323–347.

<u> PENSOFT</u>,



A comparative description of the mesosomal musculature in Sphecidae and Ampulicidae (Hymenoptera, Apoidea) using 3D techniques

Maraike Willsch¹, Frank Friedrich², Daniel Baum³, Ivo Jurisch¹, Michael Ohl¹

1 Museum für Naturkunde Berlin, Invalidenstraße 43, 10115 Berlin, Germany

2 Institut für Zoologie, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

3 Zuse Institute Berlin, Takustraße 7, 14195 Berlin, Germany

http://zoobank.org/94793352-7C43-496C-83D1-A10A355BC801

Corresponding author: Maraike Willsch (maraike.willsch@mfn.berlin)

Academic editor: D. Zimmermann • Received 17 December 2019 • Accepted 1 April 2020 • Published 11 May 2020

Abstract

Conflicting hypotheses about the relationships among the major lineages of aculeate Hymenoptera clearly show the necessity of detailed comparative morphological studies. Using micro-computed tomography and 3D reconstructions, the skeletal musculature of the meso- and metathorax and the first and second abdominal segment in Apoidea are described. Females of *Sceliphron destillatorium, Sphex (Fernaldina) lucae* (both Sphecidae), and *Ampulex compressa* (Ampulicidae) were examined. The morphological terminology provided by the Hymenoptera Anatomy Ontology is used. Up to 42 muscles were found. The three species differ in certain numerical and structural aspects. Ampulicidae differs significantly from Sphecidae in the metathorax and the anterior abdomen. The metapleural apodeme and paracoxal ridge are weakly developed in Ampulicidae, which affect some muscular structures. Furthermore, the muscles that insert on the coxae and trochanters are broader and longer in Ampulicidae. A conspicuous characteristic of Sphecidae is the absence of the metaphragma. Overall, we identified four hitherto unrecognized muscles. Our work suggests additional investigations on structures discussed in this paper.

Key Words

Aculeata, anatomy, microCT, phylogeny, propodeum, thorax

Introduction

Hymenoptera form one of the largest insect orders and comprise more than 150,000 extant species (Aguiar et al. 2013). The group of interest examined in this paper constitutes a subclade of Hymenoptera, the Aculeata (stinging wasps, bees, and ants; Sharkey et al. 2012). Derived from the modified ovipositor, the stinger is a synapomorphy of aculeate Hymenoptera and a key innovation for their evolutionary success (Sharkey et al. 2012; Schmidt 2016). The nature of phylogenetic relationships within the monophyletic Aculeata is still contested (e.g., Königsmann 1978; Lomholdt 1982; Rasnitsyn 1988; Alexander 1992; Brothers and Carpenter 1993; Ronquist et al. 1999; Peters et al. 2011, 2017; Sharkey et al. 2012; Johnson et al. 2013; Branstetter et al. 2017). Traditionally, Aculeata is divided into three lineages: Chrysidoidea, Vespoidea, and Apoidea (O'Neill 2001; Branstetter et al. 2017).

About 10,000 species of digger wasps (also named apoid wasps) as part of the species-rich superfamily Apoidea are currently known (Pulawski 2020). The most obvious synapomorphy of Apoidea is the rounded pronotal lobe (Ohl and Engel 2007). Apoidea is divided into the monophyletic Anthophila (bees) and the paraphyletic apoid wasps. The latter comprises Ampulicidae, Crabronidae, Heterogynaidae, and Sphecidae (e.g., Branstetter et al. 2017). Recent phylogenomic and molecular analyses suggest Ampulicidae is the sister to the rest of the Apoidea (Debevec et al. 2012 [ribosomal 28S and protein-coding nuclear genes]; Sann et al. 2018 [target DNA enrichment and transcriptomic sequence data]). However, contradictory evidence on the phylogenetic rela-

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

tionships within the apoid wasps (e.g., Lohrmann et al. 2008; Ohl and Spahn 2010; Debevec et al. 2012; Sharkey et al. 2012; Branstetter et al. 2017) remains unresolved. Based upon different research methods, most results suggest, that Sphecidae and Ampulicidae are well-supported clades (Ohl and Spahn 2010 [morphological study]; Branstetter et al. 2017 [ultraconserved element phylogenomics]; Peters et al. 2017 [protein-coding genes]), whereas Crabronidae are likely to be paraphyletic (Lohrmann et al. 2008 [nuclear long-wavelength-opsin and mitochondrial cytochrome-c-oxidase]; Debevec et al. 2012; Branstetter et al. 2017; Peters et al. 2017). However, Sann et al. (2018) found Crabronidae to be polyphyletic. Another unresolved issue is the position of Heterogynaidae within Apoidea (Ohl and Bleidorn 2006). Debevec et al. (2012) obtained two different results: Heterogynaidae nested within Crabronidae (maximum likelihood tree) and as sister to a monophyletic group of Sphecidae sensu stricto, Crabronidae and Anthophila (Bayesian tree). The first result was already proposed by Ohl and Bleidorn (2006 [long-wavelength opsin]). Branstetter et al. (2017) found Heterogynaidae to be sister to a grouping of paraphyletic Crabroninae and Sphecidae.

Morphological characters are still one of the major sources of phylogenetic inference (e.g., Friedrich and Beutel 2010; Ohl and Spahn 2010; Vilhelmsen et al. 2010; Zimmermann and Vilhelmsen 2016; Liu et al. 2019). Nevertheless, internal mesosomal structures are insufficiently studied across Hymenoptera, as predicated by Vilhelmsen et al. (2010), who provided detailed information for many apocritan wasps and other Hymenoptera; especially the mesosomal musculature of Pison chilense (Crabronidae) and external mesosomal characters for Pison chilense, Stangeella cyaniventris (Sphecidae), and Ampulex compressa (Ampulicidae) are described. They demonstrated, that the mesosomal region reveals considerable information for phylogenetic research. Previously, indispensable work about the mesosomal musculature in Hymenoptera was presented by Maki (1938), Snodgrass (1942; in particular, for Apis), Heraty (1989), and Matsuda (1970), followed by Prentice (1998). Recent substantial work was accomplished by Mikó et al. (2007). They dissected the musculature of the head and mesosoma in a review of the parasitic wasp family Scelionidae. Furthermore, a reinterpretation of the delimitation of the metapostnotum in Chrysidoidea was presented by Kawada et al. (2015). Moreover, Porto et al. (2016) defined internal mesosomal characters of bees and evaluated the potential of these structures, concluding that they are of great value to phylogenetic investigations. Garcia et al. (2017) described several body parts of three new species of the rare ant genus Zasphinctus, resulting in a comparative character matrix for species-level taxonomy. Subsequently, Liu et al. (2019) provided insights on the mesosoma of an ant worker of Myrmecia for comparisons with other Aculeata and to gain new information about evolution and body function.

A state-of-the-art method for morphological analyses is the three-dimensional imaging, using micro-computed tomography (microCT). It is a highly powerful technique (Faulwetter et al. 2013 and references therein; Garcia et al. 2017; Liu et al. 2019), as it makes internal structures visible without destroying the specimen. Moreover, the digital 3D models can be created repeatedly to work on different goals and the data can easily be shared worldwide.

By using 3D imaging, we aim to expand the basic morphological knowledge for phylogenetic investigations within Aculeata. In this paper we present data of muscular structures in the mesosoma of Sceliphron destillatorium (Illiger, 1807), Sphex (Fernaldina) lucae de Saussure, 1867 (both Sphecidae), and Ampulex compressa (Fabricius, 1781) (Ampulicidae) (Fig. 1). These wasps are solitary and nest-provisioning predators with different lifestyles (e.g., Williams 1942; Bohart and Menke 1976; Fouad et al. 1994; Haspel and Libersat 2003; Libersat 2003; Ohl and Spahn 2010). Both families were selected for their large number of plesiomorphic characters within digger wasps (Ohl and Spahn 2010), which might help to reconstruct the ancestral apoid anatomy. Primarily, we illustrate and describe mesosomal conformations of the skeletal musculature, with focus on the mesothorax, metathorax, and the first abdominal segment (propodeum). We also describe muscles that originate in the mesosoma and insert in the second abdominal segment (metasoma) because of strong interrelations of these muscles in this transition zone between both tagmata. The wasp waist allows for increased movability of the abdomen and, therefore, is an important anatomical cluster for various physical activities requiring precise movements of the abdomen below the body. This includes, for instance, stinging prey or enemies for defence, laying eggs (Williams 1942; Bohart and Menke 1976), carrying prey between mid or hind legs and abdomen while in flight, dragging prey forwards or backwards (Bohart and Menke 1976), and increasing balance in flight (at least when the second abdominal segment is petiolate; Bohart and Menke 1976).

Material and methods

Specimens and body parts examined

Sphex and Ampulex were taken from the collection of the Museum für Naturkunde Berlin (MfN) and Sceliphron was collected in the field (Table 1). To examine and compare the muscle sets, specimens of the same sex (females) were selected. We analysed the musculature of the mesothorax, metathorax, and the first and second abdominal segments.

Preparation, microCT, and 3D reconstruction

The extremities of the specimens were removed to minimize the scan field for optimizing the resolution of the data sets. Furthermore, the tip of the gaster was removed to facilitate the infiltration of the iodine, which intensifies the visibility of the musculature in the scan. Following Metscher (2009) and Gignac et al. (2016), our specimens were contrasted in a 25% iodine solution in pure ethanol



Figure 1. Portraits of the three specimens examined, lateral view. A. Sceliphron destillatorium, body size 20 mm; B. Sphex (Fernaldina) lucae, body size 18 mm; C. Ampulex compressa, body size 21 mm.

Table 1. Basic information about the specimen collection, classification, preparation, and settings for microCT scanning.

Specimens	Sceliphron destillatorium	Sphex (Fernaldina) lucae	Ampulex compressa
MfN collection number	MfN_Hym_Sph_I004239	MfN_Hym_Sph_I000635	MfN_Hym_Amp_I000029
Location/label data	GREECE, Crete, Afrata [little road],	USA, New Mexico, Hidalgo Co.,	GERMANY, Berlin, MfN breed,
	35°34'38.31"N, 23°4'2.3"E	Gray Ranch, 20.6 mi S Ammas	Oviposition 6 Aug. 2015, Eclosion 27
			Sept. 2015
Date of collection	24 June 2015	28 Aug. 2003	28 Sept. 2015
Leg.	M. Willsch	S. Schiller, I. Richert	L. Kirschey
Det.	M. Willsch 2015	M. Ohl 2004	L. Kirschey 2015
Family	Sphecidae	Sphecidae	Ampulicidae
Sex	Female	Female	Female
Body size (mm)	20	18	21
Storage	96% ethanol	96% ethanol	96% ethanol
Sample preparation	25% Iodine staining, critical point	25% Iodine staining, critical point	25% Iodine staining, critical point
	drying	drying	drying
Scanning medium	Air	Air	Air
Voltage (kV)	48	48	50
Current (µA)	250	250	275
Number of images	1000	1000	1440
Rotation steps	0.36	0.36	0.25
Exposure time (ms)	1000	1000	1000
Resolution (µm/pixel)	3.40	4.69	5.00

(100%) for three days and washed out with pure ethanol for 30 seconds. The wasps were dried using a critical point dryer (Leica EM CPD300; Table 1). Afterwards, the three specimens were scanned at the Visualisation Laboratory of the MfN using a Phoenix nanotom X-ray|s tube (General Electric) at 48–50 kV and 250–275 μ A. At 1 second per image 1000–1440 projections were generated per scan. The different kV- and projection-settings depended on the respective specimen size, which was also responsible for the range of the effective voxel size between 3.4–5 μ m (Table 1). The cone beam reconstruction was performed using the CT reconstruction software PHOENIX|X-RAY DATOS|X version 2.0 (GE Sensing & Inspection Technologies GmbH).

3D segmentation and post-processing

The raw microCT image data were visualised and analysed by using a Wacom Cintiq 22HD interactive pen display and the software AMIRA ZIB EDITION 2020.02 and former versions (provided by the Zuse Institute Berlin). All muscles were segmented and labelled manually by using appropriate segmentation tools in AMIRA. Segmented materials were transformed into high-resolution surfaces using the Isosurface-Tool in AMIRA. The reconstruction was accomplished for one body side of the specimens, as no structural asymmetries were observed in this region. Therefore, the number of muscles given in the results refers to one-half of the body. For post-editing (e.g., picture artefacts, file size reduction, file converting, figure compilation) we exported TIF-files from AMIRA into ADOBE PHOTOSHOP CS6.

Terminology

Skeletal musculature was categorised based on insertion sites. The muscle terminology of the Hymenoptera Anatomy Ontology (HAO; http://portal.hymao.org/projects/32/ public/ontology/) (Mikó et al. 2007; Vilhelmsen et al. 2010; Yoder et al. 2010; Seltmann et al. 2012) has been adopted here. In this connection, we provide a list of Universal Resource Identifiers (URI) for each muscular and cuticular term (Suppl. material 1: Table S1). It was created by using the "analyze" tool on the HAO website. Newly 54

detected muscles, not listed in the HAO so far or found in other literature, were also named in the HAO-scheme by the areas of origin and insertion with additional topographical orientation, if required (Table 2). The abbreviations used for the designation of muscles and sclerite structures are composed of the basic terms as follows:

Region of origin and insertion:

3ax2	third axillary sclerite of fore wing
3ax3	third axillary sclerite of hind wing
ba	basalare
cx	coxa
fu	furca
ism	intersegmental membrane
occ	occlusor
pc	pectus
ph	phragma
pl	pleuron
S	sternum
S	thoracal sternum
sa	subalare
sp	spiracle
T1	first abdominal tergite/propodeum
T2	second abdominal tergite
tr	trochanter

Divided thorax:

- 2 located on the mesothorax
- 3 located on the metathorax

Positions:

a	ante	erio
	1	1

- d dorsal I lateral
- **m** medial
- p posterior
- p posterio v ventral

Order; mostly stated for functional groups of muscles:

a or 1	first
b or 2	second
c or 3	third

Descriptions, that involve the meso- and metafurca, are based on the terminology of Porto et al. (2016). The descriptions in the results were ordered by the point of insertion from mesosoma towards metasoma and by relevant functional groups, if possible (Table 2). In this comparative work, *Sceliphron destillatorium* serves as reference species (Fig. 2). In addition, a homologisation with the generalised nomenclature for the thoracic musculature of Neoptera following Friedrich and Beutel (2008) is presented in Table 2.

Data availability

The large image data sets accomplished for this study are available online as a data publication in conjunction with this paper. Thus, our images and raw data are freely accessible via the MfN data repository (Willsch 2019; https://doi.org/10.7479/dft0-yy6m). Moreover, images will be available on the HAO portal (http://portal.hymao.org).

Results

We found 42 muscle pairs within the analysed tagmata of the three species (Table 2). There are 37 muscles in *Sceliphron* (mesothorax 18, metathorax 14, first and second abdominal segments 5), 39 in *Ampulex* (mesothorax 19, metathorax 16, first and second abdominal segments 4), and 40 muscles in *Sphex* (mesothorax 20, metathorax 15, first and second abdominal segments 5). The following description of the skeletal musculature in *Sceliphron* serves as structural basis. Subsequently, comparative descriptions of differing muscles in *Sphex* and *Ampulex* are given. Each muscle absent in one or two of the compared species examined is mentioned below (see also Table 2):

Sceliphron destillatorium (Illiger, 1807)

Mesothorax. Ventral mesofurco-profurcal muscle (fu2-fu1v; Fig. 3A) arises ventromedially from the mesofurcal bridge, then runs horizontal and inserts ventrally on the base of the profurca. First mesopleuro-mesonotal muscle (pl2-t2a; Fig. 3B) arises from the mesopectus and inserts on the mesoscutum. The muscle expands vertically and is the second largest muscle in the mesothorax. Mesopleuro-mesobasalar muscle (pl2-ba2; Fig. 3C) arises anteroventrally from the mesopleuron, fuses with ism1,2-ba2, and inserts on the mesobasalare anterior to the pleural wing articulation. Anterior thoracic spiracle occlusor muscle (splocc; Fig. 3C) arises proximally of the intersegmental membrane anteromedial to ism1,2-ba2, runs obliquely, and inserts posteriorly on the anterior thoracic spiracle. Externally, the spiracle is covered by the pronotal lobe. Intersegmental membrane-mesobasalar muscle (ism1,2-ba2; Fig. 3C) arises from both the intersegmental membrane between the pronotum and mesopectus, and from the mesopleuron, and inserts on the mesobasalare after fusing with pl2-ba2. First mesopleuro-third axillary sclerite of fore wing muscle (pl2-3ax2a; Fig. 3D) arises anterodorsally from the mesopleuron and inserts on the third axillary sclerite of the fore wing; it is short and fan-shaped. Second mesopleuro-third axillary sclerite of fore wing muscle (pl2-3ax2b; Fig. 3D) arises anterolaterally from the mesopleuron. This vertical, fan-shaped muscle is situated ventral to pl2-3ax2a and inserts on the third axillary sclerite of the fore wing. Third mesopleuro-third axillary sclerite of fore wing muscle (pl2-3ax2c; Fig. 3D) arises



Figure 2. Volume rendering of the mesosomal exoskeleton of *Sceliphron destillatorium*, anterior to the left. A. Dorsal surface view;
B. Lateral surface view; C. Ventral surface view. Abbreviations: N11 – pronotal lobe, N3 – metanotum, cx1 – procoxa, cx2 – mesocoxa, cx3 – metacoxa, pl2 – mesopleuron, pl3 – metapleuron, tr2 – mesotrochanter, S1 – prosternum, S2 – mesosternum, S3 – metasternum, scl2 – mesoscutellum, T1 – propodeum, tg – tegula. Scale bars: 0.9 mm (A, B), 1 mm (C).



Figure 3. Sceliphron destillatorium, volume rendering, mesosomal musculature, A-C: medial view, anterior to the right, D: lateral view, anterior to the left. A. Muscles discernible from the centre; B. Muscles positioned sublateral; C. Muscles located sublateral and lateral; D. Laterally positioned muscles. Abbreviations: fu2-fu1v - ventral mesofurco-profurcal; pl2-t2a - first mesopleuro-mesonotal; pl2-ba2 - mesopleuro-mesobasalar; splocc - anterior thoracic spiracle occlusor; ism1,2-ba2 - intersegmental membrane-mesobasalar; pl2-3ax2a - first mesopleuro-third axillary sclerite of fore wing; pl2-3ax2b - second mesopleuro-third axillary sclerite of fore wing; pl2-3ax2c - third mesopleuro-third axillary sclerite of fore wing; pl2-t2b - second mesopleuro-mesonotal; cx2-sa2 - mesocoxo-mesosubalar; fu2a-ph2 - anterior mesofurco-mesolaterophragmal; pl2a-fu2 - anterior mesopleuro-mesofurcal; pl2-cx2 - mesopleuro-mesocoxal; s2-cx2 - mesosterno-mesocoxal; fu2-cx2 - mesofurco-mesocoxal; fu2l-tr2 - lateral mesofurco-mesotrochanteral; fu2m-tr2 - median mesofurco-mesotrochanteral; ph1-ph2 - prophragmo-mesophragmal; pl3a-ba3 - anterior metapleuro-metabasalar; t2p-t3 - posterior mesonoto-metanotal; pl3la-t3 - anterolateral metapleuro-metanotal; pl3d-3ax3 - dorsal metapleuro-third axillary sclerite of hind wing; pl3-sa3 - metapleuro-metasubalar; cx3-sa3 - metacoxo-metasubalar; pl3m-cx3 - median metapleuro-metacoxal; fu3l-cx3 - lateral metafurco-metacoxal; fu3m-cx3 - median metafurco-metacoxal; pl3l-cx3 - lateral metapleuro-metacoxal; fu3-tr3 - metafurco-metatrochanteral; pl3-tr3 - metapleuro-metatrochanteral; ph2m-ph3 – median mesophragmo-metaphragmal; ph3-T2 – metaphragmo-second abdominal tergal; T1-S2 – propodeo-second abdominal sternal; fu3-S2 - metafurco-second abdominal sternal; s3-S2 - metasterno-second abdominal sternal. Scale bars: 0.8 mm (A–C), 0.9 mm (D).

Table 2. Terminology of the thoracic and abdominal musculature of all specimens examined. Origination and insertion are described on the basis of *Sceliphron*. If a muscle is absent in *Sceliphron*, the description refers to *Sphex* or *Ampulex*, respectively, if absent in *Sphex*. The list is sorted caudad (from thorax towards abdomen) by insertions of the muscles and by assumed functional groups. X = muscle present; - = muscle absent; ? = uncertain homology. A homologisation with the generalised nomenclature for neopteran thoracic muscles of Friedrich and Beutel (2008) is presented.

Abbreviation	Name of muscle	Origin	Insertion	Sceliphron	Sphex	Ampulex	Neoptera
				destillatorium	lucae	compressa	terminology
Mesothorax		C 11 1	C	37	37	37	117
<u>12-12 +2-</u>	Ventral mesofurco-profurcal	mesofurcal bridge	profurca	X	X 	X	IVIm /
$\frac{pl2-t2a}{rl2-t-2}$	first mesopleuro-mesonotal	mesopectus	mesoscutum	X	X 	X	IIdVm1
<u>p12-ba2</u>	mesopleuro-mesobasalar	mesopleuron	mesobasalare	X	X 	X	IIspm1
sproce	occlusor	membrane	spiracle	Λ	А	А	_
ism1,2-ba2	intersegmental membrane- mesobasalar	intersegmental membrane, mesopleuron	mesobasalare	Х	Х	X	IIppm2
pl2-3ax2a	first mesopleuro-third axillary sclerite of fore wing	mesopleuron	third axillary sclerite of fore wing	Х	Х	X	IItpm7
pl2-3ax2b	second mesopleuro-third axillary sclerite of fore wing	mesopleuron	third axillary sclerite of fore wing	Х	Х	X	IItpm9
pl2-3ax2c	third mesopleuro-third axillary sclerite of fore wing	mesopleuron	third axillary sclerite of fore wing	Х	Х	X	IItpm9
pl2-t2b	second mesopleuro-mesonotal	mesopleuron	lateral axillar area of mesonotum	Х	Х	X	IItpm5
cx2-sa2	mesocoxo-mesosubalar	mesocoxa	mesosubalare	Х	Х	X	IIdvm6
fu2a-ph2	anterior mesofurco- mesolaterophragmal	mesofurcal arm	mesolaterophragma	Х	Х	X	IIdvm8
sp3occ	posterior thoracic spiracle occlusor	mesofurcal arm	posterior thoracic spiracle	_	Х	Х	_
pl2a-fu2	anterior mesopleuro- mesofurcal	mesopleuron, mesepimeral ridge	mesofurcal arm	Х	Х	X	IIspm2
pl2-cx2	mesopleuro-mesocoxal	mesopleuron	mesocoxa (anterolateral)	Х	Х	X	IIpcm4
pl2-cx2b*	second mesopleuro-mesocoxal	mesopleuron, mesopleural spiracle apodeme	mesocoxa (dorsolateral)	_	Х	X ^d	IIpcm4?
s2-cx2	mesosterno-mesocoxal	mesodiscrimenal lamella, mesopectus	mesocoxa (anterolateral)	Х	Х	Х	IIscm3
fu2-cx2	mesofurco-mesocoxal	mesodiscrimenal lamella	mesocoxa (anteromedial)	Х	Х	X	IIscm2
fu2l-tr2	lateral mesofurco- mesotrochanteral	mesopleuron, mesofurcal arm	mesotrochanteral apodeme (lateral)	Х	X ^d	-	IIscm6
fu2m-tr2	median mesofurco- mesotrochanteral	mesofurcal arm	mesotrochanteral apodeme (lateral)	Х	Х	X ^d	IIscm6
ph1-ph2	prophragmo-mesophragmal	prophragma	mesophragma	X	Х	X	IIdlm1
Number of me	sothoracic muscles (max. 20):	110	1 0	18	20	19	
Metathorax				_			
pl3a-ba3	anterior metapleuro- metabasalar	metapleuron, paracoxal ridge	metabasalare	Х	Х	X ^d	IIIspm1
t2p-t3	posterior mesonoto-metanotal	mesoscutellum	mesophragmal spine in metanotum	Х	Х	X ^d	IIIdlm3
pl3la-t3	anterolateral metapleuro- metanotal	metapleural apodeme, metafurcal arm	metanotal apodeme	Х	Х	X ^d	IIItpm5
pl3lp-t3	posterolateral metapleuro- metanotal	metapleuron	metanotum	Х	Х	X ^d	IIItpm6
pl3v-3ax3	ventral metapleuro-third axillary sclerite of hind wing	metapleuron, mesepimeral ridge	third axillary sclerite of hind wing	Х	Х	X ^d	IIItpm9
pl3d-3ax3	dorsal metapleuro-third axillary sclerite of hind wing	mesepimeral ridge	third axillary sclerite	Х	Х	X	IIItpm7
p13-sa3	metapleuro-metasubalar	metapleuron, metapleural apodeme	metasubalare	Х	Х	X ^d	IIItpm11
cx3-sa3	metacoxo-metasubalar	metacoxa (sublateral)	metasubalare	Х	Х	X	IIIdvm6
pc31-fu3*	lateral metapecto-metafurcal	metapectus	paracoxal ridge	_	_	X	
	metafurco-metacoxal	metafurcal arm	metacoxa (medial)	-	_	X	IIIscm3?

Abbreviation	Name of muscle	Origin	Insertion	Sceliphron	Sphex	Ampulex	Neoptera
				destillatorium	lucae	compressa	terminology
pl3m-cx3	median metapleuro-metacoxal	metapectus,	metacoxa	X	Х	X	IIIscm1
		metadiscrimenal	(ventrolateral)				
		lamella					
fu31-cx3	lateral metafurco-metacoxal	paracoxal ridge,	metacoxa (lateral)	X	Х	X ^d	IIIscm2
		metadiscrimenal					
		lamella					
fu3m-cx3	median metafurco-metacoxal	metafurca,	metacoxa (medial)	X	Х	X ^d	IIIscm2
		metadiscrimenal					
		lamella					
s3-cx3*	metasterno-metacoxal	metadiscrimenal	metacoxa (medial)	-	Х	-	IIIscm1?
		lamella					
pl31-cx3	lateral metapleuro-metacoxal	metapleuron,	metacoxa	X	Х	X	IIIpcm4
		paracoxal ridge	(dorsolateral)				
fu3-tr3	metafurco-metatrochanteral	metafurcal arm	metatrochanteral	X	Х	X	IIIscm6
			apodeme (central)				
pl3-tr3	metapleuro-metatrochanteral	metapleuron,	metatrochanteral	X?	X?	X ^d ?	IIIpcm6
		metapleural	apodeme (central)				
		apodeme					
Number of met	tathoracic muscles (max. 17):			14	15	16	
First and seco	nd abdominal segment						
ph2m-ph3	median mesophragmo-	mesophragma	median process	Х	Х	-	IIIdlm1
	metaphragmal						
ph3-T2	metaphragmo-second	propodeum	second abdominal	Х	Х	X	-
	abdominal tergal		tergite				
T1-S2	propodeo-second abdominal	propodeum	second abdominal	Х	Х	X	-
	sternal		sternite (lateral)				
fu3-S2	metafurco-second abdominal	metafurcal arm	second abdominal	Х	Х	X ^d	IIIvlm2
	sternal		sternite (ventro-				
			submedial)				
s3-S2	metasterno-second abdominal	metadiscrimenal	second abdominal	Х	Х	X ^d	_
	sternal	lamella,	sternite (lateral)				
		metasternum					
Number of first	t and second abdominal segment	muscles (max. 5):		5	5	4	
Total number of	of muscles (max. 42):			37	40	39	

* = newly identified; d = difference in structure or position, amplified in chapter Results

laterally from the mesopleuron, positioned farther ventral and posterior to pl2-3ax2b, and inserts on the third axillary sclerite of the fore wing. It is the most extended and fan-shaped of the three fore wing muscles. Second mesopleuro-mesonotal muscle (pl2-t2b; Fig. 3C) arises, somewhat dorsal to pl2-3ax2c, from the mesopleuron, is fan-shaped and inserts on the ventral surface of the lateral axillar area of the mesonotum. Mesocoxo-mesosubalar muscle (cx2-sa2; Fig. 3D) arises from the mesocoxal apophysis, which corresponds with the cuticular pit and the paracoxal ridge. This muscle is slim and elongated and inserts on the mesosubalare. Anterior mesofurco-mesolaterophragmal muscle (fu2a-ph2; Fig. 3B) arises from the anterodorsal surface of the mesofurcal arm and inserts on the mesolaterophragma. Posterior thoracic spiracle occlusor muscle (sp3occ) and the corresponding spiracle (sp2) are absent. The mesopleural pit, which corresponds to the mesopleural apodeme, is visible. Anterior mesopleuro-mesofurcal muscle (pl2afu2; Fig. 3D) arises from the mesopleuron and from the mesepimeral ridge and inserts on the mesofurcal arm. Mesopleuro-mesocoxal muscle (pl2-cx2; Fig. 3D) arises from the mesopleuron and inserts anterolaterally on the mesocoxa. Second mesopleuro-mesocoxal muscle (pl2cx2b) is absent. Mesosterno-mesocoxal muscle (s2-cx2; Fig. 3B) arises mainly from the mesodiscrimenal lamella and partly from the mesopectus; it is located ventrally of pl2-cx2 and inserts anterolaterally on the mesocoxa. Mesofurco-mesocoxal muscle (fu2-cx2; Fig. 3A) arises from the mesodiscrimenal lamella as far as the transition to the free basal portion of the mesofurcal arm; it inserts anteromedial on the mesocoxal margin. Lateral mesofurco-mesotrochanteral muscle (fu2l-tr2; Fig. 3C) arises partly from the mesopleuron (posteriorly of pl2a-fu2) and partly from the anterior surface of the lateral mesofurcal arm (anteriorly of pl2a-fu2), fuses with the medially adjacent muscle fu2m-tr2, and inserts laterally on the mesotrochanteral apodeme. Median mesofurco-mesotrochanteral muscle (fu2m-tr2; Fig. 3C) arises from the posterior surface of the mesofurcal arm and is positioned medially to fu2l-tr2. After fusing with fu2l-tr2, both muscles insert laterally on the mesotrochanteral apodeme. Prophragmo-mesophragmal muscle (ph1-ph2; Fig. 3A) arises from the prophragma and inserts on the mesophragma. This horizontal, beam-shaped muscle is the largest in all species examined.

Metathorax. Anterior metapleuro-metabasalar muscle (pl3a-ba3; Fig. 3C) arises from both the metapleuron and from the anterior surface of the paracoxal ridge and inserts on the metabasalare. This longitudinal, lateral muscle extends between the mesopleural and paracoxal ridge. Posterior mesonoto-metanotal muscle (t2p-t3; Fig. 3C) arises from the mesoscutellum and inserts laterally on a spine-shaped apodeme, which is located dorsally on the mesophragma at the transition of the meso- and metascutellum; it is fan-like. Anterolateral metapleuro-metanotal muscle (pl3la-t3; Fig. 3B) arises anterolaterally from the metapleural apodeme and metafurcal arm and inserts laterally on the metanotal apodeme. It is short and fan-like. Adjacent muscles are fu3-S2 and fu3-tr3, which arise posterior to the metafurcal arm. Posterolateral metapleuro-metanotal muscle (pl3lp-t3; Fig. 3D) arises from the metapleuron and inserts on the metanotum by fusing with pl3la-t3, which lies ventral to the small pl3lp-t3. Ventral metapleuro-third axillary sclerite of hind wing muscle (pl3v-3ax3; Fig. 3D) arises from the posterior surface of the mesepimeral ridge and the metapleuron. The muscle is located lateral to pl3d-3ax3 and fuses with it, then both insert on the third axillary sclerite of the hind wing. Dorsal metapleuro-third axillary sclerite of hind wing muscle (pl3d-3ax3; Fig. 3C) arises dorso-submedial of pl3v-3ax3 from the posterior surface of the mesepimeral ridge, fuses with pl3v-3ax3 along half its length, and inserts on the third axillary sclerite of the hind wing; it is small and compact. Metapleuro-metasubalar muscle (pl3-sa3; Fig. 3C) arises from the metapleuron and partly from the metapleural apodeme and inserts on the metasubalare, ventral to the hind wing. Metacoxo-metasubalar muscle (cx3sa3; Fig. 3C) arises from the sublateral margin of the metacoxa and inserts on the metasubalare by fusing with pl3-sa3; it is long and slim. Lateral metapecto-metafurcal muscle (pc3l-fu3) and metafurco-metacoxal muscle (fu3-cx3) are absent. Median metapleuro-metacoxal muscle (pl3m-cx3; Fig. 3B) arises ventromedially from the metapectus and from the metadiscrimenal lamella, inserts ventrolaterally on the metacoxa. Lateral metafurco-metacoxal muscle (fu3l-cx3; Fig. 3C) arises sublaterally from the posterior surface of the paracoxal ridge and the metadiscrimenal lamella and inserts laterally on the metacoxa. Median metafurco-metacoxal muscle (fu3m-cx3; Fig. 3A, B) arises posteromedially from both the metafurca and metadiscrimenal lamella and inserts medially on the metacoxa. Metasterno-metacoxal muscle (s3-cx3) is absent (see Sphex). Lateral metapleuro-metacoxal muscle (pl3l-cx3; Fig. 3D) arises laterally from the metapleuron and posteriorly from the paracoxal ridge and inserts on the dorsolateral margin of the metacoxa. The muscle is located anteriorly along the metapleural ridge. Metafurco-metatrochanteral muscle (fu3-tr3; Fig. 3C) arises posteriorly of the metafurcal arm, inserts centrally on the metatrochanteral apodeme by fusing with pl3-tr3. Metapleuro-metatrochanteral muscle (pl3-tr3; Fig. 3D) arises from the metapleuron and partly from the metapleural apodeme, then fuses with fu3-tr3, and inserts centrally on the metatrochanteral apodeme. It runs parallel to, and between, pl3l-cx3 and cx3sa3 and dorsolateral of fu3-tr3.

First and second abdominal segment. Median mesophragmo-metaphragmal muscle (ph2m-ph3; Fig. 3A) arises posteromedially from the mesophragma and inserts anterior to the median process of the propodeum; it is short and square. Metaphragmo-second abdominal tergal muscle (ph3-T2; Fig. 3A-D) arises dorsolaterally from the propodeum, inserts dorsally on the second abdominal tergite; it is a large muscle. Propodeo-second abdominal sternal muscle (T1-S2; Fig. 3B, D) arises dorsolaterally from the propodeum, right above pl31-cx3 and laterally of ph3-T2; it is large and inserts on the lateral margin of the second abdominal sternite. Metafurco-second abdominal sternal muscle (fu3-S2; Fig. 3B) arises posteriorly from the submedial metafurcal arm, located dorsally of fu3-tr3, and inserts ventro-submedially on the second abdominal sternite; it is elongate and slightly fanshaped. Metasterno-second abdominal sternal muscle (s3-S2; Fig. 3A) arises from the metadiscrimenal lamella and metasternum, inserts on the lateral margin of the second abdominal sternite, and is fan-shaped and bent.

Sphex (Fernaldina) lucae de Saussure, 1867

Mesothorax. Posterior thoracic spiracle occlusor muscle (sp3occ; Fig. 4A-D) arises medial on the mesepimeral ridge, anterior to the mesofurcal arm, inserts on the posterior thoracic spiracle (sp2), which additionally is surrounded by pl2-t2b (anterodorsal), pl2a-fu2 (posterodorsal), and pl2-cx2b (ventral). The small tracheal occlusor muscle sp3occ is located submedial of pl2a-fu2. Second mesopleuro-mesocoxal muscle (pl2-cx2b; first description; Fig. 4A, C, D) arises from the mesopleuron and partly from the mesopleural spiracle apodeme, fuses with pl2-cx2 and inserts dorsolaterally on the mesocoxa; it lies anteroventral to the mesepimeral ridge. Lateral mesofurco-mesotrochanteral muscle (fu2l-tr2; Fig. 4A, D) arises from the anterior surface of the mesofurcal arm, runs lateral to fu2m-tr2 and fuses with the same, then both insert laterally on the mesotrochanteral apodeme; fu2l-tr2 is half the size of that in Sceliphron.

Metathorax. Lateral metapecto-metafurcal muscle (pc3l-fu3) and metafurco-metacoxal muscle (fu3-cx3) are absent. Metasterno-metacoxal muscle (s3-cx3; first description; Fig. 4B) arises from the metadiscrimenal lamella and inserts medially on the metacoxa.

Ampulex compressa (Fabricius, 1781)

Mesothorax. Second mesopleuro-mesocoxal muscle (**pl2-cx2b**; Fig. 5C, D, E, G, H) is slimmer than in *Sphex.* It arises from the mesopleural spiracle apodeme, fuses with pl2-cx2 (Fig. 5A, C, D, G, H), and inserts dorso-laterally on the mesocoxa. Lateral mesofurco-mesotrochanteral muscle (fu2l-tr2) is absent. Median mesofur-



Figure 4. The mesosomal musculature of *Sphex (Fernaldina) lucae* divergent to *S. destillatorium*; volume rendering, transparent exoskeleton. A. Lateral view, anterior to the left; B. Medial view, anterior to the right; C. Anterior view on the posterior thoracic spiracle occlusor; D. Dorsomedial view, anterior top right. Abbreviations: sp3occ – posterior thoracic spiracle occlusor; sp2 – posterior spiracle; pl2-cx2 – mesopleuro-mesocoxal; pl2-cx2b – second mesopleuro-mesocoxal; fu2l-tr2 – lateral mesofurco-mesotrochanteral; fu2m-tr2 – median mesofurco-mesotrochanteral; s3-cx3 – metasterno-metacoxal; pl3m-cx3 – median metapleuro metacoxal; fu3l-cx3 – lateral metafurco metacoxal; pl3l-cx3 – lateral metapleuro metacoxal; mepr – mesepimeral ridge. Scale bars: 0.7 mm (A), 0.6 mm (B), 0.3 mm (C), 0.5 mm (D).

co-mesotrochanteral muscle (**fu2m-tr2**; Fig. 5B, D, E) is larger than in Sphecidae, arises from the ventral surface of the mesofurcal arm, and inserts medially on the mesotrochanteral apodeme.

Metathorax. Anterior metapleuro-metabasalar muscle (pl3a-ba3; Fig. 5C, E) arises from the metapleuron, posterior to the mesepimeral ridge, and inserts on the metabasalare. This muscle is shorter than in *Sceliphron*, as it originates farther up. The paracoxal ridge is not very distinct. **Posterior mesonoto-metanotal muscle** (t2p-t3; Fig. 5A–D, F) arises from the upper sclerite of the mesoscutellum and inserts on the lower surface of the mesoscutellum; rectangular. There is no filament connecting it to another structure. **Anterolateral metapleuro-metanotal muscle** (pl3la-t3; Fig. 5B, E, F) mainly arises anterolaterally from the metafurcal arm (touching pl3-tr3 and partly fu3-tr3, which originate on the posterior surface of the metafurcal arm) and partly from the metapleuron and inserts on the metanotum. Posterolateral metapleuro-metanotal muscle (pl3lp-t3; Fig. 5C, D) arises from the metapleuron fuses with pl3la-t3, which is covered dorsally by pl3lp-t3, and inserts on the metanotum. It is larger than in Sceliphron and Sphex and fanshaped. Ventral metapleuro-third axillary sclerite of hind wing muscle (pl3v-3ax3; Fig. 5A, E) arises from the posterior surface of the mesepimeral ridge. This slim muscle is fused with pl3d-3ax3 and inserts on the third axillary sclerite of the hind wing. Metapleuro-metasubalar muscle (pl3-sa3; Fig. 5C, D) arises from the metapleuron at the posterior face of the mesepimeral ridge, and inserts on the metasubalare. Lateral metapecto-metafurcal muscle (pc3l-fu3; first description; Fig. 5C, E, G, H) the slender muscle arises anterior to the metacoxa laterally from the metapectus, and inserts on the posterior surface of the paracoxal ridge. Metafurco-metacoxal muscle (fu3-cx3; first description; Fig. 5C, G, H) arises medially



Figure 5. The mesosomal musculature of *Ampulex compressa* divergent to Sphecidae; volume rendering, transparent exoskeleton. **A–C** anterior to the right; **D–H** anterior to the left. **A.** Medial view, all relevant muscles visible from the centre; **B.** Medial view on submedial muscles; **C.** Medial view, further lateral located muscles; **D.** All relevant muscles discernible from lateral view; **E.** Muscles located sublateral, lateral view; **F.** Muscles located further medial, lateral view; **G.** All newly identified muscles (plus pl2-cx2), lateral view; **H.** Dorsolateral view on all newly identified muscles (plus pl2-cx2), lateral view; **H.** Dorsolateral view on all newly identified muscles (plus pl2-cx2). Abbreviations: **sp1occ** – anterior thoracic spiracle occlusor; **ism1,2-ba2** – intersegmental membrane-mesobasalar; **pl2-cx2** – second mesopleuro-mesocoxal; **pl2-cx2** – mesofurco-mesocoxal; **pl2-cx2** – mesopleuro-mesocoxal; **pl2-cx2** – mesopleuro-mesocoxal; **pl2-cx2** – mesopleuro-mesocoxal; **pl2-cx2** – metapleuro-metanotal; **pl3a-ba3** – anterior metapleuro-metabasalar; **t2p-t3** – posterior mesonoto-metanotal; **pl3la-t3** – anterolateral metapleuro-metanotal; **pl3la-t3** – netapleuro-metacoxal; **fu3-cx3** – metafurco-metacoxal; **fu3-cx3** – metafurco-metacoxal; **fu3-cx3** – metafurco-metacoxal; **fu3-cx3** – lateral metapleuro-metacoxal; **fu3-cx3** – metafurco-metacoxal; **pl3-cx3** – metafurco-metacoxal; **p**



Figure 6. Comparison of the paracoxal ridge (**pcr**) and metapleural apodeme (**pl3a**). **A.** *Sceliphron destillatorium*, anterolateral view, head left; **B.** *Sphex lucae*, anterolateral view, head left; **C.** Weakly developed structures in *Ampulex compressa*, lateral view, head left; **D.** *Ampulex compressa*, paracoxal ridge, lateral metafurcal arms (**fu3a**) fused with reduced metapleural apodeme, anterior view. Further abbreviations: **pl3lp-t3** – posterolateral metapleuro-metanotal muscle, **pl3-tr3** – metapleuro-metatrochanteral muscle, **fu3-tr3** – metafurcor-metatrochanteral muscle. Scale bars: 0.4 mm (A–C), 0.3 mm (D).

from the metafurcal arm, fuses with fu3l-cx3, and inserts medially on the metacoxa; it is slender and flattened. The median metafurco-metacoxal muscle (fu3m-cx3; Fig. 5A, F) arises posteromedially from the metafurca and from the metadiscrimenal lamella and inserts medially on the metacoxa. The lower metafurcal area runs further cranial and offers more posterior space filled by this muscle. Lateral metafurco-metacoxal muscle (fu3l-cx3; Fig. 5B, D) arises from the metapectus and inserts dorsolateral on the metacoxa. Metasterno-metacoxal muscle (s3cx3) is absent. Metapleuro-metatrochanteral muscle (pl3-tr3; Fig. 5D, E) arises posteriorly from the metafurcal arm, which merges into a spiracle at that position. The muscle is positioned laterally of fu3-tr3, fuses with it and inserts on the metatrochanteral apodeme. Metapleural apodeme and paracoxal ridge weakly developed (Fig. 6C, D); metapleural apodeme fused with lateral metafurcal arms (Fig. 6D).

Second abdominal segment. Median mesophragmo-metaphragmal muscle (ph2m-ph3) is absent. The mesophragma in *Ampulex* is rectangular like the outer cuticle and lacks a posterior notch for the insertion of a muscle. Metaphragmo-second abdominal tergal muscle (ph3-T2; Fig. 5A–C, F) arises from the metaphragma and propodeum, inserts dorsally on the second abdominal tergite; broad, large muscle extended to the posterior region. **Metafurco-second abdominal sternal muscle** (fu3-S2; Fig. 5A) arises posteriorly from the metafurcal arm, positioned posteromedial to fu3-tr3, inserts anteroventrally on the second abdominal sternite. In length and width distinctly more gracile than in *Sceliphron*. **Metasterno-second abdominal sternal muscle** (s3-S2; Fig. 5A) arises from the metadiscrimenal lamella and inserts on the anterolateral margin of the second abdominal sternite. It is noticeably smaller and neither fan-like nor bent, as in *Sceliphron*.

Discussion

The cladistic analyses by Vilhelmsen et al. (2010) inferred Crabronidae (*Pison*) as being the closest relative of Sphecidae (*Stangeella*) and Ampulicidae (*Ampulex*) and all three taxa constitute a monophyletic Apoidea. However, many anatomic structures of Ampulicidae and Sphecidae we studied differ significantly from each other, whereas the two species within Sphecidae show many similarities. Especially, the metathoracic musculature varies remarkably between the families. The muscles that insert on the notum, coxae, and trochanters show distinct structural divergences. Furthermore, the number and origin of muscles varies, due to the less distinct metapleural apodeme and paracoxal ridge in Ampulex (additional muscles inserting on the coxae in Ampulex: pl2-cx2b, fu3-cx3; in Sphex: pl2-cx2b, s3-cx3; absent muscle in Ampulex: fu2l-tr2; origin different in Ampulex: t2p-t3, pl3la-t3, fu3l-cx3, pl3tr3; Fig. 3-6; Table 2). In addition, some of the meso- and metacoxal muscles, as well as a mesotrochanteral and a metanotal muscle of Ampulex tend to be larger compared to Sphecidae (pl2-cx2, fu2-cx2, fu2m-tr2, pl3lp-t3, fu3m-cx3, pl3l-cx3). The pl3l-cx3 is also larger in Sphex (Fig. 4A) compared to Sceliphron (Fig. 3D). Strong levators and depressors attaching on the coxae might be needed for backwards dragging of large prey and speaks for an adaptation to this conspicuous hunting behaviour (Williams 1942). On the contrary, pl2-cx2b in Ampulex (Fig. 5C, D, E, G, H) is narrower than in Sphex (Fig. 4A, C, D); fu2l-tr2 in Sphex is smaller than in Sceliphron (Figs 3C, 4A, D). However, muscles supposedly involved in the movement of the notum, coxae, and trochanters should be checked carefully in subsequent studies.

Mesothorax. The mesopleural pit in Sceliphron presumably developed by muscle and spiracle reduction. According to Vilhelmsen et al. (2010), the occurrence of the mesopleural pit shows high variances within and amongst superfamilies. Spiracle reduction likely occurred independently in different groups. Snodgrass (1942), for instance, found the posterior thoracic spiracle in honeybee workers without a closing apparatus. Each of the other spiracles is equipped with an occlusor muscle (Snodgrass 1942). Vilhelmsen et al. (2010) documented the absence of the posterior thoracic spiracle in Stephanidae and Pteromalidae, while they evidenced its presence (without sp3occ) in the apoid family Crabronidae, as well as in Rhopalosomatidae (Vespoidea), and the non-aculeate families Cynipidae, Evaniidae, and Trigonalidae. Hence, not only Apoidea but also Spheciformes sensu lato bear a high variance of the development of this spiracle-muscle-complex. Duncan (1939) presented an illustration of the closing mechanism of the posterior thoracic spiracle in Vespula. The occlusor muscles we found in Sphex and Ampulex (Figs 4A-D, 5F-H) show wider attachment points than the fan-shaped muscle described in Duncan's work. In the neopteran representatives, like Zorotypus, examined by Friedrich and Beutel (2008; Table 2), sp3occ was not revealed. Concluding, other related specimens should be examined to exclude all doubts about the homologisation of the posterior thoracic spiracle and sp3occ and to gain further insights into the different formations.

In all species examined, **pl2-cx2** is located as described by the HAO, with origin on the mesopleuron and anterolateral insertion on the mesocoxa (Figs 3D, 4A, D, 5A, C, D, G, H). However, it is larger and extending farther anteriorly in *Ampulex* (Fig. 5A, C, D, G, H). *Ampulex* distinctly shows the additional and slender mesocoxal muscle **pl2-cx2b**, which we describe here for the first time (Fig. 5C–E, G, H). In *Sphex* it is broader and closely adjacent to **pl2-cx2** (Fig. 4A, C, D). It is absent in *Sceliphron*. Consequently, the development of **pl2-cx2b** should be examined in other species to clarify the phylogenetic relevance.

The muscles fu2l-tr2 and fu2m-tr2 in Ampulex, which insert on the mesotrochanter, seem to have been coalesced completely, making a separation impossible (compare Fig. 7A, B). Because of the insertion and the rather medial position, we reasonably homologized the structure with **fu2m-tr2** by excluding **fu2l-tr2** for *Ampulex*. The unambiguous identification of both muscles in Sphecidae appears to indicate an autapomorphic feature of Ampulicidae. However, Vilhelmsen et al. (2010; see also references therein) stated that both muscles were found in Evaniidae, Platygastroidea, most Proctotrupoidea, Plumarius, and Apoidea, which might include all genera they examined (i.e., Ampulex, Apis, Bombus, Pison, Stangeella). However, the authors noted the absence of fu2l-tr2 in Orthogonalys (Trigonaloidea) and of fu2m-tr2 in Ceraphronoidea, Chalcidoidea, and Stephanoidea. Nevertheless, they explained that a secondary subdivision of fu2m-tr2 may have led to the development of fu2l-tr2. In summary, the contrariness referring to fu2l-tr2 needs to be clarified by additional studies on Ampulex, in particular.

In addition, **fu2l-tr2** fills the mesopleural area in *Sceliphron* (Fig. 3C), whereas this muscle is smaller in *Sphex* (Fig. 4A, D). In contrast, **pl2-cx2b** extends over the mesopleural region in *Sphex* and *Ampulex* (Figs 4A, C, D, 5C–E, G, H). In *Ampulex*, the origin of this muscle is the same spiracle apodeme as that from which **sp3occ** arises (Fig. 5E–H); in *Sphex* it partly originates from the posterior thoracic spiracle and partly from the mesopleuron (Fig. 4A, C, D). However, we recommend a closer look at these different formations in other species before drawing phylogenetic conclusions.

Metathorax. The different constructions of the metathoracic muscles mainly depend on variations of the skeletal structures. The slight difference in the metapleural origin of pl3a-ba3 in Ampulex (Fig. 5C, E) is a consequence of the less distinct development of the paracoxal ridge (Fig. 6). As shown by Vilhelmsen et al. (2010), the paracoxal ridge is weakly developed in Ampulicidae and non-apocritan Hymenoptera, whereas it is highly variable within apocritan groups. Orthogonalys (Trigonalidae), which serves as reference species in the paper of Vilhelmsen et al. (2010), has a weakly developed paracoxal ridge, except for the ventralmost part. As no other information about the structure in Pison (Crabronidae) is available, it should be identical. We confirm the differences noted by Vilhelmsen et al. (2010), as the paracoxal ridge is weakly developed in Ampulicidae and well-marked in Sphecidae (Fig. 6). Additionally, Vilhelmsen et al. (2010) described a distinct paracoxal ridge in Chrysidoidea, Evanioidea, and Stephanoidea.

The muscle **t2p-t3** inserts laterally on a spine, which is located dorsally on the mesophragma in Sphecidae (Fig.



Figure 7. Comparison of **fu2m-tr2** – median mesofurco-mesotrochanteral muscle and **fu2l-tr2** – lateral mesofurco-mesotrochanteral muscle, anterolateral view. **A.** *Sceliphron destillatorium*; **B.** *Ampulex compressa*. Scale bars: 0.4 mm (A), 0.5 mm (B).



Figure 8. Comparison of **t2p-t3** – posterior mesonoto-metanotal muscle, posteromedial view. **A.** *Sceliphron destillatorium*; **B.** *Ampulex compressa*. Scale bars: 0.2 mm.

8A). Vilhelmsen et al. (2010) revealed in Apoidea and Vespoidea a typical lateral insertion on the metanotum, which is not yet observed in other groups; this might indicate that this feature is synapomorphic in both superfamilies. Although we found the mesoscutellum to be of similar shape in all analysed species, **t2p-t3** in *Ampulex* is instead located entirely between the upper and lower mesoscutellar sclerite (Fig. 8B). So far, this modification seems to be unique. To verify this, further representatives of Ampulicidae should be examined.

The metanotal muscle **pl3la-t3** in *Ampulex* differs from that in Sphecidae because of the weakly developed metapleural apodeme, which leads to a rather more lateral than submedial position on the thorax (Fig. 5B, F). We found a fusion of the lateral metafurcal arms with the metapleural apodeme in *Ampulex* (Fig. 6D), as already observed by Vilhelmsen et al. (2010) in the same species, other apoid taxa (*Stangeella, Apis, Bombus, Pison*), and in Vespoidea. Vilhelmsen et al. (2010) stated that most apocritan Hymenoptera have a metapleural apodeme that is often fused with the lateral metafurcal arms. In non-apocritan Hymenoptera, the metapleural apodeme shows high morphological diversity. In many cases, this may not be easy to recognize (Vilhelmsen et al. 2010). Studies on more species from both families are necessary to determine if the structures found in the present study are family-specific. Sphecidae has a well-developed metapleural apodeme, similar to Cynipoidea (Vilhelmsen et al. 2010), which is an important characteristic. Our results corroborate the conclusion by Vilhelmsen et al. (2010), that the development of the metapleural apodeme is highly variable within Apocrita and, moreover, even within Apoidea.

Additionally, the weakly developed metapleural apodeme in *Ampulex* influenced the origin of **pl3-sa3**, which only originates from the metapleuron and inserts on the metasubalare (Figs 5C, D, 9B). The origin of the metatrochanteral muscle **pl3-tr3** is also affected in *Ampulex* (Figs 5D, E, 6C, D). This muscle originates from a delicate sclerite, which provides a narrow surface of origin. This sclerite arose from the fusion of the metafurcal arm and metapleural apodeme and is equal to the medial margin of the metapleural apodeme and metafurcal arm.



Figure 9. Comparison of **pl3-sa3** – metapleuro-metasubalar muscle, dorsolateral view, anterior to the left. **A.** *Sceliphron destillatorium*; **B.** *Ampulex compressa*. Further abbreviations: **mpa** – mesopleural apodeme; **mtpa** – metapleural apodeme; **pl3** – metapleuron; **sa3** – metasubalare; **sp2** – posterior thoracic spiracle. Scale bars: 0.2 mm (A), 0.4 mm (B).



Figure 10. Illustration of the metaphragma (**ph3**) in the propodeum (**T1**) of *Ampulex compressa*. **A.** Medial view, anterior to the right; **B.** Anteromedial view on **ph3-T2** – metaphragmo-second abdominal tergal muscle; **C.** Anteromedial view on **ph3**; **D.** Posterior view on the vertical part of propodeum. Scale bars: 0.6 mm (A), 0.3 mm (B, C), 0.9 mm (D).

The homology of the metanotal muscle, which we tentatively assign to **pl3lp-t3**, according to the HAO terminology, cannot be assured. In the HAO, it is described as fan-shaped and posterolaterally originating from the metapleuron. However, size, structure, and position of **pl3lp-t3** are different among the species examined (Figs 3D, 5C, D). In *Ampulex*, **pl3lp-t3** shows great similarity to the description of it by the HAO (wide, fan-shaped, and arises laterally from the metapleuron), whereas in Sphecidae, **pl3lp-t3** is very small and compact but still fan-shaped and located sublaterally. It appears to originate from the metanotum and to insert on the metapleu-

ron. Additional examination of **pl3lp-t3** in other specimens is required to resolve the homology of this muscle.

The muscle **s3-cx3** is clearly identifiable in *Sphex* (Fig. 4B). It is located ventrally to **fu3m-cx3** and might serve to strengthen the metacoxal function from the lower centre of the body. From **fu3m-cx3**, **s3-cx3** might be subdivided. This possibly forms a genus-specific character of *Sphex*, but not of the family Sphecidae.

First and second abdominal segment. The metaphragma is conspicuously absent in Sphecidae among all studied taxa. Nevertheless, ph2m-ph3 (Fig. 3A) and ph3-T2 (Fig. 3A–D) in Sphecidae are homologue muscles. The metaphragma is usually located between the metanotum and the first abdominal segment (Snodgrass 1942). The HAO describes the metaphragma as the site of origin of the mesophragmo-metaphragmal and metaphragmo-second abdominal tergal muscles. Although the third phragma was found to be absent in honeybees by Snodgrass (1942). However, Vilhelmsen et al. (2010) stated that most Hymenoptera have at least a weak laterally developed metaphragma. This has been observed in Mymarommatoidea (Terebrantia) and Chrysidoidea (Aculeata). Vilhelmsen et al. (2010) described a metaphragma medially continuous adjacent to the lateral metapleural apodeme for other apocritan taxa (i.e., Vespoidea, Trigonaloidea, Megalyroidea, Stephanoidea, Evanioidea, most Ichneumonoidea, and Apoidea: Stangeella (Sphecidae), Pison (Crabronidae), and Ampulex (Ampulicidae)). Stangeella and Ampulex were analysed by dissection but not figured. We cannot confirm this specific pattern for Ampulex (Fig. 10A-D). The absence of the metaphragma we observed in Sceliphron and Sphex may be a potential autapomorphy or an independent reduction. Consequently, further investigation of this phragma is highly recommended.

Conclusions

We recommend additional investigations of the structures and features presented in this paper. It would be of great value to analyse the tagmata and other characteristics in the family Heterogynaidae and additional species of Crabronidae, Ampulicidae, and Sphecidae. Due to the unresolved phylogenetic position of Heterogynaidae and the paraphyly of Crabronidae, the study of more species from these taxa might be desirable. Structural investigations of more species of Vespoidea and Chrysidoidea would be helpful for clarifying controversial assumptions about phylogenetic relationships within Aculeata. Structures of phylogenetic significance were mainly found in the metathorax, i.e., the metapleural apodeme, paracoxal ridge, metaphragma, and the origin and insertion of associated muscles. Future studies should also focus on: the muscles that insert into the legs, the posterior thoracic spiracle as well as the occlusor muscle in closely related species, and the four muscles described here for the first time in Sphecidae and Ampulicidae.

Acknowledgements

We gratefully acknowledge the project funding (project OH81/13-1 for MO) by the Deutsche Forschungsgemeinschaft. Technical facilities and continuous support was provided by Science Programme I of the MfN (in particular, Kristin Mahlow, Prof. Dr Johannes Müller, Dr Nadia Fröbisch), as well as by Falko Glöckler, Dr Carsten Lüter, Anke Sänger, and the IT department. Furthermore, the research group Ohl gave reliable support, especially Annika Beckmann assisted with literature research. MW would like to thank Dr Michael Roggenbuck-Wedemeyer and Dr Martin Fritsch for useful advice. Moreover, we offer many thanks to Dr Matthew Dennis (University of Manchester) for proofreading the manuscript.

References

- Aguiar AP, Deans AR, Engel MS, Forshage M, Huber JT, Jennings JT, Johnson NF, Lelej AS, Longino JT, Lohrmann V, Mikó I, Ohl M, Rasmussen C, Taeger A, Sick Ki Yu D (2013) Order Hymenoptera. In: Zhang Z-Q (Ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness (addenda 2013). Zootaxa 3703: 51–62. https://doi.org/10.11646/zootaxa.3703.1.12
- Alexander BA (1992) A cladistic analysis of the subfamily Philanthinae (Hymenoptera: Sphecidae). Systematic Entomology 17(2): 91–108. https://doi.org/10.1111/j.1365-3113.1992.tb00324.x.
- Bohart RM, Menke AS (1976) Sphecid wasps of the world. A generic revision. University of California Press, Berkeley, Los Angeles, London, 695 pp. https://archive.org/details/bub_gb_FExMjuRhjpIC/page/n27
- Branstetter MG, Danforth BN, Pitts JP, Faircloth BC, Ward PS, Buffington ML, Gates MW, Kula RR, Brady SG (2017) Phylogenomic Insights into the evolution of stinging wasps and the origins of ants and bees. Current Biology 27(7): 1019–1025. https://doi.org/10.1016/j. cub.2017.03.027
- Brothers DJ, Carpenter JM (1993) Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). Journal of Hymenoptera Research 2(1): 227–304.
- Debevec AH, Cardinal S, Danforth BN (2012) Identifying the sister group to the bees: a molecular phylogeny of Aculeata with an emphasis on the superfamily Apoidea. Zoologica Scripta 41(5): 527– 535. https://doi.org/10.1111/j.1463-6409.2012.00549.x
- Duncan CD (1939) A contribution to the biology of North American vespine wasps. Stanford University Publication, University Series Biology and Science 8: 1–272.
- Faulwetter S, Vasileiadou A, Kouratoras M, Dailianis T, Arvanitidis C (2013) Micro-computed tomography: Introducing new dimensions to taxonomy. ZooKeys 263: 1–45. https://doi.org/10.3897/zookeys.263.4261
- Fouad K, Libersat F, Rathmayer W (1994) The venom of the cockroach-hunting wasp *Ampulex compressa* changes motor thresholds: a novel tool for studying the neural control of arousal. Zoology 98: 23–34.
- Friedrich F, Beutel RG (2008) The thorax of *Zorotypus* (Hexapoda, Zoraptera) and a new nomenclature for the musculature of Neoptera. Arthropod Structure & Development 37: 29–54. https://doi. org/10.1016/j.asd.2007.04.003

- Friedrich F, Beutel RG (2010) Goodbye Halteria? The thoracic morphology of Endopterygota (Insecta) and its phylogenetic implications. Cladistics 26(6): 579–612. https://doi.org/10.1111/j.1096-0031.2010.00305.x
- Garcia FH, Fischer G, Liu C, Audisio TL, Economo EP (2017) Next-generation morphological character discovery and evaluation: an X-ray micro-CT enhanced revision of the ant genus *Zasphinctus* Wheeler (Hymenoptera, Formicidae, Dorylinae) in the Afrotropics. ZooKeys 693: 33–93. https://doi.org/10.3897/zookeys.693.13012
- Gignac PM, Kley NJ, Clarke JA, Colbert MW, Morhardt AC, Cerio D, Cost IN, Cox PG, Daza JD, Early CM, Echols MS, Henkelman RM, Herdina AN, Holliday CM, Li Z, Mahlow K, Merchant S, Müller J, Orsbon CP, Paluh DJ, Thies ML, Tsai HP, Witmer LM (2016) Diffusible iodine-based contrast-enhanced computed tomography (diceCT): an emerging tool for rapid, high-resolution, 3-D imaging of metazoan soft tissues. Journal of Anatomy 228: 889–909. https:// doi.org/10.1111/joa.12449
- Haspel G, Libersat F (2003) Wasp venom blocks central cholinergic synapses to induce transient paralysis in cockroach prey. Developmental Neurobiology 54(4): 628–637. https://doi.org/10.1002/ neu.10195
- Heraty JM (1989) Morphology of the mesosoma of *Kapala* (Hymenoptera: Eucharitidae) with emphasis on its phylogenetic implications. Canadian Journal of Zoology 67(1): 115–125. https://doi. org/10.1139/z89-018
- Johnson BR, Borowiec ML, Chiu JC, Lee EK, Atallah J, Ward PS (2013) Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. Current Biology 23: 2058–2062. https://doi. org/10.1016/j.cub.2013.08.050
- Kawada R, Lanes GO, Azevedo CO (2015) Evolution of Metapostnotum in Flat Wasps (Hymenoptera, Bethylidae): Implications for Homology Assessments in Chrysidoidea. PLoS ONE10 (10): e0140051. https://doi.org/10.1371/journal.pone.0140051
- Königsmann E (1978) Das phylogenetische System der Hymenoptera. Teil 4: Aculeata (Unterordnung Apocrita). Deutsche Entomologische Zeitschrift, Neue Folge 25: 365–435. https://doi.org/10.1002/ mmnd.19780250408
- Libersat F (2003) Wasp uses venom cocktail to manipulate the behavior of its cockroach prey. Journal of Comparative Physiology A 189(7): 497–508. https://doi.org/10.1007/s00359-003-0432-0
- Liu S-P, Richter A, Stoessel A, Beutel RG (2019) The mesosomal anatomy of *Myrmecia nigrocincta* workers and evolutionary transformations in Formicidae (Hymenoptera). Arthropod Systematics & Phylogeny 77(1): 1–19. https://doi.org/10.26049/ASP77-1-2019-01
- Lohrmann V, Ohl M, Bleidorn C, Podsialowski L (2008) Phylogenie der "Sphecidae" (Hymenoptera: Apoidea) basierend auf molekularen Daten. Mitteilungen der Deutschen Gesellschaft für allgemeine und angewandte Entomologie 16: 99–102.
- Lomholdt O (1982) On the origin of the bees (Hymenoptera: Apidae, Sphecidae). Insect Systematics & Evolution 13(2): 185–190. https:// doi.org/10.1163/187631282X00093
- Maki T (1938) Studies on the thoracic musculature in insects. Memoirs of the Faculty of Science and Agriculture, Taihoku Imperial University 24(1): 1–343.
- Matsuda R (1970) Morphology and Evolution of the Insect Thorax. Memoirs of the Entomological Society of Canada 102(S76): 5–431. https://doi.org/10.4039/entm10276fv
- Metscher BD (2009) MicroCT for comparative morphology: simple staining methods allow high-contrast 3D imaging of diverse

non-mineralized animal tissues. BMC Physiology 9: 11. https://doi. org/10.1186/1472-6793-9-11

- Mikó I, Vilhelmsen L, Johnson NF, Masner L, Pénzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): head and mesosoma. Zootaxa 1571: 1–78. https://doi.org/10.11646/zootaxa.1571.1.1
- O'Neill KM (2001) Solitary wasps: natural history and behavior. Cornell University Press, Ithaca, NY, 406 pp.
- Ohl M, Bleidorn C (2006) The phylogenetic position of the enigmatic wasp family Heterogynaidae based on molecular data, with description of a new, nocturnal species (Hymenoptera: Apoidea). Systematic Entomology 31(2): 321–337. https://doi.org/10.1111/j.1365-3113.2005.00313.x
- Ohl M, Engel MS (2007) Die Fossilgeschichte der Bienen und ihrer nächsten Verwandten (Hymenoptera: Apoidea). Denisia 20: 687–700.
- Ohl M, Spahn P (2010) A cladistic analysis of the cockroach wasps based on morphological data (Hymenoptera: Ampulicidae). Cladistics 26: 49–61. https://doi.org/10.1111/j.1096-0031.2009.00275.x
- Peters RS, Meyer B, Krogmann L, Borner J, Meusemann K, Schütte K, Niehuis O, Misof B (2011) The taming of an impossible child: a standardized all-in approach to the phylogeny of Hymenoptera using public database sequences. BMC Biology 9: 55. https://doi. org/10.1186/1741-7007-9-55
- Peters RS, Krogmann L, Mayer C, Donath A, Gunkel S, Meusemann K, Kozlov A, Podsiadlowski L, Petersen M, Lanfear R, Diez PA, Heraty J, Kjer KM, Klopfstein S, Meier R, Polidori C, Schmitt T, Liu S, Zhou X, Wappler T, Rust J, Misof B, Niehuis O (2017) Evolutionary history of the Hymenoptera. Current Biology 27(7): 1013–1018. https://doi.org/10.1016/j.cub.2017.01.027
- Porto DS, Almeida EAB, Vilhelmsen L (2016) Comparative morphology of internal structures of the mesosoma of bees with an emphasis on the corbiculate clade (Apidae: Apini). Zoological Journal of the Linnean Society 179: 303–337. https://doi.org/10.1111/zoj.12466
- Prentice MA (1998) The comparative morphology and phylogeny of the apoid wasps (Hymenoptera: Apoidea). Ph.D. Dissertation, University of California, Berkeley, 1439 pp.
- Pulawski WJ (2020) Catalog of Sphecidae (see "Number of Species" via https://www.calacademy.org/scientists/projects/catalog-of-sphecidae)
- Rasnitsyn AP (1988) An Outline of Evolution of the Hymenopterous Insects (Order Vespida). Oriental Insects 22: 115–145. https://doi.org/1 0.1080/00305316.1988.11835485
- Ronquist F, Rasnitsyn AP, Roy A, Eriksson K, Lindgren M (1999) Phylogeny of the Hymenoptera: A cladistic reanalysis of Rasnitsyn's (1988) data. Zoologica Scripta 28: 13–50. https://doi.org/10.1046/ j.1463-6409.1999.00023.x
- Sann M, Niehuis O, Peters RS, Mayer C, Kozlov A, Podsiadlowski L, Bank S, Meusemann K, Misof B, Bleidorn C, Ohl M (2018) Phylogenomic analysis of Apoidea sheds new light on the sister group of bees. BMC evolutionary biology 18(1): 71. https://doi.org/10.1186/ s12862-018-1155-8
- Schmidt JO (2016) The sting of the wild. Johns Hopkins University Press, Baltimore, 280 pp.
- Seltmann KC, Yoder MJ, Mikó I, Forshage M, Bertone MA, Agosti D, Austin AD, Balhoff JP, Borowiec ML, Brady SG, Broad GR, Brothers DJ, Burks RA, Buffington ML, Campbell HM, Dew KJ, Ernst AF, Fernández-Triana JL, Gates MW, Gibson GAP, Jennings JT, Johnson NF, Karlsson D, Kawada R, Krogmann L, Kula RR, Mullins

PL, Ohl M, Rasmussen C, Ronquist F, Schulmeister S, Sharkey MJ, Talamas E, Tucker E, Vilhelmsen L, Ward PS, Wharton RA, Deans AR (2012) A hymenopterists' guide to the Hymenoptera anatomy ontology: utility, clarification, and future directions. Journal of Hymenoptera Research 27: 67–88. https://doi.org/10.3897/jhr.27.2961

- Sharkey MJ, Carpenter JM, Vilhelmsen L, Heraty J, Liljeblad J, Dowling APG, Schulmeister S, Murray D, Deans AR, Ronquist F, Krogmann L, Wheeler WC (2012) Phylogenetic relationships among superfamilies of Hymenoptera. Cladistics 28(1): 80–112. https://doi. org/10.1111/j.1096-0031.2011.00366.x
- Snodgrass RE (1942) The skeleto-muscular mechanisms of the honey bee. Smithsonian Miscellaneous Collections 103(2): 1–120. http:// hdl.handle.net/10088/22771
- Vilhelmsen L, Mikó I, Krogmann L (2010) Beyond the wasp-waist: structural diversity and phylogenetic significance of the mesosoma in apocritan wasps (Insecta: Hymenoptera). Zoological Journal of the Linnean Society 159(1): 22–294. https://doi.org/10.1111/j.1096-3642.2009.00576.x
- Williams FX (1942) Ampulex compressa (Fabr.), A cockroach-hunting wasp introduced from New Caledonia into Hawaii. Proceedings of the Hawaiian Entomological Society 11(2): 221–233. http://hdl.handle.net/10125/16067
- Willsch M (2019) Micro-computed tomography scanning of the mesosomal musculature in Apoidea (aculeate Hymenoptera) – segmented structures and raw data. [Dataset]. Data Publisher: Museum für Naturkunde Berlin (MfN) – Leibniz Institute for Research on Evolution and Biodiversity. https://doi.org/10.7479/dft0-yy6m
- Yoder MJ, Mikó I, Seltmann KC, Bertone MA, Deans AR (2010) A Gross Anatomy Ontology for Hymenoptera, PLOS ONE 5(12): e15991. https://doi.org/10.1371/journal.pone.0015991

Zimmermann D, Vilhelmsen L (2016) The sister group of Aculeata (Hymenoptera) – evidence from internal head anatomy, with emphasis on the tentorium. Arthropod Systematics & Phylogeny 74(2): 195– 218. https://curis.ku.dk/portal/files/171586094/05_asp_74_2_zimmermann_195_218.pdf

Supplementary material 1

Table S1

Authors: Maraike Willsch, Frank Friedrich, Daniel Baum, Ivo Jurisch, Michael Ohl

Data type: Excel file

- Explanation note: Provision of Universal Resource Identifiers (URIs) referring to structures mentioned in the paper. Automatic creation by using the Hymenoptera Anatomy Ontology "analyzer" (http://api.hymao.org/ projects/32/public/ontology/analyze).
- Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons. org/licenses/odbl/1.0). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
- Link: https://doi.org/10.3897/dez.67.49493.suppl1
<u> PENSOFT</u>.



The Nepalese species of the genus *Enicospilus* Stephens, 1835 (Hymenoptera, Ichneumonidae, Ophioninae): a preliminary revision and identification key to species

So Shimizu^{1,2,3}

- Laboratory of Insect Biodiversity and Ecosystem Science, Graduate School of Agricultural Science, Kôbe University, Rokkôdaichô 1–1, Nada, Kôbe, Hyôgo 657–8501, Japan
- 2 Research Fellow (DC1 and Overseas Challenge Program for Young Researchers), Japan Society for the Promotion of Science, Tôkyô, Japan
- 3 Department of Life Sciences, the Natural History Museum, Cromwell Road, London SW7 5BD, UK

http://zoobank.org/2B601B5D-E1BD-44B7-BA89-554E3AB5EAE1

Corresponding author: So Shimizu (parasitoidwasp.sou@gmail.com)

Academic editor: J. Fernandez-Triana • Received 20 February 2020 • Accepted 3 April 2020 • Published 11 May 2020

Abstract

A total of 10 species of *Enicospilus* (Hymenoptera, Ichneumonidae, Ophioninae) have previously been reported from Nepal. Six new species are described here (*E. alleni* Shimizu **sp. nov.**, *E. kakanicus* Shimizu **sp. nov.**, *E. nepalensis* Shimizu **sp. nov.**, *E. nikami* Shimizu **sp. nov.**, *E. phulchokiensis* Shimizu **sp. nov.**, and *E. tangi* Shimizu **sp. nov.**), and 10 are newly recorded (*E. ashbyi* Ashmead, 1904, *E. bifasciatus* (Uchida, 1928), *E. capensis* (Thunberg, 1824), *E. flavocephalus* (Kirby, 1900), *E. formosensis* (Uchida, 1928), *E. grammospilus* (Enderlein, 1921), *E. pudibundae* (Uchida, 1928), *E. purifenestratus* (Enderlein, 1921), *E. yonezawanus* (Uchida, 1928), and *E. zebrus* Gauld & Mitchell, 1981) from Nepal. A preliminary identification key to the Nepalese species of *Enicospilus* is provided. The elevational pattern of Nepalese *Enicospilus* is briefly discussed. *Enicospilus purifenestratus* is also recorded for the first time from Brunei.

Key Words

Biogeography, Darwin wasps, elevation, Nepal, new species, parasitoid wasps, systematics, taxonomy

Table of contents

Introduction	2
Material and methods	2
Results	4
Genus Enicospilus Stephens, 1835	4
Identification key to Enicospilus species of Ne	epal6
Enicospilus alleni Shimizu sp. nov	8
Enicospilus ashbyi Ashmead, 1904	10
Enicospilus bifasciatus (Uchida, 1928)	10
Enicospilus biharensis Townes,	
Townes & Gupta, 1961	13
Enicospilus capensis (Thunberg, 1824)	13
Enicospilus flavicaput (Morley, 1912)	15
Enicospilus flavocephalus (Kirby, 1900)	

Enicospilus formosensis (Uchida, 1928)	18
Enicospilus grammospilus (Enderlein, 1921)	21
Enicospilus javanus (Szépligeti, 1910)	21
Enicospilus kakanicus Shimizu, sp. nov	24
Enicospilus kanshirensis (Uchida, 1928)	26
Enicospilus laqueatus (Enderlein, 1921)	26
Enicospilus lineolatus (Roman, 1913)	29
Enicospilus melanocarpus Cameron, 1905	29
Enicospilus nepalensis Shimizu, sp. nov	33
Enicospilus nikami Shimizu, sp. nov	35
Enicospilus phulchokiensis Shimizu, sp. nov	37
Enicospilus pseudantennatus Gauld, 1977	37
Enicospilus pseudoconspersae (Sonan, 1927)	40
Enicospilus pudibundae (Uchida, 1928)	40
Enicospilus purifenestratus (Enderlein, 1921)	43

Enicospilus tripartitus Chiu, 1954	.43
Enicospilus yonezawanus (Uchida, 1928)4 Enicospilus zebrus Gauld & Mitchell, 19815 Species inquirendae and pending taxonomic acts5 Enicospilus sp. 1	.45
Enicospilus zebrus Gauld & Mitchell, 1981 5 Species inquirendae and pending taxonomic acts5 5 Enicospilus sp. 1 5 Enicospilus sp. 2 5 Enicospilus erythrocerus species-group. 5 Discussion 5 Acknowledgements 5	.48
Species inquirendae and pending taxonomic acts5 Enicospilus sp. 1	.50
Enicospilus sp. 1	.50
<i>Enicospilus</i> sp. 2	.50
<i>Enicospilus erythrocerus</i> species-group5 Discussion	.51
Discussion	.52
Acknowledgements	.54
renne agemente agemente a	.55
References	.56

Introduction

Ophioninae Shuckard, 1840 (Hymenoptera, Ichneumonidae) is a moderately large monophyletic Darwin wasp subfamily within the higher Ophioniformes, which mainly comprises solitary koinobiont endoparasitoids of Lepidoptera (Gauld 1985b; Quicke et al. 2009; Bennett et al. 2019; Klopfstein et al. 2019). The Ophioninae comprises 32 genera and over 1,100 species worldwide (e.g. Yu et al. 2016; Shimizu and Lima 2018; Shaw and Voogd 2019). Many species of Ophioninae are considered to be crepuscular or nocturnal and usually have a testaceous body, very large ocelli (posterior ocellus close to or touching eye), and long antenna, with a few exceptions (e.g. all species of Dictyonotus Kriechbaumer, 1894 are diurnal, with a black body, small ocelli, and short antenna). These characters are frequently shared with other nocturnal Ichneumonoidea (e.g. Netelia Gray, 1860 (Ichneumonidae, Tryphoninae) and Xiphozelinae van Achterberg, 1979 (Braconidae)) (e.g. Shimizu 2017). Low latitudinal tropics are considered to be the general centre of species diversity in most groups of Ophioninae (e.g. Gauld and Mitchell 1981; Gauld 1985b, 1988), but a few genera are more diverse in mid-latitudinal temperate regions (e.g. Alophophion Cushman, 1947 and Ophion Fabricius, 1798) (e.g. Gauld 1985b; Alvarado 2014; Schwarzfeld et al. 2016). Reliable and robust phylogenetic and biogeographic estimates for ophionines have not been published yet.

Enicospilus Stephens, 1835 is the largest genus of Ophioninae and predominantly tropical, with more than 700 species worldwide (e.g. Broad and Shaw 2016; Gadallah et al. 2017; Shimizu 2017; Johansson 2018). *Enicospilus* has been considered to be polyphyletic (Gauld 1985b), but there are no phylogenetic studies with comprehensive taxon sampling.

Nepal is a landlocked country between India and China's Tibet Autonomous Region (26°22'N–30°27'N, 80°4'E–88°12'E) in the central part of the Himalaya, about 800 km in latitudinal length and 140 km in longitudinal length (RAOnline 2019). Dramatic changes of altitude (from less than 100 m to more than 8,000 m) along the short longitudinal span in Nepal have created a very diverse climatic and topographic environment as well as a uniquely very rich species diversity of flora and fauna (Savada 1991; MFSC 2014; RAOnline 2019). Furthermore, Nepal is located between the Oriental and Palaearctic regions and is a melting pot of species originating from both regions (MFSC 2014). Therefore, Nepal is an interesting and important place to study biodiversity and biogeography. However, no researchers have studied Ophioninae of Nepal, although Gauld and Mitchell's (1981) great regional revision for Indo-Papuan Ophioninae included a few specimens and species from Nepal. Hence, only 10 species of *Enicospilus* have been recorded in Nepal (Gauld and Mitchell 1981), whilst 107 species have been reported from China and 73 from India (Yu et al. 2016), indicating a high potential species diversity of *Enicospilus* in Nepal.

This study aims to (1) review all previously recorded species in Nepal, (2) describe new Nepalese species, (3) newly record species from Nepal, (4) provide a preliminary identification key to the Nepalese species, and (5) briefly discuss the biogeography of the Nepalese fauna and species relationships with elevation.

Material and methods

A total of 707 specimens of Nepalese species of *Enicospilus* were examined, 148 of which are from Nepal and 559 from other countries (e.g. Brunei, China, India, Japan, Laos, and Taiwan). Specimens were observed using a stereoscopic microscope (SMZ1500, Nikon, Tôkyô, Japan). Photographs were taken using a single lens reflex camera (α 7II, Sony, Tôkyô, Japan) with a micro-lens (LAOWA 25 mm F2.8 2.5–5× ULTRA MACRO, Anhui Changgeng Optics Technology Co., Ltd, Hefei, China and A FE 50mm F2.8 Macro SEL50M28, Sony, Tôkyô, Japan) and 2× teleconverter lens (SEL20TC, Sony, Tôkyô, Japan), captured in RAW format, developed using Adobe Lightroom Creative Cloud, and stacked using Zerene Stacker. All figures were edited in Adobe Illustrator 2019 and Photoshop Creative Cloud.

Morphological terms follow those of Broad et al. (2018). Legs and wings are described separately from the mesosoma. The lower face is defined as the area between the ventral margin of the clypeus and of the antennal sockets. Terms for surface sculpture follow Eady (1968) and Gauld and Mitchell (1981). Terms for wing veins and cells follow Broad et al. (2018) and those for characters of the discosubmarginal cell follow Gauld and Mitchell (1981) (Fig. 1). 'Sclerites' refer to the sclerites of the fore wing fenestra, which are differentiated as the proximal, central and distal sclerites, all or none of which might be absent in any one species. The indices follow Shimizu and Lima (2018) and Shimizu et al. (2019) and are listed below.

Indices for head

GOI (geno-orbital index) = maximum breadth of eye in profile / maximum breadth of gena in same line

71



Figure 1. Morphological terms for the fore wing of *Enicospilus* species used in the present study. Brown characters indicate acronyms. C-1. Subbasal cell; C-2. Discosubmarginal cell; C-3. Second discal cell; C-4. Marginal cell; PS. Proximal sclerite; CS. Central sclerite; DS. Distal sclerite.

Indices for fore wing

AI (alar index) = length of 1m-cu&M between 2m-cu and bulla / length of 2rs-m

CI (cubital index) = length of CU between 1m-cu&M and 2cu-a / length of 2cu-a

DI (discoidal index) = maximum vertical distance between CU (between 2cu-a and 2m-cu) and 1m-cu&M / length of CU between 2cu-a and 2m-cu

ICI (intercubital index) = length of 2rs-m / length of M between 2m-cu and 2rs-m

SDI (second discoidal index) = length of CU between 2cu-a and 2m-cu / length of CU between M&RS and 1m-cu&M

SI (sinuousness index) = maximum length between 1m-cu&M and a straight line connecting the intersection of M, 2m-cu, and 1m-cu&M and the intersection of 1m-cu&M and CU / distance between the intersection of M, 2m-cu, and 1m-cu&M and the intersection of 1m-cu&M and CU

SRI (second recurrent index) = length of 2m-cu / length of CU between 2cu-a and 2m-cu

Indices for hind wing

NI (nervellar index) = length of CU between M and cu-a / length of cu-a

RI (radial index) = length of RS between RA and rs-m / length of rs-m

Indices for metasoma

DMI (dorsal metasomal index) = length of dorsum of tergite 2 /length of dorsum of tergite 3

PI (petiolar index) = distance between base of tergite 1 and anterior margin of spiracle / distance between posterior margin of spiracle and apex of tergite 1

THI (thyridium index) = distance between anterior margin of tergite 2 and anterior margin of thyridium / maximum diameter of thyridium

Wing characters are especially important for identifying ophionine species, but wings are almost always folded, wrinkled, and/or crooked. For accurate measurements of wing characters, the left wings have been removed from the body, placed between microscope slides in 99.9% ethanol, and photographed. Then, wings have been enclosed in paraffin paper, and the whole thing pinned under the respective specimen. Measurements were taken from photos using the software, Img-Measure ver. 1.14.

The degree of sexual dimorphism of Ophioninae is almost always very small, and most species can morphologically readily be distinguished without needing to dissect male genitalia (Gauld 1984). Therefore, the male genitalia is not dissected and new species are described based on holotype of both sexes in the present study, like previous ophionine studies (e.g. Gauld 1988; Broad and Shaw 2016; Shimizu 2017). The non-morphological abbreviations below are used in the present study.

LT	light traps
MsT	Malaise traps

Abbreviations for repositories used in the present study are as follows.

ANIC	Australian National Insect Collection, Can-
	berra, Australia
NHMUK	Natural History Museum, London, United
	Kingdom
CNC	Canadian National Collection of Insects, Ot-
	tawa, Canada
DEI	Senckenberg Deutsches Entomologisches In-
	stitut, Müncheberg, Germany
EMUS	Utah State University Insect Collection (=
	American Entomological Institute: AEI), De-
	partment of Biology, Utah State University,
	Logan, Utah, USA
EUM	Ehime University Museum, Matsuvama, Japan
FZLU	Fachbereich Zoologie, Martin-Luther-Uni-
	versität, Halle, Germany
HMNH	Hiwa Museum for Natural History, Shôbara,
	Japan
IZPAN	Instytut Zoologiczny Polska Akademia Nauk.
	Warszawa, Poland
MCZ	Museum of Comparative Zoology, Cam-
	bridge. USA
MNHA	Museum of Nature and Human Activities.
	Sanda, Japan
MNHN	Museum National d'Histoire Naturelle, Paris.
	France
MUC	Marathwada University Collection, Aurang-
	abad. India
NIAES	Institute for Agro-Environmental Sciences.
	NARO (= National Institute for Agro-Envi-
	ronmental Sciences). Tsukuba, Japan
NM	Naturhistorisches Museum, Vienna, Australia
NR	Naturhistoriska Riksmuseet, Stockholm,
	Sweden
NSMT	National Museum of Nature and Science.
	Tsukuba, Japan
OUMNH	Oxford University Museum of Natural His-
	tory (= the Hope Entomological Collection).
	Oxford, United Kingdom
SEHU	The Laboratory of Systematic Entomology
	(= Entomological Institute: EIHU). Hokkaidô
	University, Sapporo, Japan
TARI	Taiwan Agricultural Research Institute Coun-
	cil of Agriculture. Executive Yuan. Taichung.
	Taiwan
ТМ	Termeszettudomanyi Muzeum Budanest
11/1	Hungary
USNM	Smithsonian National Museum of Natural His-
	tory, Washington, DC. United States of America
ZIUU	Zoological Institute, University of Uppsala
2100	Sweden

Zoological Survey of India, Calcutta, India

Asterisks (*) are used for indicating a species newly recorded from Nepal.

Results

ZSI

Over 31 morphospecies were recognised from 148 Nepalese specimens and Gauld and Mitchell's (1981) previous records. Six of these species are new to science described below, 10 are newly recorded species from Nepal, 10 have been recorded previously from Nepal, and more than five are tentatively treated as species inquirendae, pending further taxonomic work. *Enicospilus purifenestratus* is also newly recorded from Brunei below.

Taxonomy

Class Hexapoda Blainville, 1816

Order Hymenoptera Linnaeus, 1758 Superfamily Ichneumonoidea Latreille, 1802 Family Ichneumonidae Latreille, 1802 Subfamily Ophioninae Shuckard, 1840

Genus Enicospilus Stephens, 1835

Enicospilus Stephens 1835: 126; type species, *Ophion merdarius* Gravenhorst sensu Stephens (= *Ichneumon ramidulus* Linneaus), by monotypy (Stephens 1845).

- Allocamptus Förster 1869: 150; type species, Ophion undulatus Gravenhorst, 1829, by subsequent designation (Thomson 1888: 1189).
- Dispilus Kriechbaumer 1894: 309; type species, Ophion (Dispilus) natalensis Kriechbaumer, 1894, by monotypy.
- Pleuroneurophion Ashmead 1900: 86; type species, Pleuroneurophion hawaiiensis Ashmead, 1900, by original designation.
- Banchogastra Ashmead 1900: 87; type species, Banchogastra niger Ashmead, 1900, by original designation.
- *Pycnophion* Ashmead 1900: 87; type species, *Pycnophion molokaiensis* Ashmead, 1900, by original designation.
- *Cymatoneura* Kriechbaumer 1901a: 22; type species, *Ophion undulatus* Gravenhorst, 1829, by subsequent designation (Viereck 1914: 8).
- Pterospilus Kriechbaumer 1901b: 156; type species, Ophion (Enicospilus) dubius Tosquinet, 1896, by subsequent designation (Viereck 1914: 126); junior homonym of Pterospilus Rondani, 1856.
- *Trispilus* Kriechbaumer 1901b: 156; type species, *Ophion (Enicospilus) trimaculatus* Tosquinet, 1896, by monotypy.
- Abanchogastra Perkins 1902: 141; type species, Abanchogastra debilis Perkins, 1902, by monotypy.
- Metophion Szépligeti 1905: 28; type species, Metophion bicolor Szépligeti, 1905, by subsequent designation (Viereck 1914: 94).
- Ceratospilus Szépligeti 1905: 28; type species, Ceratospilus biroi Szépligeti, 1905, by monotypy.
- Atoponeura Szépligeti 1905: 34; type species, Atoponeura concolor Szépligeti, 1905 (= Enicospilus atoponeurus Cushman, 1947), by monotypy.

Henicospilus Agassiz 1846: 138; unjustified emendation.



Figure 2. Diagnostic characters for some species of Nepalese *Enicospilus*. A–D. Outer surface of mandible: A. *E. nepalensis* Shimizu sp. nov., B. *E. tangi* Shimizu sp. nov., C. *E. tripartitus*, D. *E. yonezawanus*; E–H. Scutellum, in dorsal view: E. *E. formosensis*, F. *E. kakanicus* Shimizu sp. nov., G. *E. phulchokiensis* Shimizu sp. nov., H. *E. tangi* Shimizu sp. nov.; I, J. Hind tarsal claw: I. *E. biharensis*, J. *E. nikami* Shimizu sp. nov.

- Ophiomorpha Szépligeti 1905: 34; type species, Ophion curvinervis Cameron, 1886 (= Enicospilus cameronii Dalla Torre, 1901), by subsequent designation (Hooker 1912); junior homonym of Ophiomorpha Nilsson, 1836.
- *Cryptocamptus* Brethes 1909: 230; unnecessary replacement name for *Allocamptus* Förster, 1869.
- Amesospilus Enderlein 1914: 222; type species, Ophion unicallosus Vollenhoven, 1878, by original designation.
- *Eremotyloides* Perkins 1915: 530; type species, *Eremotylus orbitalis* Ashmead, 1901, by monotypy.
- *Schizospilus* Seyrig 1935: 79; type species, *Schizospilus divisus* Seyrig, 1935, by original designation.

Distribution. Worldwide except Antarctica (Yu et al. 2016). **Diagnosis.** Moderately to very large insects (fore wing length usually 9.0–30.0 mm). *Head*: mandible bidentate apically and weakly to strongly tapered and twisted (e.g. Fig. 2A–D); ocelli moderately to very large, and posterior ocellus often close to or touching eye (e.g. Figs 3B–D, 5B–D, 7B–D); occipital carina complete; antennae longer than fore wing length (e.g. Figs 5A, 12A, 16A), usually with more than 50 flagellomeres.

Mesosoma: pronotum unspecialised; notauli almost always absent; scutellum with lateral longitudinal carinae usually along more than 0.8× its length (e.g. Fig. 2E–H); epicnemial carina present laterally (e.g. Figs 5E, 8E, 18E); posterior transverse carina of mesosternum complete; propodeum with anterior transverse carina usually more or less complete medially, anterior area long and longitudinally striate.

Wings (e.g. Figs 1, 6F, 7F, 19F, 28F, 31B, D, F): pterostigma of fore wing fairly slender; vein 1m-cu&M of fore wing usually without ramulus; vein 2r&RS of fore wing usually more or less broadened proximally and/ or centrally, straight, sinuous, or bowed, not proximally abruptly angled; discosubmarginal cell of fore wing with fenestra, and often also with one or more sclerites; vein RS of hind wing usually straight and rarely weakly curved; vein RA of hind wing usually with 4–12 uniform hamuli.

Legs: inner mesal surface of fore tibial spur without a membranous flange; outer distal margin of mid and hind trochantelli usually simple and without a decurved tooth; hind tarsal claw moderately to strongly curved with pectinae, usually all pecten are more or less uniform shape and length and a distal one is not significantly longer than true apex of claw (e.g. Fig. 2I, J).

Metasoma (e.g. Figs 3A, 9A): very slender; tergite 1 with spiracle clearly far behind the middle; thyridium moderately to strongly developed, and oval to ellipsoidal; ovipositor straight and usually short, its length less than posterior depth of metasoma.

Colour: body usually entirely testaceous, pale yellow to reddish brown (e.g. Figs 4A–E, 11A–E, 21A–E, 26A–E), sometimes posterior metasomal segments infuscate (e.g. Figs 9A, 17A, 18A); in some species body entirely brown to black, usually with testaceous to pale yellow patterns (e.g. Figs 5A–E, 28A–E); wings entirely hyaline or weakly infuscate (e.g. Figs 3F, 9F, 10F), rarely with strong infumate patches (e.g. Figs 5F, 28F); fenestra always hyaline (e.g. Figs 10F, 19F); sclerites hyaline to black (e.g. Figs 18F, 19F, 23F).

Differential diagnosis. Adult wasps of *Enicospilus* are moderately to very large insects and distinguished from other genera of Ophioninae by the following combination of character states: inner mesal surface of the fore tibial spur lacking a membranous flange; mandibles more or less narrowed apically and moderately to strongly twisted (e.g. Fig. 2A–D); fore wing discosubmarginal cell with a fenestra (e.g. Fig. 31B, D, F), extensive glabrous area, and often one or more sclerotised and pigmented sclerites and/or quadra (e.g. Figs 3F, 15F, 27F); posterior transverse carina of mesosternum complete.

The fore wing fenestra and sclerites are usually reliable characters for recognising *Enicospilus* species. However, similar sclerites of the fore wing fenestra are also known in the genus *Dicamptus* Szépligeti, 1905 and rarely in the genus *Leptophion* Cameron, 1901. *Enicospilus* species are distinguished from both *Dicamptus* and *Leptophion* by the mandibles (i.e. mandible always weakly to strongly tapered and twisted in *Enicospilus*, but very weakly tapered and not twisted in *Dicamptus* and *Leptophion*).

Biology. Species belonging to *Enicospilus* are koinobiont endoparasitoids of Lepidoptera, such as Noctuidae (e.g. Gauld and Mitchell 1981; Gauld 1985b, 1988; Broad and Shaw 2016; Broad et al. 2018). Adult female wasps usually lay eggs within late instar larvae of Lepidoptera, with some exceptions. Broad et al. (2018) summarised the biology of Ophioninae including *Enicospilus*. Both sexes of adults are very frequently attracted to the light and considered to be nocturnal or crepuscular (e.g. Shimizu and Maeto 2016; Shimizu 2017).

Identification key to Enicospilus species of Nepal

This is a preliminary key to the Nepalese species of *Enicospilus* because there are potentially many more unrecorded or undescribed species in Nepal and its adjacent areas.

3(1)	Fore wing without sclerites and quadra (Fig. 31). Outer mandibular surface always more or less flat without a diagonal structures
-	Fore wing with more or less sclerotised sclerites and sometimes with quadra (e.g. Figs 3F, 6F, 16F, 19F). Outer man-
4 (3)	Fore wing fenestra without a proximal sclerite and only with a rather thick distal sclerite (Fig. 16F)
	Even wing fenestra always with a provinal sclerite, and if fenestra with distal sclerite, it is more or less thin (e.g.
_	Figs 6F. 8F. 9F)
5 (4)	Fore wing fenestra without a central sclerite and quadra (e.g. Figs 6F, 12F, 13F, 19F)
-	Fore wing fenestra with a central sclerite (e.g. Figs 3F, 4F, 9F, 11F)
6 (5)	Proximal sclerite more or less triangular; always strongly pigmented; its proximal margin more or less joining prox- imal margin of fenestra (Figs 13F, 24F, 25F, 27F)
_	Proximal sclerite not triangular, various (i.e. narrow and linear, or semicircular); usually weakly pigmented or not,
	except for that of <i>E. javanus</i> strongly pigmented; its proximal margin usually distinctly separated from proximal margin of fenestra by more than its own width (Figs 6F, 12F, 19F, 22F, 23F)
7 (6)	Outer mandibular surface flat without a diagonal setose deep groove E. purifenestratus (Enderlein, 1921)*
-	Outer mandibular surface with a diagonal setose deep groove between its dorsoproximal corner and base of man- dibular apical teeth (Fig. 2B, D).
8(7)	Lower face wider and 0.9× as wide as high (Fig. 25B). Upper mandibular tooth 2.1× as long as lower one (Fig. 2B).
_	Mandible very long, proximally tapered and distally parallel sided (Fig. 2B) <i>E. tangi</i> Shimizu sp. nov. Lower face narrower and 0.7–0.8× as wide as high (Figs 13B, 27B). Upper mandibular tooth 1.2–1.5× as long as
	lower one (Fig. 2D). Mandible moderately long, more or less evenly tapered (Fig. 2D)
9 (8)	Lateral longitudinal carinae of scutellum reaching anterior 0.6 of scutellum (Fig. 2F). Proximal and distal sclerites
	more or less confluent (Fig. 13F). Metapleuron entirely finely punctate, highly shiny, never with wrinkles or striae (Fig. 13E)
_	Lateral longitudinal carinae of scutellum reaching posterior end of scutellum (Fig. 2H). Proximal and distal sclerites
	separated (Fig. 27F). Metapleuron moderately punctate to striate, moderately shiny, almost always with wrinkles or striae (Fig. 27E).
10 (6)	Proximal sclerite more or less wide and semicircular (Figs 12F, 22F)
-	Proximal sclerite narrow and more or less linear (Figs 6F, 19F, 23F)
11 (10)	Fore wing with proximal sclerite confluent with distal one and its posterior end touching margin of fenestra; vein
	1m-cu&M evenly curved; AI = 1.1–1.9, CI = 0.2–0.5, SDI = 1.0–1.1 (Fig. 12F) <i>E. javanus</i> (Szépligeti, 1910)
-	Fore wing with proximal sclerite isolated and distal sclerite absent or vestigial; vein 1m-cu&M sinuous; AI = 0.7–0.9,
10 (10)	CI = 0.6-0.7, $SDI = 1.3-1.4$ (Fig. 22F)
12(10)	Hind tarsal claw uniformly pectinate (Fig. 21). Fore wing vein 1m-cu&ivi evenly curved (Fig. 6F)
_	Pecten of hind tarsal claw absent provimally (e.g. Fig. 21). Fore wing vain 1m.cu&M evenly curved to sinuous
	(Figs 19E 23F)
13 (12)	Fore wing vein 1m-cu&M moderately sinuous (Fig. 19F). 20th flagellomere 1.5× as long as wide
- ()	<i>E. nikami</i> Shimizu sp. nov.
-	Fore wing vein 1m-cu&M evenly curved (Fig. 23F). 20th flagellomere 2.0–2.2× as long as wide
	E. pudibundae (Uchida, 1928)*
14 (5)	Fore wing vein 1m-cu&M strongly angled and broadened centrally (Fig. 9F) E. flavocephalus (Kirby, 1900)*
-	Fore wing vein 1m-cu&M evenly curved or sinuous, never strongly angled and broadened (e.g. Figs 3F, 7F, 8F) 15
15 (14)	Outer mandibular surface always with a diagonal setose deep groove between its dorsoproximal corner and base of mandibular apical teeth
-	Outer mandibular surface almost flat, without a diagonal setose groove (e.g. 2A, C)
16 (15)	Proximal sclerite not confluent with distal one (Figs 7F, 15F)
-	Proximal sclerite strongly confluent with distal one (Figs 17F, 20F, 29F)
17 (16)	Meso- and metapleurae entirely very densely punctate, submatt to matt, punctures of metapleuron contiguous or
	separated by less than a puncture diameter, thus very weakly or not shiny (Fig. /A, E)
_	Meso, and metapleurae finely to moderately punctate to punctostriate, punctures never contiguous and soparated
-	by more than a puncture diameter, moderately to strongly shiny (Fig. 154 F) F laqueatus (Enderlein, 1921)
18 (16)	Central sclerite rather linear, positioned in rather anterodistal part of the fenestra (Fig. 29F). Proximal corner of
()	proximal sclerite almost right angled (Fig. 29F)
_	Central sclerite more or less oval, positioned in mediodistal part of the fenestra (Figs 17F, 20F). Proximal corner of
	proximal sclerite acutely angled (Figs 17F, 20F)

19 (18)	Posterior segments of metasoma infuscate (Fig. 17A). Scutellum smooth to punctate. Fore wing vein 1m-cu&M almost evenly curved (Fig. 17F)
_	Metasoma entirely testaceous (Fig. 20A). Anterior 0.4 of scutellum transversely striate, anterior 0.4–0.5 punctate, and posterior 0.5 longitudinally strigose (Fig. 2G). Fore wing vein 1m-cu&M more or less sinuous (Fig. 2OF)
20 (15)	Proximal sclerite not triangular (Fig. 11F). Central sclerite positioned in almost central part of fenestra; linear and parallel to vein 2r&RS (Fig. 11F)
-	Proximal sclerite more or less triangular (e.g. Figs 3F, 8F, 14F). Central sclerite positioned in distal part of fenestra; variously shaped (e.g. Figs 4F, 10F, 26F)
21 (20)	Outer mandibular surface with conspicuous very dense stout and long setae and its proximal concavity deep (Fig. 2C)
_	Outer mandibular surface with scattered slender and short to moderately long setae and its proximal concavity shallow or absent (e.g. Fig. 2A)
22 (21)	Central sclerite linear and parallel to distal margin of fenestra (Fig. 10F). Sides of scutellum rather weakly convergent posteriorly and sometimes subquadrate (Fig. 2E). Lower face wider and 0.8–0.9× as wide as high (Fig. 10B)
_	Central sclerite oval to linear, if linear it is parallel to vein 2r&RS (e.g. Figs 4F, 8F, 18F, 21F). Sides of scutellum moderately to strongly convergent posteriorly. Lower face usually narrower and 0.6–0.8× as wide as high (e.g. Figs 3B, 8B, 18B)
23 (22)	Proximal sclerite separated from distal sclerite (Figs 18F, 21F)
_	Proximal sclerite confluent with distal sclerite (Figs 3F, 4F, 8F, 14F, 30F)
24 (23)	Central sclerite weakly sclerotised and pigmented, ill-delineated, positioned in posterodistal part of fenes- tra (Fig. 18F). Posterior ocellus separated from eye by 0.3× its maximum diameter (Fig. 18B–D). Fore wing vein 1mcu&M almost evenly curved (Fig. 18F).
_	Central sclerite strongly sclerotised and pigmented, more or less well delineated, positioned in centrodistal part of fenestra (Fig. 21F). Posterior ocellus separated from eye by less than 0.2× its maximum diameter (Fig. 21B–D). Fore
25 (23)	Outer margin of propodeal spiracle separated from pleural carina (e.g. Fig. 3E)
_	Outer margin of propodeal spiracle joining pleural carina by a strong ridge (Figs 8E, 14E, 30E)
26 (25)	Propodeum with distinct posterior transverse carina laterally (Fig. 3E). Proximal corner of proximal sclerite of fore wing fenestra sharply angled at ca 40° (Fig. 3F). Fore wing fenestra with two vestigial central sclerites (Fig. 3F) <i>E. alleni</i> Shimizu sp. nov.
_	Propodeum without posterior transverse carina (Fig. 4E). Proximal corner of proximal sclerite of fore wing fenestra blunt, angled at ca 65° (Fig. 4F). Fore wing fenestra with one vestigial to strong central sclerite (Fig. 4F).
27 (25)	Central sclerite aval (Fig. 30E). Wings entirely very sparsely setase (Fig. 30E). Enirosoilus sp. 2
_ (23)	Central science ovar (Figs 8F, 14F). Wings entirely densely setose (Figs 8F, 14F).
28 (27)	Central sclerite slender (Fig. 8F). Larger species with fore wing length more than 17.0 mm <i>F. flavicaput</i> (Morley, 1912)
_	Central sclerite stouter (Fig. 14F). Smaller species with fore wing length less than 15.0 mm.

Enicospilus alleni Shimizu, sp. nov.

http://zoobank.orgBCA16349-534C-4CB2-9126-FFC9C451362B Fig. 3

Etymology. The specific name is dedicated to the collector of the holotype, Mike Allen, who collected many specimens of Nepalese Hymenoptera that are now in NHMUK.

Material examined. 12: Nepal.

Type series: holotype \mathcal{Q} , Chautasa (6,000 ft), Nepal, 24.IX.1983, M.G. Allen leg. (NHMUK) (Fig. 3).

Distribution. Nepal.

Description. Female (Holotype) (Fig.3). Body length ca 29.5 mm.

Head with GOI = 2.9 (Fig. 3C). Lower face $0.7 \times$ as wide as high, very finely coriaceous with fine punctures and setae (Fig. 3B). Clypeus $1.9 \times$ as wide as high, shiny

and very finely coriaceous with fine punctures and setae, almost flat in profile, and its lower margin acute (Fig. 3B, C). Malar space $0.2 \times$ as long as basal mandibular width (Fig. 3B, C). Mandible weakly twisted by ca 25°, moderately long, evenly narrowed, its outer surface flat and smooth without a diagonal groove or a diagonal line of punctures (Fig. 3B, C). Upper mandibular tooth 1.4× as long as lower one (Fig. 3B). Frons, vertex and gena moderately shiny with fine setae (Fig. 3B–D). Posterior ocellus large and almost touching eye (Fig. 3B–D). Ventral end of occipital carina joining oral carina. Left antenna complete with 64 flagellomeres, and right antenna apically incomplete with 53 flagellomeres; first flagellomere 1.7× as long as second; 20th flagellomere 1.6× as long as wide.



Figure 3. *Enicospilus alleni* Shimizu sp. nov., ♀, holotype. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Mesosoma entirely very weakly shiny or not (Fig. 3E). Pronotum entirely striate. Mesoscutum $1.5 \times$ as long as its maximum width, very closely coriaceous with dense setae, very weakly shiny, evenly rounded in profile, and its anterior margin almost truncate in dorsal view and rounded in profile (Fig. 3E). Notauli absent (Fig. 3E). Scutellum moderately convex, very closely coriaceous with setae, with lateral longitudinal carinae reaching posterior end (Fig. 3E). Epicnemium densely punctate with setae. Epicnemial carina weak, almost straight and inclined to anterior, its dorsal end not reaching anterior margin of mesopleuron (Fig. 3E). Mesopleuron entirely closely longitudinally strigose (Fig. 3E). Submetapleural carina very strongly broadened anteriorly and forming a lobe. Metapleuron densely punctate to reticulate with setae, moderately swollen (Fig. 3E). Propodeum very strongly and abruptly declivous in profile; anterior transverse carina complete; pleural carina almost absent; anterior area longitudinally striate; spiracular area almost smooth with setae and strongly shiny; posterior area moderately subconcentrically strigose with a pair of strong posterior carinae laterally; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge (Fig. 3E).

Wings. Fore wing length ca 19.5 mm with AI = 1.0, CI = 0.4, DI = 0.3, ICI = 0.6, SDI = 1.6, SI = 0.1, SRI = 0.2; vein 1m-cu&M almost evenly curved; vein 2r&RS very slightly sinuous and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 3F; proximal sclerite triangular, confluent with distal sclerite, strongly pigmented; central sclerite entirely weakly sclerotised, very weakly pigmented partially, positioned in anterodistal part of fenestra; distal sclerite present proximally and absent distally; proximal corner of marginal cell ca 110°; posterodistal corner of subbasal cell ca 95°; vein 1cu-a antefurcal to M&RS by 0.3×1 cu-a length (Fig. 3F). Hind wing with NI = 2.8, RI = 2.2; vein RS straight; vein RA with 10 uniform hamuli.

Legs. Outer surface of fore tibia with scattered short spines. Hind leg with coxa in profile $1.8 \times$ as long as deep; basitarsus $2.0 \times$ as long as second tarsomere; fourth tarsomere $0.6 \times$ as long as third tarsomere and $2.9 \times$ as long as wide; tarsal claw simply pectinate.

Metasoma with DMI = 1.4, PI = 2.7, THI = 3.5; dorsal margin of tergite 1 slightly sinuous in profile; thyridium elliptical (Fig. 3A).

Colour (Fig. 3). Entirely testaceous except for yellow eye orbit and vertex, apex of mandible black. Wings hyaline; fore wing sclerites and pterostigma testaceous; veins testaceous to brown.

Variation. Unknown, only known from the holotype. **Male.** Unknown

Differential diagnosis. The affinities of *E. alleni* sp. nov. are unclear, but it may be related to the *E. flavicaput* group. However, *E. alleni* sp. nov. is a very distinctive species, readily distinguished by many characters, such as the elongate lower face (Fig. 3B), sculpture of the mesosoma (Fig. 3E), shape of propodeum (Fig. 3E), and two vestigial central sclerites of the fore wing fenestra (Fig. 3F).

Enicospilus ashbyi Ashmead, 1904*

Fig. 4

Enicospilus ashbyi Ashmead 1904: 17; holotype ♂, Philippines, USNM. *Henicospilus tainanensis* Uchida 1928: 225; lectotype ♂, Taiwan, SEHU, designated by Gauld and Mitchell (1981: 446), examined; synonymised by Gauld and Mitchell (1981: 446).

Enicospilus concavus Chiu 1954: 45; holotype ♂, Taiwan, TARI, examined; synonymised by Gauld and Mitchell (1981: 446).

Material examined. 11 \bigcirc 4 \bigcirc \bigcirc : Nepal (1 \bigcirc), India (11 \bigcirc \bigcirc), Taiwan (2 \bigcirc \bigcirc).

Type series: lectotype of *Henicospilus tainanensis* Uchida, 1928, ♂, Tainan, Taiwan, S. Takano leg. (SEHU); holotype of *Enicospilus concavus* Chiu, 1954, ∂, Tai-hoku, Taiwan, 24.I.1932, J. Sonan leg. (TARI).

Non-type series: 1, Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT) (NHMUK) (Fig. 4); $9 \bigcirc \bigcirc 1$, Patancheru, Andhra Pradesh, India, VII ($7 \bigcirc \bigcirc 1$) and VIII ($2 \bigcirc \bigcirc$).1980, Bhatnagar leg. (LT) (NHMUK); $1 \bigcirc$, Jeypore, Orissa, India, IX.1958, P.S. Nathan leg. (EMUS); $1 \bigcirc$, Nilgira Hills, India, V. 1953, P.S. Nathan leg. (CNC).

Distribution. Australasian and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 4B–D): GOI = 2.1-2.4; lower face 0.7–0.8× as wide as high; clypeus flat to slightly convex in profile, its lower margin subacute; mandible rather weakly twisted by 25–30°, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.5\times$ as long as lower one; posterior ocellus almost touching eye; antenna with 45– 56 flagellomeres and 20th flagellomere $1.6-1.9\times$ as long as wide.

Mesosoma (Fig. 4E): mesopleuron longitudinally punctostriate to striate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctostriate; propodeum declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 4F): fore wing with AI = 0.7-1.2, CI = 0.2-0.3, ICI = 0.5-0.7, SDI = 1.2-1.3; fore wing vein 1m-cu&M evenly curved, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 4F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite usually partially strongly pigmented and sclerotised, strongly pigmented part linear and parallel to vein 2r&RS, positioned in anterodistal part of fenestra; distal sclerite present proximally and vestigial distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to subinterstitial to M&RS by less than 0.1×1 cu-a length.

Colour (Fig. 4): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. *Enicospilus ashbyi* is similar to *E. pallidus* (Taschenberg, 1875) and separated from it by a few characters of the central sclerite (pigmented part of central sclerite narrower in *E. ashbyi* and wider in *E. pallidus*). However, the sclerite characters (e.g. the shape and degree of sclerotisation of the central sclerite) exhibit a wide range of variation within both species, suggesting that there are cryptic species and that integrative taxonomy is needed to define species limits in this complex.

Enicospilus bifasciatus (Uchida, 1928)*

Fig. 5

Henicospilus bifasciatus Uchida 1928: 222; holotype ♀, Taiwan, SEHU, examined.



Figure 4. *Enicospilus ashbyi* Ashmead, 1904, ♂. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Material examined. $7 \stackrel{\circ}{\downarrow} \stackrel{\circ}{}_3 \stackrel{\circ}{}_{\circ} \stackrel{\circ}{}_{\circ}$: Nepal ($2 \stackrel{\circ}{\downarrow} \stackrel{\circ}{}_{\circ}$), Taiwan ($5 \stackrel{\circ}{\downarrow} \stackrel{\circ}{}_3 \stackrel{\circ}{}_{\circ} \stackrel{\circ}{}_{\circ}$).

Type series: holotype of *Henicospilus bifasciatus* Uchida, 1928, ♀, Baibara, Taiwan, Uchida leg. (SEHU).

Non-type series: $2 \bigcirc \bigcirc$, Godaveri (1,550–1,700 m), Nepal, 1.VI.1984, M.G. Allen leg. (LT) (NHMUK) (Fig. 5); 1 \bigcirc , Bukai, Taiwan, 13.VI.1934, L. Gressitt leg. (NHMUK); 1 \bigcirc , Horisha, Taiwan, V. 1927, Sonan leg. (TARI); 1 \bigcirc , Musha, Taiwan, IV.1938, Sonan leg. (TARI); 1 \circ , Shinten, Taiwan, IV.1921, Sonan leg. (TARI); 2 \bigcirc \bigcirc , Taihoku, Taiwan, I. 1924, Sonan leg. (TARI); 1 \bigcirc , Taipei, Taiwan, V.1950, Chiu leg. (TARI).

Distribution. Oriental region (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 5B–D): GOI = 3.1-3.4; lower face $0.6-0.7 \times$ as wide as high; clypeus moderately convex in profile, its lower margin acute; mandible rather strongly twisted by 55–65°, moderately long,

Figure 5. *Enicospilus bifasciatus* (Uchida, 1928), ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.3 \times$ as long as lower one; posterior ocellus close to eye; antenna with 54–56 flagellomeres and 20th flagellomere $3.1-3.3 \times$ as long as wide.

Mesosoma (Fig. 5E): mesopleuron rather coarsely longitudinally punctostriate to striate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron rather coarsely striate; propodeum evenly weakly rounded, its posterior area

dez.pensoft.net

moderately reticulate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 5F): fore wing with AI = 0.7-1.0, CI = 0.4-0.5, ICI = 0.2, SDI = 1.1-1.2; fore wing vein 1m-cu&M evenly curved, 2r&RS almost straight, centrally broadened; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 5F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite rather weakly pigmented and sclerotised, drop-shaped and its major axis parallel to vein 2r&RS, positioned in mediodistal part of fenestra; distal sclerite present proximally and vestigial distally; proximal corner of marginal cell of fore wing very sparsely setose, almost glabrous; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2×1 cu-a length.

Colour (Fig. 5): body entirely pale yellow with black marks on mesosoma, interocellar area, and posterior segments of metasoma; wings hyaline with two strongly infumate patches in the central part of the discosubmarginal cell (from anterior end of M&RS to base of 1m-cu&M) and the central part of the marginal cell (from anterocentral margin to base of RS).

Differential diagnosis. *Enicospilus bifasciatus* is a very distinctive species and no closely related species are currently known. Hence, it is easily distinguished from all *Enicospilus* by many characters listed in the above diagnosis as well as identification key, such as two strongly infumate patches in the central part of the discosubmarginal cell (from anterior end of M&RS to base of 1m-cu&M) and the central part of the marginal cell (from anterocentral margin to base of RS) of fore wing, characteristic shape of sclerites of discosubmarginal cell of fore wing (cf. Fig. 5F), very sparsely setose and almost glabrous proximal corner of marginal cell of fore wing, and small value of ICI (= 0.2).

Enicospilus biharensis Townes, Townes & Gupta, 1961

Figs 2I, 6

Henicospilus horsfieldi var glabratus Morley 1913: 395; holotype ♀, India, NHMUK, examined; junior secondary homonym of Enicospilus glabratus (Say, 1835).

Enicospilus biharensis Townes, Townes and Gupta 1961: 271; replacement name for *Henicospilus horsfieldi* var. *glabratus* Morley, 1913.

Enicospilus (Bicorniata) bicornis Rao and Nikam 1971a: 177; holotype ♀, India, MUC; synonymised by Nikam (1980: 149).

Material examined. 11 \bigcirc 13 Nepal (10 \bigcirc 13), India (1).

Type series: holotype of *Henicospilus horsfieldi* var *glabratus* Morley, 1913 (= *Enicospilus biharensis* Townes, Townes & Gupta, 1961), \bigcirc , Bihar, Chapra, India (NHMUK, Type 3b.1266).

Non-type series: 1^{\bigcirc} , Dotslghst (900 m), Nepal, 7.VII.1983, M.G. Allen leg. (Figs 2I, 6); 2^{\bigcirc}_{\bigcirc} , Kathman-

du (4,300'), Nepal, VIII.1981, M.G. Allen leg.; 1° , Kathmandu (1,300 m), Nepal, X.1982, M.G. Allen leg. (LT); 1° , Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT); 1° , Kathmandu (1,400 m), Nepal, IX.1983, M.G. Allen leg. (LT); 1° , Kathmandu (1,500 m), Nepal, III.1983, M.G. Allen leg. (LT); 1° , Kathmandu (1,500 m), Nepal, III.1983, M.G. Allen leg. (LT); 1° , Sec. Vegetation (1,390 m), B. Embassy, Kathmandu, Nepal, VI.1983, M.G. Allen leg. (LT); 2°° , Dolalghat (900 m), Nepal, 7.VII.1983, M.G. Allen leg.; 1° , Chautara (6,000'), Nepal, 24.IX.1983, M.G. Allen leg. (all NHMUK).

Distribution. Eastern Palaearctic and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 6B–D): GOI = 2.5-3.2; lower face $0.6-0.8 \times$ as wide as high; clypeus almost flat in profile, its lower margin acute; mandible moderately twisted by $30-40^\circ$, moderately long, evenly strongly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.3 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 53–64 flagellomeres and 20^{th} flagellomere $1.7-2.1 \times$ as long as wide.

Mesosoma (Fig. 6E): mesopleuron densely punctate to closely longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron densely punctate; propodeum declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 6F): fore wing with AI = 0.6-0.7, CI = 0.3-0.5, ICI = 0.7-0.8, SDI = 1.2-1.4; fore wing vein 1m-cu&M evenly curved, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 6F; fenestra of fore wing not long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite linear, separated from or vestigially confluent with distal one, weakly pigmented; central sclerite absent; distal sclerite present proximally, vestigial to moderately strong distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.2-0.3 \times 1$ cu-a length.

Colour (Fig. 6): body including interocellar area entirely testaceous; wings hyaline to slightly infuscate.

Differential diagnosis. Enicospilus biharensis is similar to *E. maruyamanus*, *E. nikami* sp. nov., *E. pudibundae*, and *E. transversus*, but can be distinguished from *E. maruyamanus*, *E. nikami* sp. nov., and *E. transversus* by the evenly curved fore wing vein 1m-cu&M (Fig. 6F) (more or less sinuous in *E. maruyamanus*, *E. nikami* sp. nov., and *E. transversus*, e.g. as in Figure 19F), and from *E. nikami* sp. nov. and sp. nov. a

Enicospilus capensis (Thunberg, 1824)* Fig. 7

Ichneumon capensis Thunberg 1824: 262; holotype ♀, South Africa, ZIUU.

Figure 6. *Enicospilus biharensis* Townes, Townes & Gupta, 1961, ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

- *Ophion lativertex* Taschenberg 1875: 435; holotype ♀, Java, FZLU; synonymised by Gauld and Mitchell (1981: 385).
- Ophion antankarus Saussure 1892: 15; type ♂, Madagascar, MNHN; synonymised by Townes and Townes (1973: 174).
- *Henicospilus montinus* Enderlein 1921: 21; holotype ♀, Java, IZPAN; synonymised by Gauld and Mitchell (1981: 385).
- *Henicospilus praedator* Enderlein 1921: 28; holotype ♀, Madagascar, IZPAN; synonymised by Townes and Townes (1973: 175).
- Henicospilus incarinatus Enderlein 1921: 30; holotype A, Madagascar, IZPAN; synonymised by Townes and Townes (1973: 175).
- Henicospilus euxoae Wilkinson 1928: 261; holotype ♀, Zimbabwe, NHMUK, examined; synonymised by Gauld and Mitchell (1978: 143).
- *Enicospilus obnoxius* Seyrig 1935: 75; lectotype ♀, Kenya, MNHN, designated by Townes and Townes (1973: 18); synonymised by Gauld and Mitchell (1978: 143).
- Henicospilus yanagiharai Sonan 1940: 371; holotype ♂, Ryûkyû Island, TARI, examined; synonymised by Gauld and Mitchell (1981: 385).
- *Enicospilus selvaraji* Rao and Kurian 1950: 174, 178, 180, 188; nomen nudum.

- *Enicospilus selvaraji* Rao and Kurian 1951: 68; holotype ♀, India, ZSI; synonymised by Gauld and Mitchell (1981: 385).
- *Enicospilus fossatus* Chiu 1954: 63; holotype ♀, Malaysia, TARI, examined; synonymised by Gauld and Mitchell (1981: 385).
- *Enicospilus indica* Rao and Grover 1960: 280; holotype ♀, India, MUC, destroyed (cf. Gauld and Mitchell 1981: 385); synonymised by Gauld and Mitchell (1981: 385).

Type series: holotype of *Henicospilus yanagiharai* Sonan, 1940, δ , Kitadaitô-jima, Okinawa Pref., Ryûkyûs, Japan, 18.III.1939, M. Yanagihara leg. (TARI); holotype of *Enicospilus fossatus* Chiu, 1954, Q, Jahore, Malaysia, 1.X.1916, J. Sonan leg. (TARI); holotype of *Henicospilus euxoae* Wilkinson, 1928, Q, Salisbury, Zimbabwe, 31.XII.1927, J.I. Roberts leg. (from *Euxoa*) (NHMUK, Type 3b.1289).

Non-type series: 1^Q, Chitwan (200 m), Terai, Nepal, 12–13.III.1983. M.G. Allen leg. (Fig. 7); 1♀5♂♂, Coimbatore, India, III–IV.1935, P.S. Nathan leg.; 55 \bigcirc 36 \bigcirc Andhra Pradesh, Patancheru, India, I $(26 \bigcirc \bigcirc 19 \bigcirc \bigcirc)$, II (1°) , VII (1°) , IX (1°) , X (2°) , XI $(7^{\circ})^{\circ}4^{\circ}\delta^{\circ}$), XII $(18 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{} 12 \stackrel{\bigcirc}{} \stackrel{\bigcirc}{} 12 \stackrel{\bigcirc}{} \stackrel{\bigcirc}{} 1980$, Bhatnagar leg. (LT) (all NHMUK); 1^Q, Agra, India, IX.1955, V.K. Gupta leg. (EMUS); 1 unsexed, Asir, Suda, Saudi Arabia, 5.VII.1962, G. Popoy leg.; 1 unsexed, Bekily, Madagascar, VIII.1933, A. Seyrig leg.; 1 \bigcirc , Madagascar, XII.1920, A. Seyrig leg.; 2 \bigcirc \bigcirc , Ruwenzori Range, Ibanda, Uganda, 20–21.VIII (1^o), 4–12. IX (1 $\stackrel{\circ}{\downarrow}$).1952, D.S. Fletcher leg.; 1 $\stackrel{\circ}{\supset}$, Nairobi, Kenya, 10–12.XII.1952, C.G.M. de Worms leg.; 1° , Kenya; 1° and 1 unsexed, Kabete, Kenya, III.1929, H.E. Box leg. (all NHMUK); 1[♀], Grahamstown, South Africa, 10–12. III.1971, F. Gess leg. (CNC).

Distribution. Afrotropical, Australasian, Oceanic, and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 7B–D): GOI = 1.5-2.0; lower face $0.8-1.0 \times$ as wide as high; clypeus rather strongly convex in profile, its lower margin impressed; mandible weakly twisted by $10-20^{\circ}$, long, proximally tapered and distally parallel sided, its outer surface with a diagonal setose groove between its dorsoproximal corner and base of mandibular apical teeth; upper mandibular tooth $2.5-3.0 \times$ as long as lower one; posterior ocellus separated from eye by $0.1-0.2 \times$ its own maximum diameter; antenna with 44–66 flagellomeres and 20^{th} flagellomere $1.6-2.0 \times$ as long as wide.

Mesosoma (Fig. 7E): mesopleuron densely punctate, submatt to matt; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron densely punctate, submatt to matt; propodeum declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge. *Wings* (Fig. 7F): fore wing with AI = 0.4-0.8, CI = 0.3-0.6, ICI = 0.4-0.6, SDI = 1.3-1.5; fore wing vein 1m-cu&M slightly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 7F; fenestra of fore wing not long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, not confluent with distal one, strongly pigmented; central sclerite rather weakly to strongly pigmented and sclerotised, and ill-delineated oval to semicircular, positioned in anteroto mediodistal part of the fenestra; distal sclerite absent proximally and strong distally; proximal corner of marginal cell of fore wing approximately uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.3×1 cu-a length.

Colour (Fig. 7): body including interocellar area entirely yellow- to red-brown; wings hyaline.

Differential diagnosis. *Enicospilus capensis* is most similar to *E. insularis* and distinguished from it by the not clearly delineated central sclerite (Fig. 7F) (well delineated in *E. insularis*), but diagnostic characters for these species are not strongly supported and need more study. *Enicospilus capensis* also more or less resembles *E. ramidulus*, but distinguished from it by the densely punctate and submatt to matt meso- and metapleurae (Fig. 7E) (meso- and metapleurae moderately punctate and never submatt to matt in *E. ramidulus*).

Enicospilus flavicaput (Morley, 1912) Fig. 8

- *Enicospilus xanthocephalus* Cameron 1907: 178; holotype ♀, Myanmar, NHMUK, examined; junior primary homonym of *Enicospilus xanthocephalus* Cameron, 1905.
- Henicospilus flavicaput Morley 1912: 45; replacement name for Enicospilus xanthocephalus Cameron, 1907.
- *Henicospilus urospilus* Enderlein 1921: 27; holotype ♀, Sumatra, IZ-PAN; synonymised by Townes et al. (1961: 72).

Material examined. $5 \bigcirc \bigcirc$ and 1 unsexed: Brunei $(3 \bigcirc \bigcirc)$, Indonesia $(1 \bigcirc)$, Myanmar $(1 \bigcirc)$, Sri Lanka (1 unsexed); no Nepalese specimens were examined.

Type series: holotype of *Enicospilus xanthocephalus* Cameron, 1907 (= *Henicospilus flavicaput* Morley, 1912), ♀, Haundraw Valley, Tenasserim, Myanmar, VIII.1894, C.T. Bingham leg. (NHMUK, Type 3b.1233).

Non-type series: $1\bigcirc$, U. Temburong (1,500 m), Bukit Retak, Brunei, IV.1981, I.D. Gauld leg. (Fig. 8); $1\bigcirc$, Montane forest (1,618 m), Bukit Retak, Brunei, V.1979, I.D. Gauld leg.; $1\bigcirc$, Pagon Ridge, Pagon, Brunei, II.1982, G. Allen leg.; $1\bigcirc$, Perliawatte (1,200–1,500 m), Mt Gede, West Java, Indonesia, I.1938; 1 unsexed, near Mahiyangana, Badulla Dist., Sri Lanka, 24.V.1974, Gans & Prasanna leg. (all NHMUK).

Distribution. Australasian and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Figure 7. *Enicospilus capensis* (Thunberg, 1822), ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Diagnosis. *Head* (Fig. 8B–D): GOI = 2.9-3.1; lower face $0.6-0.7 \times$ as wide as high; clypeus weakly convex in profile, its lower margin subacute; mandible moderately

twisted by $30-40^{\circ}$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.3-1.6 \times$ as long as lower one; posterior ocellus

Figure 8. *Enicospilus flavicaput* (Morley, 1912), ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

close to eye; antenna with 71–76 flagellomeres and 20^{th} flagellomere $2.3-2.5 \times$ as long as wide.

Mesosoma (Fig. 8E): mesopleuron rather coarsely longitudinally striate; scutellum with lateral longitudinal carinae reaching anterior 0.8–1.0 and convergent posteriorly; metapleuron rather coarsely striate to strigose; propodeum evenly rounded to slightly declivous, its posterior area coarsely reticulate, outer margin of propodeal spiracle joining pleural carina by a strong ridge. *Wings* (Fig. 8F): fore wing with AI = 0.3-0.4, CI = 0.2-0.4, ICI = 0.6-0.7, SDI = 1.2-1.4; fore wing vein 1m-cu&M weakly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 8F; fenestra of fore wing not long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite strongly pigmented and sclerotised, linear and parallel to vein 2r&RS, positioned in anterodistal part of fenestra; distal sclerite present proximally and vestigial to absent distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.1-0.2 \times 1$ cu-a length.

Colour (Fig. 8): body including interocellar area entirely testaceous; wings hyaline to weakly infuscate.

Differential diagnosis. *Enicospilus flavicaput* is most similar to *E. kanshirensis* but can be distinguished from it by the slender central sclerite (Fig. 8F) (central sclerite stouter in *E. kanshirensis*, as in Figure 14F), and larger body size (i.e. fore wing length more than 17.0 mm in *E. flavicaput* but less than 15.0 mm in *E. kanshirensis*).

Enicospilus flavocephalus (Kirby, 1900)*

Fig. 9

Ophion flavocephalus Kirby 1900: 82; lectotype ♂, Christmas Island, NHMUK, examined, designated by Gauld (1977: 79).

Henicospilus lunulatus Szépligeti 1906: 143; holotype &, Bismarck Island, TM; synonymised by Gauld and Mitchell (1981: 416).

Henicospilus albicaput Morley 1912: 50; holotype ♂, Australia, NHMUK, examined; synonymised by Townes et al. (1961: 275).

Henicospilus similis Matsumura and Uchida 1926: 221; holotype 3, Ryûkyû Island, SEHU, examined; synonymised by Uchida (1928: 221).

Material examined. $13 \bigcirc \bigcirc 11 & \bigcirc 13 \bigcirc \bigcirc 11 & \bigcirc 13 \bigcirc 011 & 01$

Type series: lectotype of *Ophion flavocephalus* Kirby, 1900, ♂, Flying Fish Cove, Christmas Island, Australia, C.W. Andrews leg. (NHMUK, Type 3b.1273); holotype of *Henicospilus albicaput* Morley, 1912, ♂, Mackay, Queensland, Australia (NHMUK, Type 3b.1254); holotype of *Henicospilus similis* Matsumura & Uchida, 1926, ♂, Okinawa, Ryûkyûs, Japan, S. Sakaguchi leg. (SEHU).

Non-type series: 1♀, Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT) (Fig. 9); 1♀, Kathmandu (1,300 m), Nepal, XI.1982, M.G. Allen leg. (LT); 1∂, Pokhara, Nepal, VIII.1982, M.G. Allen leg. (LT); $5 \bigcirc \bigcirc$, Christmas Island, Australia, 1939; 1 unsexed, Christmas Island, Australia, 1898, C.W. Andrews leg.; 1∂, Ulu Temburong (300 m), Base camp hut, Brunei, 16.II-9.III.1982, M.C. Day leg.; 1^Q, Pagon, Pagon Ridge, Brunei, II.1982, M.G. Allen leg.; 1^Q, Bukit Retak (1,618 m), Montane forest, Brunei, IX.1979, I.D. Gauld leg.; 1♀, Singapore, 1908, H.N. Ridley leg. (all NHMUK); 1[♀], Wanfeng Hill, Taichung, Taiwan, VII.1984, K.S. Lin & K.C. Chou leg. (MsT); 1∂, Kukuan (730 m), Taichung, Taiwan, 14– 17.X.1980, K.S. Lin & C.H. Wang leg.; 1♀1♂, Pingtung, Taiwan, IV.1961, K.S. Lin leg. (LT); 1♀1♂, Silo, Yunlin, Taiwan, V.1961, K.S. Lin leg. (LT); 13, Lishan, Taichung, Taiwan, 14.IX.1978; 233, Chung-ying, Taiwan, III.1961, S.C. Chiu leg. (all TARI).

Distribution. Australasian, Oceanic, and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 9B–D): GOI = 2.5-2.9; lower face $0.5-0.7 \times$ as wide as high; clypeus very slightly convex in profile, its lower margin subacute to blunt; mandi-

ble moderately twisted by $25-35^{\circ}$, moderately long, more or less evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.1-1.2 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 45–51 flagellomeres and 20^{th} flagellomere $1.8-2.3 \times$ as long as wide.

Mesosoma (Fig. 9E): mesopleuron punctate to longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron moderately strigose to striate; propodeum evenly rounded, its posterior area rather finely reticulate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 9F): fore wing with AI = 0.4-1.5, CI = 0.6-0.8, ICI = 0.4-0.6, SDI = 1.1-1.2; fore wing vein 1m-cu&M centrally strongly angulated and broadened, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 9F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite almost oval, isolated and not touching margin of fenestra, strongly pigmented; central sclerite strongly pigmented and sclerotised, linear and parallel to distal margin of the fenestra; distal sclerite absent; proximal corner of marginal cell of fore wing almost uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2×1 cu-a length.

Colour (Fig. 9): body including interocellar area entirely pale yellow with pale brown posterior segments of metasoma; wings hyaline.

Differential diagnosis. *Enicospilus flavocephalus* is a very distinctive species, but its body size, colour pattern, and profile are very similar to *E. xanthocephalus. Enicospilus flavocephalus* is easily distinguished from *E. xanthocephalus* by many characters, such as the pale yellow interocellar area (Fig. 9B, D) (black in *E. xanthocephalus*) and centrally abruptly angled and broadened fore wing vein 1m-cu&M (Fig. 9F) (evenly curved in *E. xanthocephalus*).

Enicospilus formosensis (Uchida, 1928)* Figs 2E, 10

- Henicospilus formosensis Uchida 1928: 223; holotype ♀, Taiwan, SEHU, examined.
- *Enicospilus saepis* Chiu 1954: 77; holotype ♀, Japan, TARI, examined; synonymised by Gauld and Mitchell (1981: 424).

Material examined. $2 \stackrel{\frown}{}_{\downarrow} \stackrel{\frown}{}_{?} \stackrel{\frown}{}_{?} \stackrel{\circ}{}_{?} \stackrel{\circ}{}_{$

Type series: holotype of *Henicospilus formosensis* Uchida, 1928, \bigcirc , Baibara, Taiwan, 15.VI.1926, Y. Saito & Kikuchi leg. (SEHU); holotype of *Enicospilus saepis* Chiu, 1954, \bigcirc , Nara, Honshû, Japan, 17.VIII.1918, J. Sonan leg. (TARI).

Non-type series: $1 \circlearrowleft$, mixed forest (1,550 m), Godaveri, Nepal, 6.V.1984, M.G. Allen leg. (LT) (Figs 2E, 10); $1 \circlearrowright$, Ulu Temburong (1,000 m), Brunei, II.1980, M.G.

Figure 9. *Enicospilus flavocephalus* (Kirby, 1900), Q. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Figure 10. *Enicospilus formosensis* (Uchida, 1928), A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Allen leg.; 1 unsexed, NW Himalaya, Dalhousie, India, 8.VII.1965, Tikar leg. (all NHMUK).

Distribution. Eastern Palaearctic and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 10B–D): GOI = 2.2-2.4; lower face $0.8-0.9 \times$ as wide as high; clypeus moderately convex in profile, its lower margin subacute to blunt; mandible weakly twisted by $10-20^{\circ}$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.4 \times$ as long as

dez.pensoft.net

lower one; posterior ocellus close to eye; antenna with 66-69 flagellomeres and 20^{th} flagellomere $2.1-2.2 \times$ as long as wide.

Mesosoma (Fig. 10E): mesopleuron moderately punctate; scutellum with lateral longitudinal carinae reaching anterior 0.8 or more and weakly convergent posteriorly so that subquadrate (Fig. 2E); metapleuron punctate with isolated striae; propodeum declivous in profile, its posterior area coarsely irregularly wrinkled, sometimes with posterior transverse carina laterally, outer margin of propodeal spiracle joining pleural carina by a ridge or not.

Wings (Fig. 10F): fore wing with AI = 0.2-0.6, CI = 0.2-0.9, ICI = 0.5-0.6, SDI = 1.1-1.3; fore wing vein 1m-cu&M weakly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 10F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite moderately to strongly pigmented and sclerotised, linear and parallel to distal margin of fenestra, positioned in distal part of fenestra; distal sclerite present proximally and vestigial to absent distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2×1 cu-a length.

Colour (Fig. 10): body including interocellar area testaceous; wings weakly infumate.

Differential diagnosis. *Enicospilus formosensis* is a distinctive species and can easily be distinguished by many characters, such as the wide face (Fig. 10B), shape of the central sclerite (Fig. 10F), more or less subquadrate scutellum (Fig. 2E), as listed in the diagnosis.

Enicospilus grammospilus (Enderlein, 1921)* Fig. 11

Dicamptus grammospilus Enderlein 1921: 17; holotype ♂, Sumatra, IZPAN, photos examined.

Material examined. $14 \stackrel{\circ}{\downarrow} 23 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$: Nepal $(1 \stackrel{\circ}{\downarrow})$, Indonesia $(1 \stackrel{\circ}{\circ})$, Brunei $(13 \stackrel{\circ}{\downarrow} 22 \stackrel{\circ}{\circ} \stackrel{\circ}{\circ})$.

Type series: holotype of *Dicamptus grammospilus* Enderlein, 1921, ♂, Soekaranda, Sumatra, Indonesia, Dohrn leg. (IZPAN) [photos examined].

Non-type series: $1\bigcirc$, Pokhara (950 m), Nepal, VII– VIII.1983, M.G. Allen leg. (LT) (Fig. 11); $2\bigcirc \bigcirc 1 \circlearrowleft$, Montane Forest (1,618 m), Bukit Retak, Brunei, IX.1979, I.D. Gauld leg.; $8\oslash \bigcirc 1 \textdegree$, Bukit Retak (1,500 m), U. Temburgon, Brunei, IV.1981, I.D. Gauld leg.; $2\oslash \bigcirc$, Pagon (1,700 m), U. Temburong, Brunei, IV.1981, I.D. Gauld leg.; $1\bigcirc$, Pagon Ridge, Pagon, Brunei, II.1982, M.G. Allen leg. (all NHMUK).

Distribution. Oriental region (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 11B–D): GOI = 2.5-2.7; lower face $0.7-0.8 \times$ as wide as high; clypeus almost flat in profile, its lower margin acute; mandible moderately twisted by 20–30°, moderately long, proximally tapered and distally almost subparallel sided, its outer surface without a diagonal structure; upper mandibular tooth $1.4-1.5 \times$ as long as lower one; posterior ocellus (almost) touching eye; antenna with 58–62 flagellomeres and 20^{th} flagellomere $1.7-1.9 \times$ as long as wide.

Mesosoma (Fig. 11E): mesopleuron punctate dorsally and rather closely longitudinally punctostriate to striate ventrally; scutellum with lateral longitudinal carinae reaching anterior 0.8 or more and convergent posteriorly; metapleuron rather closely striate; propodeum declivous in profile, its posterior area concentrically striate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 11F): fore wing with AI = 0.8–1.4, CI = 0.5–0.6, ICI = 0.4–0.5, SDI = 1.4–1.5; fore wing vein 1m-cu&M almost evenly curved, 2r&RS weakly bowed centrally; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 11F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite not triangular, confluent with distal one, weakly to strongly pigmented; central sclerite weakly to strongly pigmented and sclerotised, linear and parallel to vein 2r&RS, positioned in central part of fenestra; distal sclerite weak; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.1×1 cu-a length.

Colour (Fig. 11): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. *Enicospilus grammospilus* is a very distinctive species on account of its characteristic shape of fore wing vein 2r&RS and sclerites as in Figure 11F. No similar species are recognised and is very easily distinguished from all other *Enicospilus* species by the characters summarised in the above diagnosis, such as concentrically striate posterior area of propodeum and characteristic shape of sclerites of discosubmarginal cell of fore wing (cf. Fig. 11F).

Enicospilus javanus (Szépligeti, 1910) Fig. 12

Henicospilus javanus Szépligeti 1910: 93; holotype ♀, Java, TM.
Enicospilus fulacorensis Brues 1918: 117; holotype ♀, Solomon Island,
MCZ; synonymised by Gauld and Mitchell (1981: 260).

- *Enicospilus gephyrus* Chiu 1954: 32; holotype ♀, Japan, TARI, examined; synonymised by Gauld and Mitchell (1981: 260).
- *Enicospilus (Bicorniata) diurnus* Nikam 1975: 193, 194; holotype ♀, India, MUC; synonymised by Gauld and Mitchell (1981: 260).

Material examined. $44 \ constant 44 \ co$

Non-type series: $2 \bigcirc \bigcirc 1 \oslash$, Kakani (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); $3 \bigcirc \bigcirc$, Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT) (Fig. 12); $1 \oslash$, Pokhara, Nepal, VIII.1982, M.G. Allen leg. (LT); $2 \bigcirc \bigcirc 1 \oslash$, Gn. Pagon (1,700 m), U. Temburong, Brunei, IV.1981, I.D. Gauld leg.; $24 \oslash \bigcirc$, Bukit Retak (1,500 m), U. Temburong, Brunei, IV.1981, I.D. Gauld leg.; $24 \oslash \bigcirc$, Bukit Retak (1,500 m), U. Temburong, Brunei, IV.1981, I.D. Gauld leg.; $2 \oslash \bigcirc$, Pagon Ridge, Pagon, Brunei, II.1982, I.D. Gauld leg.; $2 \oslash \bigcirc$, 1' forest (500 m), U. Temburong, Brunei, IV.1981, I.D. Gauld leg.; $1 \oslash$, Thekkadi, Periyar Dam, Travancore, India, 6–10.V.1937; $1 \heartsuit$, Andhra Pradesh, Patancheru, India, XII.1980, Bhatnagar leg. (LT); $1 \heartsuit$, Wau (1,200 m),

Figure 11. *Enicospilus grammospilus* (Enderlein, 1921), \bigcirc . **A.** Habitus; **B.** Head, frontal view; **C.** Head, lateral view; **D.** Head, dorsal view; **E.** Mesosoma, lateral view; **F.** Central part of fore wing.

Morobe Dist., Papua New Guinea, X.1979, I.D. Gauld leg.; $3 \bigcirc \bigcirc$, Mt Lawes (400 m), Port Moresby, Papua New Guinea, 5.III–12.V.1963, W.W. Brandt leg.; $1\bigcirc$, Singapore, 1901, H.N. Kidley leg.; $1\bigcirc$, Peradeniya, Sri Lanka, 25.VII.1919, N.K. Jardine leg.; $1\bigcirc$, Matale (1,500 m), Sri Lanka, 10.V.1919, N.K. Jardine leg. (all NHMUK).

Distribution. Australasian, Eastern Palaearctic, and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Figure 12. *Enicospilus javanus* (Szépligeti, 1910), Q. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Diagnosis. *Head* (Fig. 12B–D): GOI = 2.7-3.2; lower face $0.7-0.8 \times$ as wide as high; clypeus moderately convex in profile, its lower margin blunt; mandible moderately twisted by $15-30^\circ$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.5 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 55-62 flagellomeres and 20^{th} flagellomere $2.0-2.5 \times$ as long as wide.

Mesosoma (Fig. 12E): mesopleuron dorsally punctate to longitudinally striate and ventrally longitudinally striate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron striate; propodeum declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 12F): fore wing with AI = 1.1-1.8, CI = 0.2-0.5, ICI = 0.4-0.6, SDI = 1.0-1.1; fore wing vein 1m-cu&M evenly curved, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 12F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite not triangular, confluent with distal one, at least anteriorly very strongly pigmented; central sclerite absent; distal sclerite more or less strong and rather thick; proximal corner of marginal cell of fore wing more or less uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than $0.1 \times$ 1cu-a length.

Colour (Fig. 12): body including interocellar area entirely testaceous; wings hyaline to slightly infumate.

Differential diagnosis. *Enicospilus javanus* is distinctive and one of the most easily distinguishable species on account of the proximally extended fore wing fenestra and the shape of the sclerites (cf. Fig. 12F).

Enicospilus kakanicus Shimizu, sp. nov.

http://zoobank.orgCF0FE094-738D-4491-8EBA-3C673E97C238 Figs 2F, 13

Etymology. The specific name is derived from the type locality, Kakani, Nepal.

Material examined. 1*^(†)*: Nepal.

Type series: holotype ♂, Kakani (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT) (NHMUK) (Figs 2F, 13). **Distribution.** Nepal.

Description. Male (Holotype) (Fig. 13). Body length ca 24.0 mm.

Head with GOI = 2.8 (Fig. 13C). Lower face $0.7 \times$ as wide as high, moderately punctate with setae, strongly shiny (Fig. 13B). Clypeus $1.5 \times$ as wide as high, moderately punctate with setae, moderately convex in profile, and its lower margin impressed (Fig. 13B, C). Malar space $0.4 \times$ as long as basal mandibular width (Fig. 13B, C). Malar space $0.4 \times$ as long as basal mandibular width (Fig. 13B, C). Mandible moderately twisted by ca 30°, moderately long, more or less evenly tapered, its outer surface with a diagonal setose groove between its dorsoproximal corner to base of mandibular apical teeth (Fig. 13B, C). Upper mandibular tooth 2.0 \times as long as lower one (Fig. 13B).

Frons, vertex and gena strongly shiny with fine setae (Fig. 13B–D). Posterior ocellus close to eye (Fig. 13B–D). Ventral end of occipital carina joining oral carina. Antenna with 73 flagellomeres; first flagellomere $1.7 \times$ as long as second; 20th flagellomere $2.8 \times$ as long as wide.

Mesosoma entirely moderately to strongly shiny with setae (Fig. 13E). Pronotum punctate with wrinkles centrally. Mesoscutum 1.4× as long as its maximum width, finely punctate with setae, and evenly rounded in lateral profile (Fig. 13E). Notauli absent (Fig. 13E). Scutellum moderately convex, finely punctate with setae, with lateral longitudinal carinae reaching anterior 0.6 (Fig. 2F). Epicnemium densely punctate. Epicnemial carina strongly present, evenly and moderately curved to anterior, its dorsal end reaching anterior margin of mesopleuron (Fig. 13E). Mesopleuron entirely punctate with longitudinal wrinkles or striae (Fig. 13E). Submetapleural carina almost parallel sided (Fig. 13E). Metapleuron entirely finely punctate with setae (Fig. 13E). Propodeum weakly evenly rounded in profile; anterior transverse carina complete; anterior area longitudinally striate; spiracular area finely punctate with setae; posterior area moderately longitudinally strigose centrally and irregularly wrinkled to reticulate laterally; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge (Fig. 13E).

Wings. Fore wing length ca 17.0 mm with AI = 0.4, CI = 0.4, DI = 0.3, ICI = 0.5, SDI = 1.4, SI = 0.1, SRI = 0.3; vein 1m-cu&M almost evenly curved; vein 2r&RS straight and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 13F; proximal sclerite triangular, confluent with distal sclerite, strongly pigmented; central sclerite absent; distal sclerite more or less entirely present from base to apex, weakly to moderately pigmented; proximal corner of marginal cell evenly setose; posterodistal corner of second discal cell ca 95°; posterodistal corner of subbasal cell ca 95°; vein 1cu-a antefurcal to M&RS by 0.2× 1cu-a length (Fig. 13F). Hind wing with NI = 1.8, RI = 1.8; vein RS straight; vein RA with six uniform hamuli.

Legs. Outer surface of fore tibia with scattered spines. Hind leg with coxa in profile $1.9 \times$ as long as deep; basitarsus $2.0 \times$ as long as second tarsomere; fourth tarsomere $0.6 \times$ as long as third tarsomere and $4.2 \times$ as long as wide; tarsal claw simply pectinate.

Metasoma with PI = 3.8, DMI = 1.2, THI = 3.6; dorsal margin of tergite 1 not sinuous; thyridium elongate (Fig. 13A).

Colour (Fig. 13). Entirely testaceous except for apex of mandible black. Wings hyaline; sclerites of fenestra and veins testaceous.

Variation. Unknown.

Female. Unknown.

Differential diagnosis. Enicospilus kakanicus sp. nov. is similar to and can be confused with *E. longitarsis* Tang, 1990, *E. tangi* sp. nov., and *E. yonezawanus* (Uchida, 1928). These species all belong to the *E. ramidulus* complex and share the following characters: outer surface of mandible with a diagonal setose deep groove

Figure 13. *Enicospilus kakanicus* Shimizu sp. nov., \mathcal{O} . A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

between its dorsoproximal corner and base of mandibular apical teeth (e.g. Fig. 2B, D), fore wing fenestra without central sclerite (e.g. Figs 13F, 25F, 27F), and proximal sclerite triangular (e.g. Figs 13F, 25F, 27F). *Enicospilus kakanicus* sp. nov. is distinguished from the above species by the rather short lateral longitudinal carinae of the scutellum, i.e. reaching the anterior 0.6 of the scutellum in *E. kakanicus* sp. nov., as in Figure 2F, but almost always reaching the posterior end of the scutellum in *E. longitarsis* Tang, 1990, *E. tangi* sp. nov., and *E. yonezawanus*, as in, e.g., Figure 2H, and also by the characters used in the above key, such as width of lower face, mandibular shape and length, and surface sculptures of metapleuron.

Enicospilus kanshirensis (Uchida, 1928) Fig. 14

- Henicospilus kanshirensis Uchida 1928: 226; holotype 3, Taiwan, SEHU, examined.
- *Enicospilus sauteri* Cushman 1937: 310; holotype ♂, Taiwan, DEI; junior secondary homonym of *Enicospilus sauteri* Enderlein, 1921; synonymised by Gauld and Mitchell (1981: 459).
- *Enicospilus cushmani* Chiu 1954: 45; replacement name for *Enicospilus sauteri* Cushman, 1937; synonymised by Gauld and Mitchell (1981: 459).

Type series: holotype of *Henicospilus kanshirensis* Uchida, 1928, ♂, Kanshirei [= Gauziling], Tainan, Taiwan, 15.IV.1908, S. Matsumura leg. (SEHU).

Non-type series: 1 \bigcirc , Dharan Sal & 2^y forest (330m), Terai, Nepal, 14–15.XI.1983, M.G. Allen leg. (Fig. 14); 1 \bigcirc , Anamalai Hills (3,500'), Cinchona, India, V.1957, P.S. Nathan leg.; 1 \bigcirc , Tjigaeha, Mt Djampang, West Java, Indonesia, I.1938, K.M. Walsh leg.; 1 \bigcirc , Tengah, Mt Tjioeng, Djampang Mts, West Java, Indonesia, I.1938, K.M. Walsh leg.; 1 \bigcirc , Sunmoon Lake, Taiwan, 22–29.IX.1970, Shui-Chen Chiu leg. (all NHMUK).

Distribution. Australasian and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 14B–D): GOI = 2.8-3.1; lower face $0.7 \times$ as wide as high; clypeus moderately convex in profile, its lower margin subacute to blunt; mandible moderately twisted by $20-30^{\circ}$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.4-1.6 \times$ as long as lower one; posterior ocellus close to eye; antenna with 63-66 flagellomeres and 20^{th} flagellomere $2.1-2.3 \times$ as long as wide.

Mesosoma (Fig. 14E): mesopleuron entirely closely to rather coarsely longitudinally striate; scutellum with lateral longitudinal carinae reaching anterior 0.8 or more and convergent posteriorly; metapleuron rather coarsely striate to strigose; propodeum weakly declivous, its posterior area coarsely reticulate to concentrically striate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 14F): fore wing with AI = 0.4-0.5, CI = 0.2-0.3, ICI = 0.5-0.7, SDI = 1.1-1.3; fore wing vein 1m-cu&M moderately sinuate, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 14F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite almost triangular, confluent with distal one, strongly pigmented; central sclerite strongly pigmented and sclerotised, linear and parallel to vein 2r&RS, positioned in anterodistal part of fenestra; distal sclerite present proximally and vestigial to absent distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.1-0.2 \times 1$ cu-a length.

Colour (Fig. 14): body including interocellar area entirely testaceous; wings hyaline.

dez.pensoft.net

Differential diagnosis. *Enicospilus kanshirensis* is most similar to *E. flavicaput* but can be distinguished from it by the stouter central sclerite (Fig. 14F) (central sclerite slender in *E. flavicaput* as in Figure 8F), and smaller body size (i.e. fore wing length less than 15.0 mm in *E. kanshirensis* but more than 17.0 mm in *E. flavicaput*).

Enicospilus laqueatus (Enderlein, 1921) Fig. 15

Enicospilus leetoni Chiu 1954: 38; holotype ♀, Taiwan, TARI, examined; synonymised by Gauld and Mitchell (1981: 396).

Material examined. $29 \bigcirc 97 & 3 \\ 3 \bigcirc 94 \\ 3 \\)$, India $(2 \bigcirc 91 \\ 3 \\)$, Taiwan $(23 \bigcirc 92 \\ 3 \\ 3 \\)$ and 2 unsexed), Zambia $(1 \bigcirc)$.

Type series: holotype of *Enicospilus leetoni* Chiu, 1954, ♀, Taihoku, Taiwan, 1.IX.1925, J. Sonan leg. (TARI).

Non-type series: 13° , Gokarna (1,450 m), Nepal, VI.1983, M.G. Allen leg. (Fig. 15); 1^{\bigcirc}_{+} , Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT); 1∂, Kathmandu, Nepal, M.G. Allen leg.; 2♀♀, Kakani (2,070 m), Nepal, VII.1983, M.G. Allen leg. (LT); 13, Kakani (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); 13, Phulchoki (2,500 m), Nepal, IX.1982, M.G. Allen leg. (LT); 2♀♀, Delhi, India, 14.XI.1967 (1♀), 5.III.1968 (1^{\bigcirc}) ; 1 $^{\bigcirc}$, U.P. Garjia, India, 22.IV.1967, Gupta leg. (all NHMUK); 1♀1♂ and 1unsexed, Taitung, Taiwan, 31.V-6.VI (1♀), 7–13.VI (1♂), 1–14.XI (1 unsexed).1971 (MsT); 21 \bigcirc \bigcirc 1 \bigcirc and 1 unsexed, Kuanhsi, Taiwan, 16. VIII (1°) , 19.VIII (1 unsexed), 29.VIII (2°) , IX (13°) , 10.X (3♀♀), 24–30.XII (1♀).1968, 11–17.III.1969 (1♀), 30.VIII.1970 (1♀) (MsT) (all TARI); 1♀, 15 km E Lusaka, Zambia, 22-31.I.1980, R.A. Beaver leg. (NHMUK).

Distribution. Afrotropical and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 15B–D): GOI = 2.9-3.1; lower face $0.7-0.8 \times$ as wide as high; clypeus moderately convex in profile, its lower margin acute; mandible weakly twisted by $10-25^{\circ}$, moderately long, evenly tapered, its outer surface with a diagonal setose groove between its dorsoproximal corner and base of mandibular apical teeth; upper mandibular tooth $1.3-1.4 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 56-62 flagelomeres and 20^{th} flagellomere $2.0-3.0 \times$ as long as wide.

Mesosoma (Fig. 15E): mesopleuron punctate to longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctostriate; propodeum weakly declivous in profile, its posterior area moderately reticulate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 15F): fore wing with AI = 0.4-0.6, CI = 0.4, ICI = 0.4-0.6, SDI = 1.2-1.4; fore wing vein 1m-cu&M almost evenly curved or very slightly sinuous, 2r&RS al-

Henicospilus laqueatus Enderlein 1921: 26; holotype ♂, Taiwan, IZPAN.

Figure 14. *Enicospilus kanshirensis* (Uchida, 1928), *A*. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

most straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 15F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, separated from distal one, strongly pigmented; central sclerite strongly pigmented, sclerotised, well-delineated D-shaped to semi-circular, positioned in almost mediodistal part of fenestra; distal sclerite absent proximally and more or less strong distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.1-0.3 \times 1$ cu-a length.

Colour (Fig. 15): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. *Enicospilus laqueatus, E. pseudoantennatus, E. vestigator*, and *E. tripartitus* share similar fenestra, sclerites, and fore wing venation (e.g.

Figure 15. *Enicospilus laqueatus* (Enderlein, 1921), \Im . A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Figs 15F, 21F, 26F). However, *E. laqueatus* can be readily separated from *E. pseudoantennatus*, *E. vestigator*, and *E. tripartitus* by a diagonal setose deep groove of the out-

er surface of the mandible between its dorsoproximal corner and base of mandibular apical teeth (outer mandibular surface without a distinct diagonal setose deep groove in *E. pseudoantennatus, E. vestigator,* and *E. tripartitus,* as in e.g. Figure 2C).

Enicospilus lineolatus (Roman, 1913)

Fig. 16

Enicospilus striatus Cameron 1899: 103; holotype ♀, India, OUMNH; junior secondary homonym of *Enicospilus striatus* (Brullé); synonymised by Gauld and Mitchell (1981: 304).

Henicospilus lineolatus Roman 1913: 30; holotype 3, Philippines, NR.

Enicospilus uniformis Chiu 1954: 25; holotype ^Q, Taiwan, TARI, examined; synonymised by Gauld and Mitchell (1981: 304).

- *Enicospilus flatus* Chiu 1954: 28; holotype ♀, Taiwan, TARI, examined; synonymised by Gauld and Mitchell (1981: 304).
- *Enicospilus gussakovskii* Viktorov 1957: 185; holotype ♀, Ussr, Moscow; synonymised by Gauld and Mitchell (1981: 304).
- *Enicospilus striolatus* Townes, Townes and Gupta 1961: 290; replacement name for *Enicospilus striatus* Cameron, 1899; synonymised by Gauld and Mitchell (1981: 304).
- *Enicospilus unicornis* Rao and Nikam 1969: 343; lectotype ♂, India, NHMUK, examined, designated by Gauld and Mitchell (1981: 304); synonymised by Gauld and Mitchell (1981: 304).
- *Enicospilus unicornis* Rao and Nikam 1970: 103; holotype ♀, India, MUC; junior primary homonym of *Enicospilus unicornis* Rao & Nikam, 1969; synonymised by Gauld and Mitchell (1981: 305).

Type series: holotype of *Enicospilus uniformis* Chiu, 1954, \bigcirc , Taihoku, Taiwan, 14.IV.1921, S. Aoki leg. (TARI); holotype of *Enicospilus flatus* Chiu, 1954, \bigcirc , Taihoku, Taiwan, 28.V.1931, J. Sonan leg. (TARI); lectotype of *Enicospilus unicornis* Rao & Nikam, 1969, \bigcirc , Himayatbagh, Aurangabad, Maharashtra, India, VIII.1968, Nikam leg. (NHMUK, Type 3b.2858).

Non-type series: 1°_{\circ} , Kathmandu (4,300'), Nepal, VIII.1981, M.G. Allen leg. (Fig. 16A–E); 1♀, Kathmandu (4,300'), Nepal, VIII.1982, M.G. Allen leg.; 1♀2♂♂, Phulchoki (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT) (Fig. 16F by 3); 2, Godavarl (6,000'), Kathmandu, Nepal, 1–2 (1 $\stackrel{\circ}{\downarrow}$), 3 (1 $\stackrel{\circ}{\downarrow}$). VIII.1967 (MsT); 1[♀], Godavarl (5,000'), Kathmandu, Nepal, 10.VIII.1967 (MsT); 1^o, near Simra (180 m), Adhabhar, Nepal, 23–28.VIII.1967 (MsT); 1♀, Kakani (2,070 m), Nepal, VII.1983, M.G. Allen leg. (LT); 2♀♀, Kakani (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); $1 \bigcirc 1 \circlearrowright$, Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT); 1°_{+} , Victoria, Toolangi, Australia, I–II.1983, Farrugia & Gauld leg.; $2 \bigcirc \bigcirc$, U. Temburong (1,500 m), Bukit Retak, Brunei, IV.1881, I.D. Gauld leg.; $34 \bigcirc \bigcirc 6 \bigcirc \bigcirc$ and 1 unsexed, Andhra Pradesh, Patancheru, India, VI (1^{\bigcirc}) , VII (1^{\bigcirc}) , VIII $(4^{\bigcirc}_{+}^{\bigcirc})$, IX $(27 \stackrel{\circ}{\downarrow} \stackrel{\circ}{\downarrow} \stackrel{\circ}{\circ} \stackrel{\circ}{\circ} \stackrel{\circ}{\circ}$ and 1 unsexed), X $(1 \stackrel{\circ}{\downarrow}).1980$ $(1 \stackrel{\circ}{\circ})$, Bhatnagar leg. (LT) (all NHMUK); 17, Hitsujigaoka (43°00'N, 141°24'E), Sapporo, Hokkaidô, Japan, 16-23. VIII $(1 \mathscale{Q})$, 30.VIII–6.IX $(1 \mathscale{Q})$.2007, 28.VII–4.VIII $(1 \mathscale{Q})$, 4–11 $(6 \mathscale{Q} \mathscale{Q})$, 11–18 $(4 \mathscale{Q} \mathscale{Q})$.VIII, 1–8.IX $(4 \mathscale{Q} \mathscale{Q})$.2008, K. Konishi leg. (MsT) (EUM); 1 \mathscale{Q} , Kokoda (365 m), Papua New Guinea, VI.1933, L.E. Cheesman leg.; 1 \mathscale{Q} , Wau (1,200 m), Morobe District, Papua New Guinea, 24–26. II.1963, J. Sedlacek leg. (MsT); 1 \mathscale{Q} , Peak View Motel (550 m), Kandy, Sri Lanka, 15–24.I.1970, Davis & Rowe leg. (all NHMUK); $3\mathscale{Q} \mathscale{Q} \m$

Distribution. Australasian, Eastern Palaearctic, Oceanic, and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 16B–D): GOI = 2.2-2.7; lower face $0.7-0.8 \times$ as wide as high; clypeus almost flat in profile, its lower margin acute to subacute; mandible rather weakly twisted by $10-20^{\circ}$, moderately long, proximally tapered and distally more or less parallel sided, its outer surface without a diagonal structure; upper mandibular tooth $1.3-1.5 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 51-61 flagellomeres and 20^{th} flagellomere $1.9-2.2 \times$ as long as wide.

Mesosoma (Fig. 16E): mesopleuron punctate; scutellum with lateral longitudinal carinae reaching at least anterior 0.8 and convergent posteriorly; metapleuron punctate to punctostrigose; propodeum weakly declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 16F): fore wing with AI = 0.5-0.9, CI = 0.5-0.9, ICI = 0.7-1.0, SDI = 1.3-1.5; fore wing vein 1m-cu&M moderately sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 16F; fenestra of fore wing not long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal and central sclerites absent; distal sclerite strong and more or less centrally broadened; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a interstitial to antefurcal to M&RS by less than 0.3×1 cu-a length.

Colour (Fig. 16): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. Some species of Oriental *Enic*ospilus (e.g. *E. fusiformis* and *E. unicolor*) have a centrally broadened distal sclerite and lack proximal and central sclerites, as in Figure 16F. Among them, *E. lineolatus* is most similar to *E. unicolor*, but distinguished by the narrower distal sclerite than that of *E. unicolor* and testaceous fore wing pterostigma and sclerite (brown in *E. unicolor*).

Enicospilus melanocarpus Cameron, 1905 Fig. 17

Enicospilus reticulatus Cameron 1902: 52; holotype ♂, Maldives, NHMUK, examined; synonymised by Gauld and Mitchell (1981: 377); junior primary homonym of *Enicospilus reticulatus* Cameron, 1899.

Figure 16. *Enicospilus lineolatus* (Roman, 1913), \Diamond . A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

- *Eniscospilus* (sic) *melanocarpus* Cameron 1905: 122; holotype ♀, Sri Lanka, NHMUK, examined.
- Henicospilus nigrinervis Szépligeti 1906: 142; holotype ♀, New Guinea, TM; synonymised by Gauld and Mitchell (1981: 377); junior secondary homonym of *Enicospilus nigrinervis Cameron*, 1901.
- *Ophion (Henicospilus) nocturnus* Kohl 1908: 315; holotype ♀, Samoa, NM; synonymised by Gauld and Mitchell (1981: 378).
- *Henicospilus batavianus* Szépligeti 1910: 92; holotype Q, Java, TM; synonymised by Gauld and Mitchell (1981: 378).

- *Henicospilus turneri* Morley 1912: 51; lectotype ♀, Australia, NHMUK, examined, designated by Townes et al. (1961: 291); synonymised by Gauld and Mitchell (1981: 378).
- Henicospilus atricornis var. zeylanicus Morley 1913: 392; holotype ♀, Sri Lanka, NHMUK, examined; synonymised by Gauld and Mitchell (1981: 378).
- *Henicospilus uncivena* Enderlein 1921: 23; holotype ♀, India, IZPAN; synonymised by Gauld and Mitchell (1981: 378).
- *Henicospilus crassivena* Enderlein 1921: 24; holotype ♀, Sumatra, IZ-PAN; synonymised by Townes et al. (1961: 281).
- *Enicospilus nigrivenalis* Cushman 1937: 307; holotype ♀, Taiwan, DEI; synonymised by Gauld and Mitchell (1981: 378).
- *Enicospilus quintuplex* Chiu 1954: 61; holotype ♀, China, TARI, examined; synonymised by Gauld and Mitchell (1981: 378).
- *Enicospilus (Polycorniata) brunnis* Rao and Nikam 1971b: 105; holotype ♀, India, MUC; synonymised by Gauld and Mitchell (1981: 378).

Material examined. $105 \bigcirc \bigcirc 21 \textcircled{3}$ and 6 unsexed: Nepal $(5 \bigcirc \bigcirc 2 \textcircled{3} \textcircled{3})$, Australia $(1 \bigcirc)$, China $(1 \bigcirc)$, Maldives $(1 \Huge{3})$, India $(26 \bigcirc \bigcirc)$, Indonesia $(4 \bigcirc \bigcirc 2 \Huge{3} \Huge{3})$ and 1 unsexed), Japan $(2 \bigcirc \bigcirc)$, Malaysia $(1 \bigcirc)$, Papua New Guinea $(7 \bigcirc \bigcirc 1 \Huge{3})$, Philippines $(7 \bigcirc \bigcirc)$, Singapore (1 unsexed), Sri Lanka $(8 \bigcirc \bigcirc)$, Taiwan $(43 \bigcirc \bigcirc 15 \Huge{3} \Huge{3})$ and 4 unsexed).

Type series: holotype of *Enicospilus reticulatus* Cameron, 1902, \Diamond , Hulule, Maldive Islands, 20.VI.1900 (NHMUK, Type 3b.1268); holotype of *Eniscospilus* (sic) *melanocarpus* Cameron, 1905, \heartsuit , Sri Lanka (NHMUK, Type 3b.1234); lectotype of *Henicospilus turneri* Morley, 1912, \heartsuit , Mackay, Queensland, Australia, 1899, Turner leg. (NHMUK, Type 3b.1261); holotype of *Henicospilus atricornis* var. *zeylanicus* Morley, 1913, \heartsuit , Kandy, Sri Lanka, 11.VII.1910, Green leg. (NHMUK, Type 3b.2098); holotype of *Enicospilus quintuplex* Chiu, 1954, \heartsuit , Shaowu, Fukien, China, 8.X.1945, S.H. Chao leg. (TARI).

Non-type series: 1∂, Godaveri (1,550–1,700 m), Nepal, VI.1983, M.G. Allen leg. (LT) (Fig. 17); 13, Pokhara (950 m), Nepal, VII-VIII.1983, M.G. Allen leg. (LT); 1°_{+} , montane and oak forest (2,760 m), Phulchoki, Nepal, VIII.1983, M.G. Allen leg. (LT); 1♀, Phulchoki (2,500 m), Nepal, IX.1982, M.G. Allen leg. (LT); 1^Q, Phulchoki (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); 1^Q, Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT); 1^Q, Kakani (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); $18^{\bigcirc}_{+}^{\bigcirc}$, Pradesh, Patancheru, India, I (1 \bigcirc), II (1 \bigcirc), VIII (2 \bigcirc \bigcirc), IX (5 \bigcirc \bigcirc), X (9 \bigcirc \bigcirc).1980, Bhatnagar leg. (LT); $8 \stackrel{\bigcirc}{_{+}} \stackrel{\bigcirc}{_{+}}$, Mysore, Mudigere, India, X-XI.1979, J.S. Noyes leg.; $3 \bigcirc \bigcirc$, Radjamandula, Java, Indonesia, XI.1937, K.M. Walsh leg.; 13 and 1 unsexed, Mt Djampang, Tjigaeha, Java, Indonesia, I.1938, K.M. Walsh leg.; 1^Q, Mt Melang, Djampang Wetan, Java, Indonesia, VIII.1937, K.M. Walsh leg.; 1∂, Gunung Gede, Lebak Sioe, Java, Indonesia, IX.1937, K.M. Walsh leg. (all NHMUK); 1[♀], Buzena, Nago City, Kunigami County, Okinawa-hontô, Okinawa Pref., Japan, 15.IV.1991, M. Hayashi leg.; 1^Q, Uebaru, Nakijin Vil., Kunigami County, Okinawa-hontô, Okinawa Pref., Japan, 23.IV.1991, M. Hayashi leg. (LT) (all NIAES); 1^Q, Clearing, Perak,

Malaysia, 1.VI.1941, F. Gerald leg.; 5, 2, 3, Bulolo forestry Reserve, Papua New Guinea, IX.1979, I.D. Gauld leg.; 2♀♀, Wau (1,000 m), Morobe, Papua New Guinea, X.1979, I.D. Gauld leg.; $7 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{\downarrow}$, Bay Bay, Leyte, Visca forest, Philippines, VIII (1 $\stackrel{\circ}{\downarrow}$), 30.VIII–4.IX (4 $\stackrel{\circ}{\downarrow}\stackrel{\circ}{\downarrow}$), 5–13.IX $(2 \oplus \oplus)$.1980, L. Tuangganr leg.; 1 unsexed, Singapore, 2.XII.1967, C.G. Roche leg.; $6 \bigcirc \bigcirc$, Peak View Motel, Kandy, Kan. Dist. Sri Lanka, 7–14 $(3 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{\downarrow})$, 14–24 ($3 \stackrel{\bigcirc}{\downarrow} \stackrel{\bigcirc}{\downarrow}$).I.1970, Davis & Rowe leg. (all NHMUK); (233, 17-23. VIII (3 unsexed), 26. VIII-4. XI (12), 12-19(2♀♀), 14–19 (1♂).XI.1972, 16–22.IV.1973 (2♀♀3♂♂ and 1 unsexed) (MsT); $12 \stackrel{\circ}{\downarrow} 2 \stackrel{\circ}{\triangleleft} \stackrel{\circ}{\triangleleft}$, Sunmoon Lake, Taichung, Taiwan, 2.X (1♀), 8.XI (1♀).1968, 9 (1♀), 31 (1 O).IV, 11 (1 O), 14 (1 Q).VII, 1 (3 Q Q), 2–8 (2 Q Q), 7–13 (1 $^{\circ}$), 9–15 (1 $^{\circ}$).IX, 4–10.XI (1 $^{\circ}$).1969 (MsT); $26 \stackrel{\bigcirc}{_{\sim}} 7 \stackrel{\bigcirc}{_{\sim}}$, Wufeng, Taichung, Taiwan, 25–28.VI ($2 \stackrel{\bigcirc}{_{\sim}} \varphi$), 1-3 (1 \bigcirc 1 \bigcirc), 7-11 (1 \bigcirc), 16-20 (1 \bigcirc).VII, 19-26.X (1 \bigcirc), 29.X–5.XI. (2♀♀), 5–10 (3♀♀), 10–15 (1♀2♂♂), 17–22 $(1 \oplus 1 \textcircled{3})$.XI, 27.XI–3.XII.1979 $(2 \oplus \oplus 1 \textcircled{3})$, 7–14 $(1 \oplus 1 \textcircled{3})$, 15–21 (1♀), 20–26 (2♀♀).XII.1979, 1–4 (3♀♀), 4–11 (1♀), 25–31 (2♀♀).I.1980, 9–20.II (2♀♀).1980, K.C. Chou leg. (all TARI).

Distribution. Australasian, Eastern Palaearctic, Oceanic, and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 17B–D): GOI = 2.5-3.1; lower face $0.7-0.8 \times$ as wide as high; clypeus slightly to strongly convex in profile, its lower margin acute; mandible weak-ly twisted by $10-20^{\circ}$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.5 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 53–65 flagellomeres and 20^{th} flagellomere $1.8-2.4 \times$ as long as wide.

Mesosoma (Fig. 17E): mesopleuron punctate to longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctate to punctostriate; propodeum almost evenly rounded, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 17F): fore wing with AI = 0.4-1.1, CI = 0.3-0.5, ICI = 0.4-0.5, SDI = 1.1-1.4; fore wing vein 1m-cu&M more or less evenly curved, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 17F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, strongly confluent with distal one, strongly pigmented; central sclerite moderately to strongly pigmented and sclerotised, usually well-delineated oval, positioned in antero- to medio-distal part of fenestra; distal sclerite more or less evenly strong from proximal to distal; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.3×1 cu-a length.

Colour (Fig. 17): body including interocellar area entirely testaceous with black posterior segments of metasoma; wings hyaline.

Figure 17. *Enicospilus melanocarpus* Cameron, 1905, A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Differential diagnosis. *Enicospilus melanocarpus* is very similar to *E. sauteri*, but distinguished by the uniformly setose marginal cell of the fore wing (Fig. 17F)

(marginal cell of fore wing proximally glabrous in *E. sauteri*) and the oval central sclerite (Fig. 17F) (central sclerite linear in *E. sauteri*). Many species were synony-

mised with *E. melanocarpus* under Gauld's conservative species criteria, but their wide distribution and considerable range of morphological variation indicate this name includes many species. Therefore, further researches are needed to reveal the true species diversity under the name '*melanocarpus*'.

Enicospilus nepalensis Shimizu, sp. nov.

http://zoobank.org7C19F1EE-EC88-4090-A25B-0089401B750A Figs 2A, 18

Etymology. The specific name is derived from the type locality.

Type series: holotype \bigcirc , Pokhara (950 m), Nepal, VII– VIII.1983, M.G. Allen leg. (LT) (NHMUK) (Figs 2A, 18); paratype \bigcirc , same label and repository as holotype.

Distribution. Nepal.

Description. Female (Holotype) (Fig. 18). Body length ca 16.5 mm.

Head with GOI = 2.5 (Fig. 18C). Lower face $0.8 \times$ as wide as high, finely punctate with setae, strongly shiny (Fig. 18B). Clypeus 1.6× as wide as high, finely punctate with setae, moderately convex in profile, its lower margin impressed (Fig. 18B, C). Malar space 0.4× as long as basal mandibular width (Fig. 18B, C). Mandible weakly twisted by ca 15°, moderately long, its proximal half evenly narrowed and distal half subparallel sided, its outer surface entirely almost flat with long and rather stout setae (Figs 2A, 18B, C). Upper mandibular tooth 1.7× as long as lower one, very slender and cylindrical (Figs 2A, 18B). Frons, vertex and gena strongly shiny with fine setae (Fig. 18B-D). Posterior ocellus rather small and separated from eye by $0.3 \times$ its own maximum diameter (Fig. 18B-D). Ventral end of occipital carina joining oral carina. Antenna with 49 flagellomeres; first flagellomere $1.6 \times$ as long as second; 20^{th} flagellomere $2.3 \times$ as long as wide.

Mesosoma entirely strongly shiny with setae (Fig. 18E). Pronotum punctostriate dorsally and finely coriaceous ventrally (Fig. 18E). Mesoscutum $1.5 \times$ as long as its maximum width, almost smooth with very fine punctures with setae, and evenly rounded in profile (Fig. 18E). Notauli absent (Fig. 18E). Scutellum moderately convex, almost smooth with very fine and sparse punctures with setae, with lateral longitudinal carinae reaching posterior end (Fig. 18E). Epicnemium from densely strigose dorsally to densely punctate ventrally with setae. Epicnemial carina present, evenly curved to anterior, its dorsal end not reaching anterior margin of mesopleuron (Fig. 18E). Mesopleuron finely punctate dorsally and longitudinally punctostriate to strigose ventrally (Fig. 18E). Submetapleural carina almost parallel sided centrally and weakly broadened anteriorly (Fig. 18E). Metapleuron moderately punctate with setae (Fig. 18E). Propodeum evenly rounded in profile; anterior transverse carina complete centrally, its lateral end almost joining pleural carina; anterior area longitudinally striate; spiracular area almost smooth with very fine and sparse punctures and setae; posterior area rather finely subconcentrically striate; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge (Fig. 18E).

Wings. Fore wing length ca 11.0 mm with AI = 0.4, CI = 0.3, DI = 0.4, ICI = 0.4, SDI = 1.2, SI = 0.2, SRI = 0.3; vein 1m-cu&M almost evenly curved; vein 2r&RS slightly sinuous and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 18F; proximal sclerite triangular, not confluent with distal sclerite, very strongly pigmented; central sclerite small and its major diameter subequal to thickness of vein 2r&RS, suboval, weakly sclerotised and pigmented, positioned in posterodistal part of fenestra; distal sclerite moderately pigmented; proximal corner of marginal cell evenly setose; posterodistal corner of second discal cell ca 95°; posterodistal corner of subbasal cell ca 95°; vein 1cu-a slightly antefurcal to M&RS by 0.1×1 cu-a length (Fig. 18F). Hind wing with NI = 1.2, RI = 1.7; vein RS straight; vein RA with 6 uniform hamuli.

Legs. Outer surface of fore tibia without dense and long spines. Hind leg with coxa in profile $1.7 \times$ as long as deep; basitarsus $2.0 \times$ as long as second tarsomere; fourth tarsomere $0.6 \times$ as long as third tarsomere and $3.5 \times$ as long as wide; tarsal claw simply pectinate.

Metasoma with PI = 2.8, DMI = 1.3, THI = 2.5; dorsal margin of tergite 1 more or less sinuous; thyridium elongate (Fig. 18A).

Colour (Fig. 18). Entirely testaceous except for apex of mandible, posterior part of T5, and T6–8 black. Wings hyaline; proximal sclerite brown; central and distal sclerites amber; veins brown.

Variations (n = 2): body length 15.5–16.5 mm; head with GOI = 2.4–2.5; clypeus 1.6–1.7× as wide as high; malar space 0.3–0.4× as long as basal mandibular width; mandible twisted by 15–25°; upper mandibular tooth 1.6–2.1× as long as lower one; antenna with first flagellomere 1.6–1.7× as long as second; pronotum punctostriate dorsally and finely coriaceous ventrally or entirely almost smooth to weakly coriaceous with very sparse and fine punctures; metapleuron sparsely to moderately punctate; fore wing length 10.0–11.0 mm; hind coxa in profile 1.6–1.7× as long as deep; fourth tarsomere 3.5–3.7× as long as wide; metasoma with PI = 2.7–2.8; THI = 2.5–2.8; mandible proximally testaceous and apically black or entirely dark brown to black.

Male. Unknown.

Differential diagnosis. Enicospilus nepalensis sp. nov. is probably closely related to or belongs to the *E. ramidulus* complex. Among the complex, *E. nepalensis* sp. nov. is most closely related to *E. tricorniatus* Rao & Nikam, 1970 based on the rather small ocelli relative to other *Enicospilus* (posterior ocellus separated from eye by more than $0.3 \times$ its own maximum diameter) (e.g. Fig. 18B–D), highly shiny body (e.g. Fig. 18A–E), shape

Figure 18. *Enicospilus nepalensis* Shimizu sp. nov., Q, holotype. **A.** Habitus; **B.** Head, frontal view; **C.** Head, lateral view; **D.** Head, dorsal view; **E.** Mesosoma, lateral view; **F.** Central part of fore wing.

of body (e.g. Fig. 18A), shape and position of the fore wing veins and sclerites (e.g. Fig. 18F), distribution, etc. However, *E. nepalensis* sp. nov. is readily distinguishable from *E. tricorniatus* by the following characters: lower face more or less elongate and $0.8 \times$ as wide as high (Fig. 18B) (lower face subquadrate to transverse and $1.0-1.1 \times$ as wide as high in *E. tricorniatus*), the central sclerite weakly sclerotised and pigmented (Fig. 18F) (moderately to strongly sclerotised and pigmented in *E. tricorniatus*), moderate-sized, fore wing length 10.0– 11.0 mm (small, fore wing length less than 8.5 mm in *E. tricorniatus*), posterior ocellus separated from eye by $0.3 \times$ its own maximum diameter (Fig. 18B–D) (posterior ocellus separated from eye by almost its own maximum diameter in *E. tricorniatus*).

Enicospilus nikami Shimizu, sp. nov.

http://zoobank.org26026EC4-711F-49F7-AFA8-C4772D6E0F99 Figs 2J, 19

Etymology. The specific name is dedicated to Dr P.K. Nikam who studied Ophioninae as well as other groups of Hymenoptera mainly of India.

Material examined. 1 \bigcirc : Nepal.

Type series: holotype $\stackrel{\bigcirc}{_{+}}$, Kathmandu (1,300 m), Nepal, XI.1982, M.G. Allen leg. (LT) (NHMUK) (Figs 2J, 19).

Distribution. Nepal.

Description. Female (Holotype) (Fig. 19). Body length ca 23.0 mm.

Head with GOI = 2.9 (Fig. 19C). Lower face $0.6 \times$ as wide as high, shiny, rather finely punctate with setae (Fig. 19B). Clypeus 1.6× as wide as high, sparsely and finely punctate with setae, almost flat in profile, and its lower margin acute (Fig. 19B, C). Malar space 0.2× as long as basal mandibular width (Fig. 19B, C). Mandible weakly twisted by ca 25°, long, proximally strongly narrowed, centrally to apically subparallel sided, its outer surface flat and smooth without a diagonal groove and line of punctures (Fig. 19B, C). Upper mandibular tooth $1.3 \times$ as long as lower one (Fig. 19B). Frons, vertex and gena moderately shiny with fine setae (Fig. 19B-D). Posterior ocellus almost touching eye (Fig. 19B-D). Ventral end of occipital carina joining oral carina. Antenna with 59 flagellomeres; first flagellomere $1.9 \times$ as long as second; 20^{th} flagellomere $1.5 \times$ as long as wide.

Mesosoma entirely moderately shiny with setae (Fig. 19E). Pronotum finely coriaceous with punctures to closely strigose (Fig. 19E). Mesoscutum $1.5 \times$ as long as its maximum width, finely punctate with setae, strongly shiny, and evenly rounded in profile (Fig. 19E). Notauli absent (Fig. 19E). Scutellum moderately convex, with lateral longitudinal carinae almost reaching posterior end, and moderately punctate with setae (Fig. 19E). Epicnemium densely punctate with setae.

Epicnemial carina present, evenly weakly curved to anterior, its dorsal end not reaching anterior margin of mesopleuron (Fig. 19E). Mesopleuron entirely moderately punctate, and ventral margin longitudinally finely strigose (Fig. 19E). Submetapleural carina broadened anteriorly (Fig. 19E). Metapleuron diagonally closely strigose (Fig. 19E). Propodeum declivous in profile; anterior transverse carina complete centrally, its lateral end not joining pleural carina; pleural carina absent posteriorly; anterior area longitudinally striate medially and smooth laterally; spiracular area finely coriaceous; posterior area concentrically striate; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge (Fig. 19E).

Wings. Fore wing length ca 15.0 mm with AI = 0.5, CI = 0.6, DI = 0.3, ICI = 0.8, SDI = 1.5, SI = 0.1, SRI = 0.3; vein 1m-cu&M moderately sinuous; vein 2r&RS very slightly bowed but almost straight, and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 19F; proximal sclerite linear, weakly pigmented and virtually unsclerotised so that vestigial, separated from distal sclerite; central sclerite absent; distal sclerite almost absent but anterodistal part slightly pigmented; proximal corner of marginal cell uniformly setose; posterodistal corner of subbasal cell ca 65°; vein 1cu-a antefurcal to M&RS by $0.2 \times 1cu$ -a length (Fig. 19F). Hind wing with NI = 2.6, RI = 1.7; vein RS straight; vein RA with 11 uniform hamuli.

Legs. Outer surface of fore tibia with very few spines. Hind leg with coxa in profile $1.7 \times$ as long as deep; basitarsus $2.2 \times$ as long as second tarsomere; fourth tarsomere $0.6 \times$ as long as third tarsomere and $2.6 \times$ as long as wide; tarsal claw simply pectinate except lacking pecten proximally.

Metasoma with PI = 3.2, DMI = 1.3, THI = 2.5; dorsal margin of tergite 1 not sinuous; thyridium elongate (Fig. 19A).

Colour (Fig. 19). Entirely testaceous except for apex of mandible black. Wings hyaline; sclerites of fore wing fenestra very slightly pigmented, testaceous; veins black to testaceous.

Variation. Unknown

Male. Unknown

Differential diagnosis. Enicospilus nikami sp. nov. is similar to *E. biharensis*, *E. maruyamanus*, *E. pudibundae*, and *E. transversus* and these species are rather difficult to separate from each other. However, *E. nikami* sp. nov. can be distinguished from *E. biharensis*, *E. maruyamanus* and *E. transversus* by the proximally incomplete pectinae of hind tarsal claw (Fig. 2J) (hind tarsal claw completely pectinate from its base to apex in *E. biharensis*, *E. maruyamanus* and *E. transversus*, as in e.g. Figure 2I), from *E. biharensis* and *E. pudibundae* by the sinuous fore wing vein 1m-cu&M (Fig. 19F) (1m-cu&M evenly curved in *E. biharensis* and *E. pudibundae* as in Figures 6F, 23F), from *E. maruyamanus* by

Figure 19. *Enicospilus nikami* Shimizu sp. nov., ♀, holotype. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

the entirely moderately punctate mesopleuron (Fig. 19E) (mesopleuron entirely longitudinally punctostriate in *E. maruyamanus*) and the angle of posterodistal corner of second discal cell (i.e. ca 90° in *E. nikami* sp. nov. as in

Figure 19F, but ca 115° in *E. maruyamanus*), and from *E. transversus* by the entirely moderately punctate mesopleuron (Fig. 19E) (mesopleuron entirely longitudinally striate in *E. transversus*).
Enicospilus phulchokiensis Shimizu, sp. nov.

http://zoobank.org23580571-7C71-49F7-B2BE-5EDC87CAC2C3 Figs 2G, 20

Etymology. The specific name is derived from the type locality.

Material examined. 12: Nepal.

Type series: holotype \bigcirc , Phulchoki, M.G. Allen leg. (NHMUK) (Figs 2G, 20).

Distribution. Nepal.

Description. Female (Holotype) (Fig. 20). Body length ca 21.5 mm.

Head with GOI = 2.9 (Fig. 20C). Lower face $0.7 \times$ as wide as high, rather finely punctate with setae, strongly shiny (Fig. 20B). Clypeus 1.3× as wide as high, finely punctate with setae, moderately convex in profile, and its lower margin impressed (Fig. 20B, C). Malar space $0.4\times$ as long as basal mandibular width (Fig. 20B, C). Mandible weakly twisted by ca 20°, moderately long, evenly narrowed, its outer surface with a diagonal setose deep groove between its dorsoproximal corner to base of mandibular apical teeth (Fig. 20B, C). Upper mandibular tooth 1.6× as long as lower one, slender and cylindrical (Fig. 20B). Frons, vertex and gena strongly shiny with fine setae (Fig. 20B-D). Posterior ocellus almost touching eye (Fig. 20B-D). Ventral end of occipital carina joining oral carina. Antenna with 64 flagellomeres; first flagellomere 1.7× as long as second; 20th flagellomere 2.2× as long as wide.

Mesosoma entirely strongly shiny with setae (Fig. 20E). Pronotum finely punctate dorsally and strigose to rugose ventrally (Fig. 20E). Mesoscutum 1.5× as long as its maximum width, almost smooth with very fine punctures with setae, and evenly rounded in profile (Fig. 20E). Notauli absent (Fig. 20E). Scutellum moderately convex, anterior 0.4 transversely striate, anterior 0.4-0.5 punctate, and posterior 0.5 longitudinally strigose, with lateral longitudinal carinae reaching posterior end (Figs 2G, 20E). Epicnemium densely punctate with setae. Epicnemial carina present, evenly curved to anterior, its dorsal end close to anterior margin of mesopleuron (Fig. 20E). Mesopleuron entirely finely punctate, longitudinally strigose ventrally (Fig. 20E). Submetapleural carina weakly evenly broadened anteriorly (Fig. 20E). Metapleuron entirely finely punctate with setae (Fig. 20E). Propodeum almost evenly rounded in profile; anterior transverse carina complete; anterior area longitudinally striate; spiracular area almost smooth with very fine and sparse punctures with setae; posterior area rather finely irregularly rugose; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge.

Wings. Fore wing length ca 13.5 mm with AI = 0.4, CI = 0.4, DI = 0.4, ICI = 0.5, SDI = 1.2, SI = 0.1, SRI = 0.3; vein 1m-cu&M weakly sinuous; vein 2r&RS almost straight and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 20F; proximal sclerite triangular, confluent with distal sclerite, moderately pigmented; central sclerite rather small and its minor diameter smaller than thickness of vein 2r&RS, elliptical, moderately sclerotised and pigmented, positioned in mediodistal part of fenestra; distal sclerite moderately pigmented; proximal corner of marginal cell evenly setose; posterodistal corner of second discal cell ca 105° ; posterodistal corner of subbasal cell ca 85° ; vein 1cu-a subinterstitial to M&RS (Fig. 20F). Hind wing with NI = 1.3, RI = 1.7; vein RS straight; vein RA with 7 uniform hamuli.

Legs. Outer surface of fore tibia with sparse spines. Hind leg with coxa in profile $2.0 \times$ as long as deep; basitarsus $2.0 \times$ as long as second tarsomere; fourth tarsomere $0.6 \times$ as long as third tarsomere and $4.6 \times$ as long as wide; tarsal claw simply pectinate.

Metasoma with PI = 2.9, DMI = 1.4, THI = 2.9; dorsal margin of tergite 1 weakly sinuous; thyridium elongate (Fig. 20A).

Colour (Fig. 20). Entirely testaceous except for apex of mandible black. Wings hyaline; sclerites amber; veins brown.

Variation. Unknown

Male. Unknown

Differential diagnosis. Mandibular structure and mesosoma sculpture of E. phulchokiensis sp. nov. indicate that it belongs to the E. ramidulus complex. Enicospilus phulchokiensis sp. nov. runs to couplet 230 (including E. melanocarpus and E. xavius) of Gauld and Mitchell's (1981: 143) key, and to couplet 61 (including E. melanocarpus and E. sauteri) of Tang's (1990: 34, 181) key. However, E. phulchokiensis sp. nov. is distinguishable from E. melanocarpus, E. sauteri and E. xavius by the strongly sculptured scutellum (Fig. 2G), sinuous fore wing vein 1m-cu&M (Fig. 20F), and entirely testaceous metasoma without black posterior segments (Fig. 20A). Moreover, E. phulchokiensis sp. nov. is possibly related to E. puncticulatus Tang, 1990 and its related species-group, but distinguished from E. puncticulatus by the confluent proximal and distal sclerites (Fig. 20F) (separated in E. puncticulatus).

Enicospilus pseudantennatus Gauld, 1977 Fig. 21

Enicospilus pseudantennatus Gauld 1977: 92; holotype ♀, Australia, ANIC.

Type series: paratypes of *Enicospilus pseudantennatus* Gauld, 1977, 1♀, Paramatta, NSW, Australia, 16.I.1921 (EMUS); 5♂♂,Tambourine Mts, SE Queensland, Australia, 1–9.V.1935, R.E. Turner leg.; 1♂, Cabramatta, NSW, Australia, 6.IV.1963, M. Nikitin leg.; 1♀, Merrylands, NSW, Australia, 25.XI.1964, M. Nikitin leg. (all NHMUK).

Non-type series: 1, D.P.I Research Stn, Gatton, SE Queensland, Australia, 13–21.IV.1981 (MsT) (Fig. 21); 1, Mt Tanbourine, Queensland, Australia, 12–18.X.1978, I.D. Galloway leg.; 1, Canberra, ACT, Australia, IX.1981, I.D. Gauld leg. (all NHMUK); 1, Ambon, Indonesia, 29.IX.1960, A.M.R. Wegner leg. (EMUS).



Figure 20. *Enicospilus phulchokiensis* Shimizu sp. nov., Q, holotype. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Distribution. Australasian, Oceanic and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 21B–D): GOI = 2.2-2.8; lower face $0.7-0.8 \times$ as wide as high; clypeus moderately convex in profile, its lower margin impressed; mandible rather weakly twisted by $10-20^{\circ}$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.3-1.6 \times$ as long as lower one; posterior ocellus close to eye; antenna with 56–63 flagellomeres and 20^{th} flagellomere $2.2-2.4 \times$ as long as wide.

Mesosoma (Fig. 21E): mesopleuron entirely punctate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctate; propodeum evenly weakly rounded, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.



Figure 21. *Enicospilus pseudantennatus* Gauld, 1977, ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Wings (Fig. 21F): fore wing with AI = 0.3-0.6, CI = 0.3-0.4, ICI = 0.5-0.7, SDI = 1.2-1.4; fore wing vein 1m-cu&M moderately sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore

wing as in Figure 21F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, separated from distal one, strongly pigmented; central sclerite partially strongly pigmented and sclerotised, ill-delineated oval, positioned in almost medio-distal part of fenestra; distal sclerite strong distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2 1cu-a length.

Colour (Fig. 21): body including interocellar area entirely red-brown; wings hyaline.

Differential diagnosis. As mentioned under *E. laqueatus*, four Oriental species of *Enicospilus* (*E. laqueatus*, *E. pseudantennatus*, *E. vestigator*, and *E. tripartitus*) have similar fenestra, sclerites, and fore wing veins (e.g. Figs 15F, 21F, 26F). Among them, *E. pseudantennatus* is distinguished from *E. laqueatus* by the flat outer surface of the mandible (outer surface of mandible with a diagonal deep setose groove between dorsoproximal corner and base of mandibular apical teeth in *E. laqueatus*), from *E. tripartitus* by the not densely setose and proximally more or less flat outer mandibular surface (outer surface of mandible with very dense setae and sharp and rather deep proximal concavity in *E. tripartitus*, as in Figure 2C), and from *E. vestigator* by the weakly twisted mandible (10–20°) (mandible strongly twisted by 60–80° in *E. vestigator*).

Enicospilus pseudoconspersae (Sonan, 1927) Fig. 22

Henicospilus pseudoconspersae Sonan 1927: 48; holotype ♂, Taiwan, TARI, examined.

Henicospilus mushanus Uchida 1928: 216; holotype ♀, Taiwan, SEHU, examined; synonymised by Gauld and Mitchell (1981: 344).

Enicospilus tenuinubeculus Chiu 1954: 34; holotype ♀, China, TARI, examined; synonymised by Gauld and Mitchell (1981: 345).

Material examined. $7 \begin{array}{l} & & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \\ & \\ & \end{array}$ Nepal $(5 \begin{array}{l} & \end{array}$ Nepal $(5 \begin{array}{l} & \\ \end{array}$ Nepal (5 \begin{array}{l} & \end{array} Nepal $(5 \begin{array}{l} & \end{array}$ Nepal (5 \begin{array}{l} & \end{array} Nepal (5 \begin{array}{l} \end{array} Nepal (5 \begin{array}{l} & \end{array} Nepal (5 \begin{array}{l} & \end{array} Nepal (5 \begin{array}{l} \end{array} Nep (5 \begin{array}{l} \end{array} Nepal (5 \begin{array}{l} \end{array}

Type series: holotype of *Henicospilus pseudoconspersae* Sonan, 1927, \Diamond , Taihoku, Taiwan, 25.IV.1927, J. Sonan leg. (TARI); holotype of *Henicospilus mushanus* Uchida, 1928, \heartsuit , Musha, Taiwan, 24.VII.1925, Matsumura (SEHU); holotype of *Enicospilus tenuinubeculus* Chiu, 1954, \heartsuit , Fukien, Shaown, China, 23–29.V.1944, H.F. Chao leg. (TARI).

Non-type series: 1♀, Kakani (2,070 m), Nepal, VII.1983, M.G. Allen leg. (LT) (Fig. 22); 1^o, Kathmandu (1,300 m), Nepal, XI.1982, M.G. Allen leg. (LT); 1♀, Godaveri (1,550–1,700 m), Nepal, V.1983, M.G. Allen leg. (LT); 1β , Godaveri (5,000'), Nepal, 5.VIII.1967; 1^Q, Phulchoki (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT); 1♀, Kathmandu (4300'), Nepal, VIII.1982; 1∂, Sal & 2y forest (330 m), Dharan, Terai, Nepal, 14-15.XI.1983, M.G. Allen leg.; 1∂, Godavari, Kathmandu, Nepal, 5.VIII.1967; 1Å, 1 mi. S of Ulleri (5,500–7,000'), Nepal, 16.V.1954, J. Ouinlan leg.; 1∂, China (all NHMUK); 1∂, Hiji agricultural road (85 m, 26°43'16.8"N, 128°10'43.4"E), Hiji, Kunigami Village, Kunigami County, Okinawa-hontô, Okinawa Pref., Japan, 3-4.VII.2016, S. Shimizu et al. leg. (LT) (NIAES).

Distribution. Eastern Palaearctic and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Fig. 22B–D): GOI = 2.8-3.1; lower face $0.6-0.7 \times$ as wide as high; clypeus almost flat in profile, its lower margin acute to subacute; mandible rather weakly twisted by $15-25^{\circ}$, moderately long, proximally tapered and distally approximately parallel sided, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.4 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 52-65 flagellomeres and 20^{th} flagellomere $1.7-2.3 \times$ as long as wide.

Mesosoma (Fig. 22E): mesopleuron punctate to longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctostriate; propodeum evenly rounded, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 22F): fore wing with AI = 0.7-0.9, CI = 0.6-0.7, ICI = 0.4-0.6, SDI = 1.3-1.4; fore wing vein 1m-cu&M moderately sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 22F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite semicircular, isolated and not touching margin of fenestra, almost always (very) weakly pigmented; central sclerite absent; distal sclerite absent or vestigial; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.2-0.3 \times 1$ cu-a length.

Colour (Fig. 22): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. *Enicospilus pseudoconspersae* is one of the most distinctive and easily distinguishable species among the Oriental species of *Enicospilus* on account of the characteristic isolated and weakly pigmented semicircular proximal sclerite (Fig. 22F). There are no known morphologically similar species.

Enicospilus pudibundae (Uchida, 1928)* Fig. 23

Henicospilus pudibundae Uchida 1928: 219; lectotype ♂, Japan, SEHU, designated by Townes et al. (1965: 330), examined.

Material examined. $18 \begin{array}{l} \bigcirc \begin{array}{l} \bigcirc 2 \end{array} \begin{array}{l} \bigcirc \end{array} \begin{array}{l} \bigcirc \end{array} \begin{array}{l} \bigcirc \end{array} \begin{array}{l} \bigcirc \end{array}$ (2 $\bigcirc \begin{array}{l} \bigcirc 1 \end{array} \begin{array}{l} \bigcirc \end{array} \end{array} \begin{array}{l} \bigcirc \end{array} \begin{array}{l} \bigcirc \end{array} \end{array}$

Type series: lectotype of *Henicospilus pudibundae* Uchida, 1928, ♂, Sapporo, Hokkaidô, Japan, 4.VI.1925, Tamanuki leg. (emerged from *Dasychira pudibunda* L.) (SEHU).

Non-type series: $2 \bigcirc \bigcirc$, Kakani, Nepal, 1–30.V.1984, M.G. Allen leg. (Fig. 23); 1 \checkmark , Sal & 2^y forest (330 m), Dharan, Terai, Nepal, 14–15.XI.1983, M.G. Allen leg.; $2 \bigcirc \bigcirc$, U. Temburong (1,700 m), Gn. Pagon, Brunei, IV.1981, I.D. Gauld leg.; 1 \bigcirc , U. Temburong (1,500 m), Bukit Retak, Brunei, IV.1981, I.D. Gauld leg. (all NHMUK); 1 \bigcirc , Anamalai Hills (3,500'), Cinchona, India, IV.1956, P.S. Nathan leg. (CNC); 1 \bigcirc , Takadomari, Fuk-



Figure 22. *Enicospilus pseudoconspersae* (Sonan, 1927), Q. **A.** Habitus; **B.** Head, frontal view; **C.** Head, lateral view; **D.** Head, dorsal view; **E.** Mesosoma, lateral view; **F.** Central part of fore wing.

agawa City, Hokkaidô, Japan, 5–19.VIII.2007, H. Hara leg. (MsT) (NSMT); 1 \bigcirc , Yoshigahira, Niigata Pref., Japan, 25.VI.1954, K. Baba leg. (MNHA); 1 \bigcirc , Kurokawa, Niigata Pref., Japan, 22.VI.1954, K. Baba leg. (MNHA); 1 \bigcirc , Oyamada, Machida City, Tôkyô, Japan, IX.2008, S. Ohsato leg. (NHMUK); 1 \bigcirc , Dokan-Shinmichi, Imperial Palace, Chiyoda Ward, Tôkyô, Japan, 27.VII–3. VIII.2010 (MsT) (NSMT); 1 \bigcirc , Mt Futatabi-san, Kôbe City, Hyôgo Pref., Japan, 28.VIII.1990, N. Sugiura leg. (MNHA); $6 \bigcirc \bigcirc$, Mori, Tôjyô Town, Shôbara City, Hiroshima Pref., Japan, 21.VII.2015 (1 \bigcirc), 6 ($2 \bigcirc \bigcirc$), 8 (1 \bigcirc). IX, 3.X (1 $\stackrel{\circ}{\downarrow}$).2016, 17.IX.2017 (1 $\stackrel{\circ}{\downarrow}$), N. Takashiba leg. (LT) (HMNH).

Distribution. Eastern Palaearctic and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. Head (Fig. 23B–D): GOI = 2.6-2.8; lower face $0.7 \times$ as wide as high; clypeus almost flat in profile, its lower margin acute to subacute; mandible weakly twisted by $10-20^\circ$, moderately long, evenly tapered, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.5 \times$ as long as lower one; posterior ocellus (almost) touching eye; antenna with



Figure 23. *Enicospilus pudibundae* (Uchida, 1928), ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

54–59 flagellomeres and 20th flagellomere 2.0–2.1× as long as wide.

Mesosoma (Fig. 23E): mesopleuron entirely punctate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctate; propodeum weakly declivous, its posterior area irregularly wrinkled, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 23F): fore wing with AI = 0.5-1.0, CI = 0.5-0.7, ICI = 0.5-0.7, SDI = 1.4-1.5; fore wing vein 1m-cu&M evenly curved, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 23F;

fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite more or less linear, very weakly confluent with distal one or not, very weakly to strongly pigmented; central sclerite absent; distal sclerite more or less weak to absent; proximal corner of marginal cell of fore wing sparsely to uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2× 1cu-a length.

Colour (Fig. 23): body including interocellar area entirely testaceous, sometimes posterior segments of metasoma weakly infuscate; wings hyaline to very slightly infuscate.

Differential diagnosis. Enicospilus pudibundae resembles E. biharensis, E. maruyamanus, E. nikami sp. nov., and E. transversus, but can be distinguished from E. biharensis, E. maruyamanus, and E. transversus by the proximally incomplete pectination of the hind tarsal claw (pectination of hind tarsal claw complete from base to apex of the claw in E. biharensis, E. maruyamanus, and E. transversus, as in e.g. Figure 2I) and also from E. maruyamanus, E. nikami sp. nov., and E. transversus by the evenly curved fore wing vein 1m-cu&M (Fig. 23F) (1m-cu&M more or less sinuous in E. maruyamanus, E. nikami sp. nov. and E. transversus, as in e.g. Figure 19F). The Nepalese and some other Oriental specimens exhibit a rather wider proximal sclerite and sparser setosity in the proximal corner of the fore wing fenestra than the holotype and Eastern Palaearctic specimens, suggesting that the Oriental specimens are potentially cryptic species. However, at present, I have not enough evidence to describe them as a new species and tentatively follow Gauld and Mitchell's (1981) species criteria.

Enicospilus purifenestratus (Enderlein, 1921)* Fig. 24

Amesospilus purifenestratus Enderlein 1921: 17; holotype ♀, Sumatra, IZPAN.

Material examined. $4 \bigcirc \bigcirc 4 & \bigcirc 3 \\ \bigcirc & \bigcirc & \bigcirc 3 \\ \bigcirc & \bigcirc & \bigcirc 3 \\ \bigcirc & \bigcirc & \bigcirc & \bigcirc 3 \\ \bigcirc & \bigcirc & \bigcirc & \bigcirc & 0 \\ & \bigcirc & \bigcirc & 0 \\ \bigcirc & \bigcirc & \bigcirc & 0 \\$

Non-type series: 1° , Kathmandu (1,350 m), Nepal, VII.1983, M.G. Allen leg. (LT); $4^{\circ}_{\circ}^{\circ}$, Phulchoki (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT) (Fig. 24); $2^{\circ}_{\circ}^{\circ}$, Seria, Brunei, XII.1979, Allen leg.; 1°_{\circ} , Singapore, 1905, H.N. Ridley leg. (all NHMUK).

Distribution. Australasian, Eastern Palaearctic, and Oriental regions (Yu et al. 2016). Newly recorded from Nepal and Brunei.

Diagnosis. *Head* (Fig. 24B–D): GOI = 2.7-3.0; lower face $0.6-0.7\times$ as wide as high; clypeus slightly convex in profile, its lower margin subacute to blunt; mandible weakly twisted by $10-20^\circ$, moderately long, proximally tapered and distally more or less parallel sided, its outer surface without a diagonal structure; upper mandibular tooth $1.3-1.5\times$ as long as lower one; posterior ocellus almost touching eye; antenna with 56–59 flagellomeres and 20^{th} flagellomere $1.6-1.9\times$ as long as wide.

Mesosoma (Fig. 24E): mesopleuron punctate to longitudinally punctostriate; scutellum with lateral longitudinal carinae reaching anterior 0.8 or more and convergent posteriorly; metapleuron punctostriate to striate; propodeum weakly declivous, its posterior area irregularly to subconcentrically wrinkled, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 24F): fore wing with AI = 0.5–0.6, CI = 0.2–0.4, ICI = 0.6–0.8, SDI = 1.3–1.4; fore wing vein 1m-cu&M moderately sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 24F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite absent; distal sclerite more or less entirely pigmented; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.1–0.3 \times 1$ cu-a length.

Colour (Fig. 24F): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. Enicospilus purifenestratus is very similar to *E. urocerus* Gauld & Mitchell, 1981, but distinguished from it by the unswollen segments 3 and 4 of the maxillary palp (segments 3 and 4 of the maxillary palp swollen in *E. urocerus*) and thinner distal sclerite (Fig. 24F) (distal sclerite thicker in *E. urocerus*).

Enicospilus tangi Shimizu, sp. nov.

http://zoobank.org3CFC30CE-94A9-4D5E-A3D7-F40D221C6127 Figs 2B, H, 25

Etymology. The specific name is dedicated to Dr Yuqing Tang who described *E. longitarsis*, which is morphologically the most similar species to the one that is hereby described, and has contributed to the taxonomy of Ophioninae in Asia, represented by the monograph of Chinese *Enicospilus* (Tang 1990).

Material examined. 1*^(†)*: Nepal.

Type series: holotype ♂, Kakani (2,070 m), Nepal, 1–23. VIII.1983, M.G. Allen leg. (NHMUK) (Figs 2B, H, 25).

Distribution. Nepal.

Description. Male (Holotype) (Figs 2B, H, 25). Body length ca 24.5 mm.

Head with GOI = 2.5 (Fig. 25C). Lower face $0.9 \times$ as wide as high, moderately punctate with setae and shiny (Fig. 25B). Clypeus $1.7 \times$ as wide as high, moderately punctate with setae, moderately convex in profile, lower margin impressed (Fig. 25B, C). Malar space $0.4 \times$ as long as basal mandibular width (Fig. 25B, C). Mandible weakly twisted by ca 25°, very long, proximally strongly narrowed, centrally to apically subparallel sided, its outer surface with a diagonal setose deep groove between dorsoproximal corner to base of mandibular apical teeth (Figs 2B, 25B, C). Upper mandibular tooth 2.1 × as long as lower one, stouter than lower one (Figs 2B, 25B). Frons, vertex and gena moderately shiny with fine setae



Figure 24. *Enicospilus purifenestratus* (Enderlein, 1921), 3. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

(Fig. 25B–D). Posterior ocellus close to eye, separated from eye by less than $0.1 \times$ its own maximum diameter (Fig. 25B–D). Ventral end of occipital carina joining oral carina. Antenna incomplete apically, right antenna with 64 flagellomeres and left antenna with 65 flagellomeres; first flagellomere $1.9 \times$ as long as second; 20^{th} flagellomere $2.2 \times$ as long as wide.

Mesosoma entirely moderately shiny with setae (Fig. 25E). Pronotum punctate dorsally and punctostrigose centrally to ventrally (Fig. 25E). Mesoscutum $1.5 \times$ as long as its maximum width, densely and finely punctate with setae, rather weakly shiny, and evenly rounded in profile (Fig. 25E). Notauli absent (Fig. 25E). Scutellum moderately convex, moderately punctate with setae, with lateral longitudinal carinae almost reaching posterior end (Figs 2H, 25E). Epicnemium densely punctate with setae. Epicnemial carina present, evenly weakly curved to anterior, its dorsal end not reaching anterior margin of mesopleuron (Fig. 25E). Mesopleuron entirely weakly to moderately punctostriate to reticulate-strigose longitudinally (Fig. 25E). Submetapleural carina almost parallel sided centrally and weakly broadened anteriorly (Fig. 25E). Metapleuron densely punctostriate with setae (Fig. 25E). Propodeum almost evenly rounded in profile; anterior transverse carina complete centrally, its lateral end almost joining pleural carina; pleural carina vestigial; anterior area longitudinally striate; spiracular area strongly shiny and finely punctures with setae; posterior area rather moderately rugose; propodeal spiracle elliptical, its outer margin not joining pleural carina by a ridge (Fig. 25E).

Wings. Fore wing length ca 15.5 mm with AI = 0.4, CI = 0.4, DI = 0.3, ICI = 0.5, SDI = 1.3, SI = 0.1, SRI = 0.3; vein 1m-cu&M almost evenly curved; vein 2r&RS almost straight and RS evenly curved; fenestra and sclerites of discosubmarginal cell as in Figure 25F; proximal sclerite triangular, confluent with distal sclerite, moderately pigmented; central sclerite absent; distal sclerite weakly pigmented; proximal corner of marginal cell uniformly setose; posterodistal corner of second discal cell ca 95°; posterodistal corner of subbasal cell ca 90°; vein 1cu-a antefurcal to M&RS by 0.3×1 cu-a length (Fig. 25F). Hind wing with NI = 1.8, RI = 1.5; vein RS straight; vein RA with 6 uniform hamuli.

Legs. Ventral 0.7 of outer surface of fore tibia with rather dense spines. Hind leg with coxa in profile $1.8 \times$ as long as deep; basitarsus $2.0 \times$ as long as second tarsomere; fourth tarsomere $0.7 \times$ as long as third tarsomere and $5.0 \times$ as long as wide; tarsal claw simply pectinate.

Metasoma with PI = 2.8, DMI = 1.3, THI = 2.1; dorsal margin of tergite 1 slightly sinuous; thyridium elongate (Fig. 25A).

Colour (Fig. 25). Entirely testaceous except for apex of mandible black. Wings hyaline; proximal sclerite testaceous, distal sclerite very weakly pigmented; veins brown. Variation. Unknown.

Female. Unknown.

Differential diagnosis. Enicospilus tangi sp. nov. can be confused with E. kakanicus sp. nov., E. longitarsis, and E. yonezawanus, all of which belong to the E. ramidulus complex. Among these species, E. tangi sp. nov. is most closely related to E. longitarsis, and these species are distinguished from the other Oriental species of Enicospilus by the triangular proximal sclerite (e.g. Fig. 25F), the absence of the central sclerite (e.g. Fig. 25F), moderately large value of SDI (over 1.3) (e.g. Fig. 25F), a diagonal setose deep groove of the mandibular outer surface (e.g. Fig. 2B), moderately large fore wing fenestra (e.g. Fig. 25F), rather dense spines on the outer surface of the fore tibia, etc. Enicospilus tangi sp. nov. is distinguished from E. longitarsis by the following character states: scutellum narrowed posteriorly (Fig. 2H) (subquadrate in E. longitarsis); fore wing vein 1m-cu&M evenly curved (Fig. 25F) (slightly sinuous in *E. longitarsis*); lower face $0.9 \times$ as wide as high (Fig. 25B) (0.8 in *E. longitarsis*); GOI = 2.5 (Fig. 25C) (1.8 in *E. longitarsis*).

Enicospilus tripartitus Chiu, 1954 Figs 2C, 26

Enicospilus tripartitus Chiu 1954: 36; holotype ♀, Taiwan, TARI, examined.

Material examined. $27 \bigcirc \bigcirc 10 \textcircled{3}$ and 2 unsexed: Nepal $(24 \bigcirc \bigcirc 8 \textcircled{3}$ and 1 unsexed), China $(1 \bigcirc)$, India (1 3), Japan (1 unsexed), Taiwan $(2 \heartsuit \bigcirc)$, unknown (1 3).

Type series: holotype of *Enicospilus tripartitus* Chiu, 1954, \bigcirc , Taihoku, Taiwan, 27.VIII.1937, J. Sonan leg. (TARI); paratype of same species, 1 \bigcirc , no data (NHMUK).

Non-type series: $24 \bigcirc \$ \$ \$ \$$, Kakani (2,000 m), Nepal, VIII.1982 ($2 \bigcirc \diamondsuit$), VI ($4 \bigcirc \circlearrowright 1 \$$), VII ($4 \bigcirc \circlearrowright 3 \$ \$ \$$), 1–23 ($2 \bigcirc \circlearrowright 2 \$ \$$).VIII ($3 \bigcirc \circlearrowright 1 \$$), IX ($4 \oslash \circlearrowright$), X ($2 \bigcirc \circlearrowright$).1983, 1–30.V ($1 \circlearrowright 1 \$$), 1–14.VII ($2 \oslash \circlearrowright$).1984, M.G. Allen leg. (Figs 2C, 26); 1 unsexed, Sangu (ca 6,200'), Taplejung district, Nepal, 16–29.X.1961; 1 \circlearrowright , ShinKaiSi (1,340 m), Mt Omei, Szechuen, China; 1\$, Kangra Valley (1,370 m), India, X.1899, Dudgeon leg. (all NHMUK); 1 unsexed, Genka-yama, Okinawa-hontô, Okinawa Pref., Japan, 4.V.1964, T. Takara & T. Kakinohana leg. (MNHA); $1 \circlearrowright$, Kuanhsi, Taiwan, 29.VIII.1968 (MsT) (TARI).

Distribution. Eastern Palaearctic and Oriental regions (Yu et al. 2016). Gauld and Mitchell (1981) recorded this species from Nepal.

Diagnosis. *Head* (Figs 2C, 26B–D): GOI = 2.2-2.9; lower face $0.7-0.8 \times$ as wide as high; clypeus moderately to strongly convex in profile, its lower margin more or less blunt; mandible rather weakly twisted by $10-20^{\circ}$, moderately long, proximally tapered and distally parallel sided, its outer surface flat but with conspicuous dense setae and a proximal deep concavity; upper mandibular



Figure 25. *Enicospilus tangi* Shimizu sp. nov., ♂, holotype. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

tooth 1.2–1.6× as long as lower one; posterior ocellus close to eye; antenna with 55–66 flagellomeres and 20^{th} flagellomere 2.2–2.4× as long as wide.

Mesosoma (Fig. 26E): mesopleuron entirely more or less densely punctate and submatt; scutellum with lateral longitudinal carinae reaching posterior end and conver-



Figure 26. *Enicospilus tripartitus* Chiu, 1954, ♀. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

gent posteriorly; metapleuron densely punctate as mesopleuron; propodeum weakly declivous, its posterior area moderately reticulate, outer margin of propodeal spiracle not joining pleural carina by a ridge.

Wings (Fig. 26F): fore wing with AI = 0.3-0.6, CI = 0.3-0.4, ICI = 0.5-0.7, SDI = 1.2-1.6; fore wing vein 1m-cu&M almost evenly curved to slightly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 26F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, separated from distal one, strongly pigmented; central sclerite strongly pigmented and sclerotised, well-delineated oval and its major axis parallel to distal margin of fenestra, positioned in mediodistal part of fenestra; distal sclerite absent to weak; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a subinterstitial to antefurcal to M&RS by less than 0.2×1 cu-a length.

Colour (Fig. 26): body including interocellar area entirely reddish brown; wings hyaline.

Differential diagnosis. Four Oriental *Enicospilus* species, *E. laqueatus*, *E. pseudantennatus*, *E. vestigator*, and *E. tripartitus*, have similar fenestra, sclerites, and fore wing veins (e.g. Figs 15F, 21F, 26F), as mentioned under *E. laqueatus* and *E. pseudantennatus*. Among them, *E. tripartitus* is readily distinguishable from other species by the outer mandibular surface: outer surface of mandible with very dense setae and sharp and rather deep proximal concavity in *E. tripartitus* (Figs 2C, 26B, C), but more or less flat proximally with scattered setae in *E. laqueatus* (Fig. 15B, C) *E. pseudantennatus* (Fig. 21B, C) and *E. vestigator*.

Enicospilus yonezawanus (Uchida, 1928)*

Figs 2D, 27

Henicospilus yonezawanus Uchida 1928: 218; lectotype ♀, Japan, SEHU, designated by Townes et al. (1965: 337), examined.

Enicospilus microstriatellus Uchida 1956: 95; holotype ♂, Ryûkyû Island, SEHU, examined; synonymised by Gauld and Mitchell (1981: 337).

Material examined. $27 \Im \Im 3$?: Nepal (1 \Im), India (10 \Im), Indonesia (1 \Im), Japan (2 \Im 733), Laos (8 \Im \Im), Malaysia (4 \Im \Im), Papua New Guinea (1 \Im), Taiwan (13).

Type series: lectotype of *Henicospilus yonezawanus* Uchida, 1928, \bigcirc , Yonezawa, Yamagata Pref., Honshû, Japan, 23.VII.1919, S. Matsumura leg. (SEHU); holotype of *E. microstriatellus* Uchida, 1956, \circlearrowleft , Sinmura, Amami-ôshima, Kagoshima Pref., Ryûkyûs, Japan, 7.IV.1954, T. Kumata leg. (SEHU).

Non-type series: 1 \bigcirc , Godaveri (1,550–1,700 m), Nepal, IX.1983, M.G. Allen leg. (LT) (Figs 2D, 27); 10 \bigcirc \bigcirc , Andhra Pradesh, Patanchneru, India, IX.1980, Rhatnagar leg. (LT); 1 \bigcirc , Medan, L. Fulmek, Sumatra, Indonesia (all NHMUK); 1 \bigcirc , Isa (32°8'29.3"N, 130°33'13.7"E), Kagoshima Pref., Kyûshû, Japan, 7.IX.2012, Y. Matsubara & K. Fukuda leg. (MsT) (NSMT); 500, Isa (32°6'41.8"N, 130°31'38.4"E), Kagoshima Pref., Kyûshû, Japan, 7.IX.2012, Y. Matsubara & K. Fukuda leg. (MsT) (CNC); 1° , Hiji agricultural road (85 m, 26°43'16.8"N, 128°10'43.4"E), Hiji, Kunigami Vil., Kunigami County, Okinawa-hontô, Okinawa Pref., Ryûkyûs, Japan, 2-3. VII.2016, S. Shimizu et al. leg. (LT) (MNHA); $4^{\bigcirc}_{\downarrow}^{\bigcirc}$, Phou Khoun (19.250697 N, 102.254204 E), Luang Phabang, Laos, 21-22.IV.2018, H. Yoshitomi leg. (EUM); $4^{\circ}_{\pm}^{\circ}_{\mp}$, Sala Phou Khoun (19°25'7.57"N, 102°25'41.6"E), Luang Phabang, Laos, 21.IV.2018, K. Yasuda leg. (LT) (EUM); 1^Q, Serdang, Malaysia, IX.1979, Khashiyah leg.; 1[♀], Carambola Farm, Serdang, Selangor, Malaysia, XI.1979; $2^{\bigcirc}_{\downarrow}$, Serdang, Selangor, Malaysia, X ($1^{\bigcirc}_{\downarrow}$) and XI (1 $^{\circ}$).1979, I.D. Gauld leg.; 1 $^{\circ}$, Morobe (1,000 m), Wau, Papua New Guinea, X.1979, I.D. Gauld leg. (all NHMUK); 1∂, Chihpen, Taitung, Taiwan, 17–18. II.1982, L.Y. Chou & K.C. Chou leg. (TARI).

Distribution. Australasian, Eastern Palaearctic, and Oriental regions (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Figs 2D, 27B–D): GOI = 2.9-3.2; lower face $0.7-0.8 \times$ as wide as high; clypeus moderately convex in profile, its lower margin impressed; mandible weakly twisted by $10-20^{\circ}$, moderately long, evenly tapered, its outer surface with a diagonal setose groove between its dorsoproximal corner and base of mandibular apical teeth; upper mandibular tooth $1.2-1.5 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 63–70 flagellomeres and 20^{th} flagellomere $2.0-2.2 \times$ as long as wide.

Mesosoma (Fig. 27E): mesopleuron punctate to rather closely longitudinally striate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron punctate to striate; propodeum almost evenly rounded, its posterior area moderately reticulate, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 27F): fore wing with AI = 0.3-0.7, CI = 0.2-0.4, ICI = 0.4-0.6, SDI = 1.2-1.3; fore wing vein 1m-cu&M almost evenly curved to very slightly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 27F; fenestra of fore wing not very long and its anterodistal corner distinctly separated from proximal end of vein RS; proximal sclerite triangular, separated from distal one, strongly pigmented; central sclerite absent; distal sclerite absent proximally and weak distally; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by $0.1-0.3 \times 1$ cu-a length.

Colour (Fig. 27): body including interocellar area entirely testaceous; wings hyaline.

Differential diagnosis. *Enicospilus yonezawanus* is one of the most common in the Eastern Palaearctic and Oriental regions and more or less distinctive species based on some characters, such as mandibular and



Figure 27. *Enicospilus yonezawanus* (Uchida, 1928), Q. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

clypeal structure, shape of fore wing sclerites, and surface sculpture of mesopleuron, but can be confused with *E. kakanicus* sp. nov., *E. longitarsis*, and *E. tangi* sp. nov. However, *E. yonezawanus* is distinguishable from *E. kakanicus* sp. nov. by the complete lateral longitudinal carinae of the scutellum (lateral longitudinal carinae of the scutellum posteriorly absent in *E. kakanicus* sp. nov., as in Figure 2F), from *E. longitarsis* and *E. tangi* sp. nov. by the scattered spines on the outer fore tibial surface (spines rather dense in *E. longitarsis* and *E. tangi* sp. nov.) and the separated proximal and distal sclerites (Fig. 27F) (proximal and distal sclerites confluent in *E. longitarsis* and *E. tangi* sp. nov. as in e.g. Figure 25F).

Enicospilus zebrus Gauld & Mitchell, 1981*

Fig. 28

Enicospilus zebrus Gauld and Mitchell 1981: 406; holotype ^Q₊, Myanmar, EMUS, examined.

Type series: holotype of *Enicospilus zebrus* Gauld & Mitchell, 1981, \bigcirc , Mt Victoria (2,800 m), Myanmar, V.1938, G. Heinrich leg. (EMUS); paratypes of *E. zebrus*, $2\bigcirc \bigcirc$, same data as holotype except for 2,400 m (NHMUK and EMUS).

Non-type series: 1Å, Choche Lekh (3,500 m), Chautara Dist., Nepal, 17.VI.1983, G. Robinson leg.; 1Å, Phulchoki peak (2,700 m), Nepal, X.1983, M.G. Allen leg. (LT); 1 \bigcirc , Phulchoki (2,500 m), Nepal, IX.1982, M.G. Allen leg. (LT) (Fig. 28); 1 \bigcirc , montane & oak forest (2,760 m), Phulchoki, Nepal, VIII.1983, M.G. Allen leg. (LT); 1 \bigcirc , Nauling Lekh (9,000'), Gobre, Nepal, VI.1983, M.G. Allen leg. (LT); 2 \bigcirc 2 \bigcirc 1Å, Yu Lung Mountain (3,200 m), Likiang, Yunnan, P.R. China, 15–21.VI.2009, A.C. Galsworthy leg. (LT) (all NHMUK).

Distribution. Oriental region (Yu et al. 2016). Newly recorded from Nepal.

Diagnosis. *Head* (Fig. 28B–D): GOI = 3.0-3.2; lower face $0.6-0.7 \times$ as wide as high; clypeus slightly convex in profile, its lower margin acute; mandible weakly twisted by $10-20^{\circ}$, moderately long, proximally tapered and distally more or less parallel sided, its outer surface without a diagonal structure; upper mandibular tooth $1.2-1.3 \times$ as long as lower one; posterior ocellus almost touching eye; antenna with 58–61 flagellomeres and 20^{th} flagellomere 2.6–2.7× as long as wide.

Mesosoma (Fig. 28E): mesopleuron punctate to rather coarsely longitudinally striate; scutellum with lateral longitudinal carinae reaching posterior end and convergent posteriorly; metapleuron rather coarsely striate; propodeum evenly weakly rounded, its posterior area more or less coarsely irregularly wrinkled with strong posterior transverse carina laterally, outer margin of propodeal spiracle joining pleural carina by a ridge.

Wings (Fig. 28F): fore wing with AI = 0.5, CI = 0.3-0.4, ICI = 0.4-0.5, SDI = 1.4-1.5; fore wing vein 1m-cu&M

very slightly sinuous, 2r&RS almost straight; fenestra and sclerites of discosubmarginal cell of fore wing as in Figure 28F; fenestra of fore wing very long and its anterodistal corner very close to proximal end of vein RS; proximal sclerite triangular, confluent with distal one, strongly pigmented; central sclerite moderately pigmented and sclerotised, ill-delineated semicircular to oval, its major axis parallel to distal margin of fenestra, positioned in very distal and slightly anterior part of fenestra; distal sclerite entirely moderately pigmented; proximal corner of marginal cell of fore wing uniformly setose; vein 1cu-a antefurcal to M&RS by 0.1× 1cu-a length.

Colour (Fig. 28): body entirely black with pale yellow patterns, interocellar area not infuscate; wings hyaline but fore wing with three strongly infumate areas around anterocentral part of discosubmarginal cell, proximal part of second discal cell, and central part of marginal cell.

Differential diagnosis. Gauld and Mitchell (1981) suggested that *E. zebrus* is related to the *E. signativentris* species-group and very close to *E. biumbratus* (Morley, 1912) on body and wing colour pattern as well as other characters, but *E. zebrus* is distinguished from *E. biumbratus* by many characters, such as the longer fore wing fenestra (Fig. 28F), smaller and semicircular to oval central sclerite (Fig. 28F), etc.

Species inquirendae and pending taxonomic acts

Some morphospecies and species-groups listed below are tentatively treated as species inquirendae pending taxonomic acts. Two morphospecies (*Enicospilus* sp. 1 (Fig. 29) and *Enicospilus* sp. 2 (Fig. 30)) are likely to be undescribed species, but the only available specimens are in poor condition, so they are not be described here. Also, the *E. erythrocerus* species-group is currently taxonomically challenging. Type specimens must be re-examined and integrative taxonomic methods should be included to delimit and redefine species. Three morphospecies are included in Nepalese specimens of the *E. erythrocerus* group (Fig. 31), and at least one of these is potentially an undescribed species.

Enicospilus sp. 1

Fig. 29

Material examined. 1 unsexed: Nepal.

1 unsexed, Phulchoki (2,000 m), Nepal, VIII.1982, M.G. Allen leg. (LT) (NHMUK) (Fig. 29).

Comments. The mandibular structure of this species indicates it is associated with the *E. ramidulus* complex. *Enicospilus* sp. 1 does not key out to any species in Gauld and Mitchell's (1981) and Tang's (1990) keys and is possibly an undescribed species. It may potentially be found to be closely related to *E. choui* Tang, 1990 or *E. sinicus* Tang, 1990. However, only one broken specimen is known, so I tentatively treat this species as a species inquirenda.



Figure 28. *Enicospilus zebrus* Gauld & Mitchell, 1981, Q. A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.

Enicospilus sp. 2

Fig. 30

Material examined. 1∂: Nepal.

13, Terai (200 m), Chitwan, Nepal, 12–13.III.1983, M.G. Allen leg. (NHMUK) (Fig. 30).

Comments. The material examined is not in bad condition except for incomplete antennae. However, antennal

characters are often useful and important for distinguishing *Enicospilus* species, as previous studies suggested (e.g. Broad and Shaw 2016). Therefore, antennae should be complete to describe a new species.

The affinities of this species are not clear, but, as with *Enicospilus* sp. 1, it also does not key out to any species in Gauld and Mitchell's (1981) or Tang's (1990) keys, indicating that it is potentially an undescribed species.



Figure 29. *Enicospilus* sp. 1, unsexed, Q. A. Habitus; **B.** Head, frontal view; **C.** Head, lateral view; **D.** Head, dorsal view; **E.** Mesosoma, lateral view; **F.** Central part of fore wing.

Enicospilus erythrocerus species-group

Fig. 31

Material examined. $8 \bigcirc \bigcirc 19 \bigcirc \bigcirc$: Nepal.

1♀1♂, Godaveri (1,550–1,700 m), Nepal, VI (1♂), IX (1♀).1983, M.G. Allen leg. (LT); 1♂, Chauta-

sa (6,000'), Nepal, 24.IX.1983, M.G. Allen leg. (Fig. 31A, B); 1° , Kakani (2,070 m), Nepal, VII.1983, M.G. Allen leg. (LT); 1° , secondary vegetation (1,500 m), Kathmandu, Nepal, 10.VI.1984, M.G. Allen leg. (LT); 1° , Godaveri (1,550–1,700 m), Nepal, 5.VIII.1984, M.G. Allen leg. (LT) (Fig. 31C, D); 1° , Kakani



Figure 30. *Enicospilus* sp. 2, \Diamond . A. Habitus; B. Head, frontal view; C. Head, lateral view; D. Head, dorsal view; E. Mesosoma, lateral view; F. Central part of fore wing.



Figure 31. Nepalese specimens of the *Enicospilus erythrocerus* species-group spp. **A-B.** \Diamond from Chautasa: **A.** habitus, **B.** central part of fore wing; **C-D.** \Diamond from Godaveri: **C.** habitus, **D.** central part of fore wing; **E-F.** \Diamond from Kathmandu: **E.** habitus, **F.** central part of fore wing.

Comments. The *E. erythrocerus* species-group is moderately large and one of the most taxonomically confusing groups within *Enicospilus*. It consists of rather large wasps with the fore wing fenestra lacking any trace of sclerites, SDI more than 1.2, lateral longitudinal carinae of the scutellum almost always reaching the posterior end, moderately sized fore wing fenestra, etc. In this study, I examined 27 Nepalese specimens of this species-group and recognised at least three morphospecies (Fig. 31). However, further research is needed to identify or describe them. Therefore, I tentatively treat all specimens of the *E. erythrocerus* species-group as species inquirenda.

Discussion

Many species of Nepalese Enicospilus were recognised from middle elevations, and the median value of elevation for 83% of Nepalese Enicospilus fauna is between 950-2,070 m (Fig. 32). These species are generally widely distributed in the mountainous areas of the (sub)tropical Oriental region and, in some species, such as E. lineolatus and E. yonezawanus, also in the Eastern Palaearctic region. On the other hand, three species (i.e. E. capensis, E. kanshirensis, and E. pudibundae) have been collected only at lower elevations, from 200-330 m (Fig. 32). These species are also widely distributed in the Oriental region, as with the middle-elevation species, and in particular E. capensis is a very widespread Old World species known from the Afrotropical, Australasian, Oceanic, and Oriental regions (Gauld and Mitchell 1981). However, E. zebrus has been collected only at higher elevations (Fig. 32), above 2,500 m, suggesting that this species is restricted



Figure 32. Elevational distribution pattern of the Enicospilus in Nepal.

to the northern high-elevational margin of the continental Oriental region and endemic to the southern slope and eastern highlands of the Himalayas. This is a preliminary study of the Nepalese fauna of *Enicospilus*, as well as of Ophioninae; the sample size is small and the sampling bias of the materials used in the present study is not known, but trends of elevational distribution patterns are indicated. These elevational and distribution patterns of Nepalese *Enicospilus* species are fairly consistent with those proposed by Gauld and Mitchell (1981) and Gauld (1985a).

The Nepalese fauna of Enicospilus has trebled through this study, even though it is a preliminary work. Based on species represented by more than two specimens, no endemicity of the Nepalese fauna is recognised, with most species common to other Oriental countries. Moreover, several common Oriental Enicospilus species, such as E. abdominalis (Szépligeti, 1906), E. aciculatus (Taschenberg, 1875), E. concentralis Cushman, 1937, E. dasychirae Cameron, 1905, E. dolosus (Tosquinet, 1896), E. exaggeratus Chiu, 1954, E. nigropectus Cameron, 1905, E. riukiuensis (Matsumura & Uchida, 1926), E. shinkanus (Uchida, 1928) and E. signativentris (Tosquinet, 1903), have not been found in Nepal yet, but they may be present in the country. Considering the Enicospilus fauna of adjacent areas of Nepal and that of the Old World, at least 60 species are potentially found in Nepal. Therefore, additional studies and greater sampling efforts are needed to reveal the true Enicospilus diversity in Nepal.

Acknowledgements

I thank José Fernández-Triana, Kazuhiko Konishi, Davide Dal Pos, and Kyohei Watanabe for reviewing and commenting the manuscript of this paper; Gavin Broad (NHMUK) for commenting on and checking the English grammar on an early draft of this paper; Akihiko Shinohara (NSMT), Andrew Bennett (CNC), Chi-Feng Lee (TARI), David Wahl (EMUS), Hiraku Yoshitake (NIAES), Hiroyuki Yoshitomi (EUM), José Fernández-Triana (CNC), Junsuke Yamasako (NIAES), Kazuhiko Konishi (EUM), Masahiro Ohara (SEHU), Shinichi Yoshimatsu (NIAES), Yoshiaki Hashimoto (MNHA), and Yoshihiro Senda (HMNH) for their kind help during investigations in collections; Alessandro Rodrigues Lima (Universidade Federal de Minas Gerais, Belo Horizonte, Brazil) for providing photos of the type of E. grammospilus; Hiroaki Fujikawa (Okinawa), Masato Ito (Kôbe University), and Yôto Komeda (Kyûshû University) for their kind help during fieldwork in Okinawa, Japan; and finally my parents, Mr Ryo Shimizu and Ms Yumiko Shimizu (Niigata), for encouraging my Darwin wasp studies.

This research is partially supported by the Grant-in-Aid for JSPS Fellows (Grant Number 18J20333) from the Japan Society for the Promotion of Science and the JSPS Overseas Challenge Program for Young Researchers to carry out research at NHMUK.

References

- Agassiz LJR (1846) Nomenclator zoologicus, index universalis. Jent et Gassman, Soloduri, 1135 pp.
- Alvarado M (2014) Revision of the South American wasp genus Alophophion Cushman, 1947 (Hymenoptera: Ichneumonidae: Ophioninae).
 Revista Peruana de Biología 21(1): 3–60. https://doi.org/10.15381/rpb.v21i1.8245
- Ashmead WH (1900) Classification of the *Ichneumon* flies, or the superfamily Ichneumonoidea. Proceedings of the United States National Museum 23(1206): 1–220. https://doi.org/10.5479/si.00963801.23-1206.1
- Ashmead WH (1904) A list of Hymenoptera of the Philippine Islands with descriptions of new species. Journal of the New York Entomological Society 12: 1–22.
- Bennett AMR, Cardinal S, Gauld ID, Wahl DB (2019) Phylogeny of the subfamilies of Ichneumonidae (Hymenoptera). Journal of Hymenoptera Research 71: 1–156. https://doi.org/10.3897/jhr.71.32375
- Brèthes J (1909) Hymenoptera Paraguayensis. Anales del Museo Nacional de Historia Natural de Buenos Aires 12: 225–256.
- Broad GR, Shaw MR (2016) The British species of *Enicospilus* (Hymenoptera: Ichneumonidae: Ophioninae). European Journal of Taxonomy 187: 1–31. https://doi.org/10.5852/ejt.2016.187
- Broad GR, Shaw MR, Fitton MG (2018) Ichneumonid wasps (Hymenoptera: Ichneumonidae): their classification and biology. Handbooks for the Identification of British Insects 7(12): 1–418.
- Brues CT (1918) Parasitic Hymenoptera from the British Solomon Islands collected by Dr. W.M.Mann. Bulletin of the Museum of Comparative Zoology at Harvard University 62: 97–130.
- Cameron P (1899) Hymenoptera Orientalia, or contributions to a knowledge of the Hymenoptera of the Oriental Zoological Region. Part VIII. The Hymenoptera of the Khasia Hills. First paper. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 43(3): 1–220. https://doi.org/10.5962/bhl.title.8802
- Cameron P (1902) Hymenoptera. In: Gardiner JS (Ed.) The Fauna and Geography of the Maldive and Laccadive Archipelagoes. Cambridge University Press, Cambridge, 51–63. https://doi.org/10.5962/ bhl.title.10215
- Cameron P (1905) On the phytophagous and parasitic Hymenoptera collected by Mr. E. Green in Ceylon. Spolia Zeylanica 3: 67–143.
- Cameron P (1907) On some undescribed phytophagous and parasitic Hymenoptera from the Oriental Zoological Region. Annals and Magazine of Natural History (Series 7) 19: 166–192. https://doi. org/10.1080/00222930709487250
- Chiu SC (1954) On some *Enicospilus*-species from the Orient (Hymenoptera: Ichneumonidae). Bulletin of the Taiwan Agricultural Research Institute 13: 1–79.
- Cushman RA (1937) H. Sauter's Formosa-collection: Ichneumonidae. Arbeiten über Morphologische und Taxonomische Entomologie 4: 283–311.
- Eady RD (1968) Some illustrations of microsculpture in the Hymenoptera. Proceedings of the Royal Entomological Society of London. Series A, General Entomology 43(4–6): 66–72. https://doi. org/10.1111/j.1365-3032.1968.tb01029.x
- Enderlein G (1914) Hymenoptera IV: Ichneumonidae. In: Michaelsen W (Ed.) Beiträge zur Kenntnis der Land-und Süsswasserfauna Deutsch-Südwestafrikas. Band 1. L. Friederichsen, Hamburg, 211–233.
- Enderlein G (1921) Beiträge zur Kenntnis aussereuropäischer Ichneumoniden V. Über die Familie Ophionidae. Stettiner Entomologische Zeitung 82: 3–45.

- Förster A (1869) Synopsis der Familien und Gattungen der Ichneumonen. Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens 25: 135–221.
- Gadallah NS, Soliman AM, Rousse P, Al Dhafer HM (2017) The genus *Enicospilus* Stephens, 1835 (Hymenoptera, Ichneumonidae, Ophioninae) in Saudi Arabia, with twelve new species records and the description of five new species. European Journal of Taxonomy 365: 1–69. https://doi.org/10.5852/ejt.2017.365
- Gauld ID (1977) A revision of the Ophioninae (Hymenoptera: Ichneumonidae) of Australia. Australian Journal of Zoology (Supplementary Series) 49: 1–112. https://doi.org/10.1071/AJZS049
- Gauld ID (1984) The Australian Ophioninae (Insecta; Hymenoptera): a historical biogeographic study. Journal of Biogeography 11: 269– 288. https://doi.org/10.2307/2845005
- Gauld ID (1985a) A preliminary survey of the Ophioninae (Hymenoptera: Ichneumonidae) of Brunei. Brunei Museum Journal 6(1): 169–188.
- Gauld ID (1985b) The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). Bulletin of the British Museum of Natural History, Entomological Series 51(2): 61–185.
- Gauld ID (1988) A survey of the Ophioninae (Hymenoptera: Ichneumonidae) of tropical Mesoamerica with special reference to the fauna of Costa Rica. Bulletin of the British Museum (Natural History) (Entomology) 57(1): 1–309.
- Gauld ID, Mitchell PA (1978) The Taxonomy, Distribution and Host Preferences of African Parasitic Wasps of the Subfamily Ophioninae. CAB: Slough / Commonwealth Institute of Entomology, London, 287 pp.
- Gauld ID, Mitchell PA (1981) The Taxonomy, Distribution and Host Preferences of Indo-Papuan Parasitic Wasps of the Subfamily Ophioninae. CAB, Slough, 611 pp.
- Hooker CW (1912) The *Ichneumon* flies of America belonging to the tribe Ophionini. Transactions of the American Entomological Society 38(1–2): 1–176.
- Johansson N (2018) Review of the Swedish *Enicospilus* (Hymenoptera; Ichneumonidae; Ophioninae) with description of three new species and an illustrated key to species. European Journal of Taxonomy 483: 1–21. https://doi.org/10.5852/ejt.2018.483
- Kirby WF (1900) Hymenoptera. In: Andrews CW (Ed.) A Monograph of Christmas Island (Indian Ocean). Physical Features and Geology. With Description of the Fauna and Flora by Numerous Contributors. British Museum of Natural History, London, 81–88.
- Klopfstein S, Santos BF, Shaw MR, Alvarado M, Bennett AMR, Dal Pos D, Giannotta M, Herrera Florez AF, Karlsson D, Khalaim AI, Lima AR, Mikó I, Sääksjärvi IE, Shimizu S, Spasojevic T, van Noort S, Vilhelmsen L, Broad GR (2019) Darwin wasps: new name heralds renewed efforts to unravel evolutionary history of Ichneumonidae. Entomological Communications 1: ec01006. https://doi. org/10.37486/2675-1305.ec01006
- Kohl FF (1908) VII. Hymenopteren. In: Rechinger K (Ed.) Botanische und zoologische Ergebnisse einer wissenschaftlichen Forschungsreise nach den Samoa-Inseln, dem Neuguinea-Archipel und Solomons-Inseln. Denkschriften der Akademie der Wissenschaften 81: 306–317.
- Kriechbaumer J (1894) Hymenoptera Ichneumonidae a medico nautico Dr. Joh. Brauns in itinere secundo ad oras Africae lecta. Berliner Entomologische Zeitschrift 39: 297–318. https://doi.org/10.1002/ mmnd.18940390215

- Kriechbaumer J (1901a) Bemerkungen über Ophioniden (Hym.). Zeitschrift für Systematische Hymenopterologie und Dipterologie 1: 18–24.
- Kriechbaumer J (1901b) Ueber die Gattungen der von Tosquinet in seinen Ichneumonides d'Afrique beschrieben Ophionarten. Zeitschrift für Systematische Hymenopterologie und Dipterologie 1: 155–156.
- Matsumura S, Uchida T (1926) Die Hymenopteran-Fauna von den Riukiu-Inseln. Insecta Matsumurana 1: 63–77.
- MFSC (2014) Nepal Fifth National Report to Convention on Biological Diversity. Ministry of forests and soil conservation, Government of Nepal, Kthmandu, 77 pp.
- Morley C (1912) A Revision of the Ichneumonidae Based on the Collection in the British Museum (Natural History) with Descriptions of new Genera and Species Part I. Tribes Ophionides and Metopiides. British Museum, London, 88 pp. https://doi.org/10.5962/bhl.title.8761
- Morley C (1913) The Fauna of British India Including Ceylon and Burma, Hymenoptera (Vol. 3). Ichneumonidae. British Museum, London, 531 pp.
- Nikam PK (1975) Studies on Indian Ichneumonidae. Four new species of *Enicospilus* Stephens (Ophioninae) from Marathwada. Marathwada University Journal of Sciences 14(7): 193–202.
- Nikam PK (1980) Studies on Indian species of *Enicospilus* Stephens (Hymenoptera: Ichneumonidae). Oriental Insect 14(2): 131–219. https://doi.org/10.1080/00305316.1980.10433632
- Perkins RCL (1902) Four new species and a new genus of parasitic Hymenoptera (Ichneumonidae, sub-fam. Ophioninae) from the Hawaiian Islands. Transactions of the Entomological Society of London 50: 141–144. https://doi.org/10.1111/j.1365-2311.1902.tb01378.x
- Perkins RCL (1915) On Hawaiian Ophioninae (Hymenoptera, Fam. Ichneumonidae). Transactions of the Entomological Society of London 62: 521–535. https://doi.org/10.1111/j.1365-2311.1915.tb02991.x
- Quicke DLJ, Laurenne NM, Fitton MG, Broad GR (2009) A thousand and one wasps: a 28S and morphological phylogeny of the Ichneumonidae (Insecta: Hymenoptera) with an investigation into alignment parameter space and elision. Journal of Natural History 43(23– 24): 1305–1421. https://doi.org/10.1080/00222930902807783
- Rao SN, Grover P (1960) Studies on Indian Ichneumonidae (Parasitic Hymenoptera). Proceedings of the National Academy of Sciences India (B) 30: 276–288.
- Rao SN, Kurian C (1950) Descriptions of eleven new and records of fifteen known species of Ichneumonoidea (Hymenoptera Parasitica) from India. Indian Journal of Entomology 12: 167–190.
- Rao SN, Kurian C (1951) Descriptions of eleven new and records of fifteen known species of Ichneumonidae (Hymenoptera Parasitica) from India – Part II. Indian Journal of Entomology 13: 65–78.
- Rao SN, Nikam PK (1969) Studies on Indian parasitic Hymenoptera (Ichneumonidae) from Marathwada, II. Subfam. Ophioninae. Bulletin of Entomology (India) 10: 12–17.
- Rao SN, Nikam PK (1970) Studies on Indian parasitic Hymenoptera (Ichneumonidae) from Marathwada I. Marathwada University Journal of Sciences 9: 103–105.
- Rao SN, Nikam PK (1971a) Studies on Indian parasitic Hymenoptera (Ichneumonidae) from Marathwada VII. Subfamily Ophioninae. Marathwada University Journal of Sciences 10: 177–179.
- Rao SN, Nikam PK (1971b) Two new species of *Enicospilus* Stephens (Ichneumonidae, Ophioninae) from Marathwada. Annals of Zoology (Agra) 7: 103–110.
- RAOnline (2019) Nepal Nature. https://www.raonline.ch/pages/np/nat/ np_geology02.html#foot [Accessed on: 2019-12-20]

- Roman A (1913) Philippinische Schlupfwespen aus dem schwedischen Reichsmuseum 1. Arkiv för Zoologi 8(15): 1–51. https://doi. org/10.5962/bhl.part.1064
- Saussure H de (1892) Histoire naturelle des Hyménoptères (Vol. 20). In: Grandidier A (Ed.) Histoire Physique, Naturelle et Politique de Madagascar. L'Impimerie nationale, Paris, 590 pp. https://doi. org/10.5962/bhl.title.1599
- Savada AM (1991) Nepal: a country study. http://countrystudies.us/nepal/ [Accessed on: 2019-12-20]
- Schwarzfeld MD, Broad GR, Sperling FAH (2016) Molecular phylogeny of the diverse parasitoid wasp genus *Ophion* Fabricius (Hymenoptera: Ichneumonidae: Ophioninae). Systematic Entomology 41(1): 191–206. https://doi.org/10.1111/syen.12152
- Seyrig A (1935) Mission scientifique de l'Omo. Tome III. Fascicule 18. Hymenoptera, II. Ichneumonidae: Cryptinae, Pimplinae, Tryphoninae et Ophioninae. Mémoires du Muséum National d'Histoire Naturelle, Paris 4: 1–100.
- Shaw MR, Voogd J (2019) Notes on the biology, morphology and generic placement of "*Hellwigia*" obscura Gravenhorst (Hymenoptera: Ichneumonidae, Ophioninae). Journal of Hymenoptera Research 69: 39–53. https://doi.org/10.3897/jhr.69.33662
- Shimizu S (2017) Description of a new species and revised key to species of the *Enicospilus antefurcalis* species-group from Japan (Hymenoptera: Ichneumonidae: Ophioninae). Acta Entomologica Musei Nationalis Pragae 57(1): 183–194. https://doi.org/10.1515/aemnp-2017-0067
- Shimizu S, Bennett AMR, Ito M, Maeto K (2019) A systematic revision of the Japanese species of the genus *Therion* Curtis, 1829 (Hymenoptera: Ichneumonidae: Anomaloninae). Insect Systematics & Evolution 50(1): 36–66. https://doi.org/10.1163/1876312X-00002180
- Shimizu S, Lima A (2018) Taxonomic revision of the genus Stauropoctonus Brauns, 1889 (Hymenoptera: Ichneumonidae: Ophioninae) in Japan. Entomological Science 21(1): 34–47. https://doi.org/10.1111/ ens.12279
- Shimizu S, Maeto K (2016) Three Oriental species of the genus *Enicospilus* Stephens (Hymenoptera: Ichneumonidae: Ophioninae) newly recorded from Japan. Japanese Journal of Systematic Entomology 22(2): 203–207.
- Sonan J (1927) Studies on the insect pests of the tea plant, Part II. Report of the Department of Agriculture Government Research Institute of Formosa 29: 1–132. [in Japanese]
- Sonan J (1940) M. Yanagihara's collection from Daito-Islands, Okinawa: Hymenoptera. Transactions of the Natural History Society of Formosa. Taihoku 30: 369–375.
- Stephens JL (1835) Illustrations of British Entomology. Mandibulata 7. London, 312 pp.
- Stephens JF (1845) Index, List of Plates and Errata of "Illustrations of British Entomology. Mandibulata (Vol. VII)." Baldwin & Cradock, London, 307–312.
- Szépligeti GV (1905) Hymenoptera. Ichneumonidae (Gruppe Ophionoidea), subfam. Pharsaliinae-Porizontinae. Genera Insectorum 34: 1–68.
- Szépligeti GV (1906) Neue exotische Ichneumoniden aus der Sammlung des Ungarischen National Museums. Annales Musei Nationalis Hungarici 4: 119–156.
- Szépligeti GV (1910) E. Jacobons'sche Hymenopteren aus Java und Krakatau. Braconiden und Ichneumoniden. Notes from the Leyden Museum 32: 85–104.
- Tang YQ (1990) A monograph of Chinese *Enicospilus* Stephens (Hymenoptera: Ichneumonidae: Ophioninae). Chongqing Publishing

House, Chongqing, China. 208 pp. [in Chinese with English key and list of new species]

- Taschenberg EL (1875) Zur Kenntnis der Gattung Ophion Fab. Zeitschrift für die Gesammten Naturwissenschaften 46: 421–438.
- Thomson CG (1888) Öfversigt af de i Sverige funna arter af *Ophion* och *Paniscus*. Opuscula Entomologica, Lund 12: 1185–1201.
- Thunberg CP (1824) Ichneumonidea, Insecta Hymenoptera illustrata. Mémoires de l'Académie Imperiale des Sciences de Saint Petersbourg 8: 249–281.
- Townes HK, Momoi S, Townes M (1965) A catalogue and reclassification of the Eastern Palearctic Ichneumonidae. Memoirs of the American Entomological Institute 5: 1–661.
- Townes HK, Townes M (1973) A catalogue and reclassification of the Ethiopian Ichneumonidae. Errata for 1944–1945 Nearctic catalogue, 1965 Eastern Palearctc catalogue and 1966 Neotropic catalogue. Memoirs of the American Entomological Institute 19: 1–416.
- Townes HK, Townes M, Gupta VK (1961) A catalogue and reclassification of the Indo-Australian Ichneumonidae. Memoirs of the American Entomological Institute 1: 1–522.

- Uchida T (1928) Zweiter Beitrag zur Ichneumoniden-Fauna Japans. Journal of the Faculty of Agriculture, Hokkaido University 21: 177–297.
- Uchida T (1956) Ueder die Gattung Spilophion Cameron (Hym. Ichneumonidae). Insecta Matsumurana 20 (1–2): 17–18.
- Viereck HL (1914) Type species of the genera of Ichneumon flies. United States National Museum Bulletin 83: 1–186. https://doi. org/10.5479/si.03629236.83.1
- Viktorov GA (1957) Species of the genus *Enicospilus* Stephens in USSR. Entomologicheskoye Obozreniye 36: 179–210. [in Russian with English summary]
- Wilkinson DS (1928) New parasitic Hymenoptera. Bulletin of Entomological Research 19(3): 261–265. https://doi.org/10.1017/ S0007485300020599
- Yu DSK, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015 Database on flash-drive. Nepean, Ontario. http:// www.taxapad.com [Accessed on: 2020-2-10]