

A new species of *Lycodon* Boie, 1826 (Serpentes, Colubridae) from northern Vietnam

Helen Y. Janssen^{1,2}, Cuong T. Pham³, Hanh Thi Ngo⁴, Minh Duc Le^{5,6,7},
Truong Q. Nguyen^{3,8}, Thomas Ziegler^{1,2}

1 AG Zoologischer Garten Köln, Riehler Strasse 173, D-50735 Cologne, Germany **2** Institute of Zoology, University of Cologne, Zùlpicher Strasse 47b, D-50674 Cologne, Germany **3** Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam **4** Faculty of Biology, Hanoi University of Science, Vietnam National University, 334 Nguyen Trai Road, Hanoi, Vietnam **5** Faculty of Environmental Sciences, Hanoi University of Science, Vietnam National University, 334 Nguyen Trai Road, Hanoi, Vietnam **6** Central Institute for Natural Resources and Environmental Studies, Hanoi National University, 19 Le Thanh Tong, Hanoi, Vietnam **7** Department of Herpetology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024, USA **8** Graduate University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam

Corresponding author: *Truong Q. Nguyen* (nqt2@yahoo.com); *Thomas Ziegler* (ziegler@koelnerzoo.de)

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Abstract

A new species of the genus *Lycodon* is described from Cao Bang Province, Vietnam, based on three individuals with distinct differences in morphology and molecular data. The new species is differentiated from its congeners by a combination of the following characters: dorsal scales in 17-17-15 rows, smooth throughout; supralabials usually eight (rarely nine); infralabials ten; one elongated loreal on each side, in contact with the eye; preloacal plate single; ventral scales 212–218 (plus one or two preventral scales); subcaudals 90 or 91; maxillary teeth 13 or 14; dorsal surface of body with 28 or 29 light body bands; dorsal surface of tail with 13 cream bands, forming a distinct blotch in the vertebral region. Based on phy-

logenetic analyses of mitochondrial cytochrome *b* sequence data, the new species is recovered as the sister species to a clade containing *L. multizonatus* and *L. liuchengchaoi* with strong support from the Bayesian analysis. The new species is at least 7.5% divergent from other species within this clade in uncorrected pairwise distance calculated using a fragment of more than 1000 bp of the mitochondrial cytochrome *b*. This discovery increases the number of *Lycodon* species known from Vietnam to 16.

Keywords

Cao Bang Province, *Lycodon pictus* sp. nov., morphology, phylogeny, taxonomy

Introduction

The genus *Lycodon* Boie, 1827 is one of the most diverse genera of colubrid snakes, with 61 currently recognised species (Uetz et al. 2019, Luu et al. 2019). Recent phylogenetic studies showed that the genera *Dinodon*, *Dryocalamus* and *Lepturophis* nested within *Lycodon* and suggested to place them into the genus *Lycodon* sensu lato (Guo et al. 2013; Siler et al. 2013; Figueroa et al. 2016). The members of this genus have a broad distribution from eastern Iran to southern China and Japan, southward to the Philippines as well as the Indo-Australian Archipelago (Lanza 1999; Siler et al. 2013; Neang et al. 2014). Six species of *Lycodon* have been described in the last five years, namely *L. zoosvictoriae* Neang, Hartmann, Hun, Souter & Furey, 2014 from Cambodia; *L. cavernicolus* Grismer, Quah, Anuar, Muin, Wood & Nor, 2014 from Malaysia; *L. sidiki* Wostl, Hamidy, Kurniawan & Smith, 2017 from Indonesia; *L. banksi* Luu, Bonkowski, Nguyen, Le, Calame & Ziegler, 2018 from Laos, *L. namdongensis* Luu, Ziegler, Ha, Le & Hoang, 2019 from Vietnam and *L. gibsonae* Vogel & David, 2019 from Thailand. From Vietnam, fifteen species of *Lycodon* have been reported to date, comprising *L. capucinus* (Boie, 1827), *L. cardamomensis* (Daltry & Wüster, 2002), *L. davisonii* (Blanford, 1878), *L. fasciatus* (Anderson, 1879), *L. flavozonatus* (Pope, 1928), *L. futsingensis* (Pope, 1928), *L. laoensis* Günther, 1864, *L. meridionalis* (Bourret, 1935), *L. namdongensis* Luu, Ziegler, Ha, Le & Hoang, 2019, *L. paucifasciatus* Rendahl in Smith, 1943, *L. rosozonatus* (Hu & Zhao, 1972), *L. rufozonatus* Cantor, 1842, *L. ruhstrati abditus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009, *L. septentrionalis* (Günther, 1875), and *L. subcinctus* Boie, 1827 (Uetz et al. 2019, Luu et al. 2019).

Our recent field surveys in the Ha Lang and Trung Khanh districts, Cao Bang Province, northern Vietnam, revealed a snake population that was referable to the genus *Lycodon* based on the following characters: nostril enlarged; robustly arched upper maxillary bone with an inward curve in the anterior part; anterior and posterior maxillary teeth interrupted by a diastema; dorsal scales smooth or weakly keeled, in 17 rows anteriorly and at midbody, and posteriorly 15 rows (Lanza 1999; Grismer et al. 2014). However, the series of three individuals from Cao Bang were morphologically distinct from other named species. These morphological results were further corroborated by the analysis of a fragment of the mitochondrial cytochrome *b* gene, and so herein we describe the population from Cao Bang Province, northern Vietnam, as a new *Lycodon* species.

Materials and methods

Sampling

The field surveys were led by TQN in October 2011 and from April to May 2012. The collected specimens were euthanised with ethyl-acetate, fixed in approximately 85% ethanol for 10 hours, and subsequently transferred to 70% ethanol for permanent storage. Liver tissue samples were preserved separately in 95% ethanol. The specimens were deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam and of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.

Morphological analysis

Identification of sex was performed by dissection (inspection of gonads and presence of hemipenes). Maxillary teeth were counted by dissecting the right maxilla for teeth / sockets. Scallation and maxillary teeth number were examined with a binocular dissecting microscope. Measurements were taken following Ziegler et al. (2018) with a measuring tape to the nearest 1 mm.

Abbreviations of morphological characters are as follows:

SVL	Snout-vent length (from tip of snout to vent);
TaL	tail length;
TaL / TL	ratio of tail length / total length;
TL	total length;
DSR	dorsal scale rows number at one head length posterior to the head – number of dorsal scale rows at midbody – number of dorsal scale rows at one head length anterior to the vent;
SL	supralabials (counted on upper lips);
SL / orbit	number of supralabials entering orbit;
IL	infralabials (counted on lower lips);
Lor	loreal;
Lor / eye	loreal scale touching the eye (yes or no);
PreOc	preoculars;
PostOc	postoculars;
Atem	number of anterior temporals;
PTem	number of posterior temporals;
BodySc	scallation of the body (keeled or smooth);
PreVen	number of preventral scales;
Ven	number of ventral scales;
SubC	number of subcaudal scales;
Prec	precloacal (or cloacal) plate (single or divided);
Teeth max	number of maxillary teeth / alveoli.

Scale counts were taken following Vogel et al. (2009). Ventral scales (Ven) were counted according to Dowling (1951). Bilateral scale counts were given as left / right.

Comparisons were mainly based on the data provided by Boulenger (1893), Pope (1928), Smith (1943), Leviton (1965), Ota and Ross (1994), Manthey and Grossmann (1997), Lanza (1999), Vogel et al. (2009), Vogel and David (2010) and Neang et al. (2014), with additional references provided in the comparisons and legends of the tables. Additionally, studied specimens are listed in the Appendix 1.

Molecular data and phylogenetic analyses

Representative taxa of the genus *Lycodon* were included in the study. Sequences of the species were downloaded from GenBank. Two samples of the population from Cao Bang Province (ZFMK 93746, ZFMK 93747) were incorporated in the analysis. *Boiga cynodon* (Boie 1827) and *Dipsadoboa flavida broadleyi* (Broadley & Stevens, 1971) were used as outgroups based on Figueroa et al. (2016).

DNA was extracted using DNeasy Blood and Tissue kit (Qiagen, Germany) following the manufacturer's instructions. A fragment of the mitochondrial cytochrome *b* gene was amplified using the primer pair L14910 (5'-GACCTGTGATMTGAAAACCAACCGTTGT-3') and H16064 (5'-CTTTGGTTTACAAGAACAATGCTTTA-3'; Burbrink et al. 2000). Extracted DNA was amplified using HotStarTaq Mastermix (Qiagen, Germany) with 21 µl volume consisting of 10 µl of Mastermix, 5 µl of water, 2 µl of each primer at 10 pmol/ml and 2 µl of DNA. PCR conditions were 95 °C for 15 minutes to activate the Taq, with 40 cycles of 95 °C for 30 s, 45 °C for 45 s, 72 °C for 60 s, and a final extension at 72 °C for six minutes. The mitochondrial cytochrome *b* gene was utilised in this study because it has been widely used in previous molecular analyses of *Lycodon* (e.g., Guo et al. 2013, Siler et al. 2013), and has been shown to be informative in revealing new species of *Lycodon* (e.g., Grismer et al. 2014, Luu et al. 2018, 2019).

PCR products were visualised using gel electrophoresis through a 2% low melting-point agarose gel stained with ethidium bromide. Successful amplifications were purified to eliminate PCR components using GeneJET™ PCR Purification kit (ThermoFisher Scientific, Lithuania). Purified PCR products were sent to FirstBase (Malaysia) for sequencing.

The obtained sequences were aligned in ClustalX 1.8.3 (Thompson et al. 1997) using the default settings. Data were analysed using maximum parsimony (MP) as implemented in PAUP*4.0b10 (Swofford 2001) and Bayesian inference (BI) as implemented in MrBayes v3.2 (Ronquist et al. 2012). Settings for these analyses followed Le et al. (2006), except that the number of generations in the Bayesian analysis was increased to 1×10^7 . For the maximum likelihood (ML) analysis, we used IQ-TREE v.1.6.7.1 (Nguyen et al. 2015) with a single model and 10,000 ultrafast bootstrap replications. For ML and BI, the optimal model for nucleotide evolution was set to TrN+I+G by Modeltest v3.7 (Posada and Crandall 1998). For BI, the analysis was conducted with

a random starting tree and run for 10^7 generations. Four Markov chains, one cold and three heated (utilising default heating values), were sampled every 1000 generations. Log-likelihood scores of sample points were plotted against generation time to detect stationarity of the Markov chains. The burn-in value was set to 26 in the BI analysis, as $-\ln L$ scores reached stationarity after 26,000 generations in both runs. Two independent analyses were run simultaneously. Nodal support was evaluated using Bootstrap replication (BP) as estimated in PAUP*4.0b10 and IQ-TREE v1.6.7.1 and posterior probability (PP) in MrBayes v3.2. $BP \geq 70$ and $PP \geq 95\%$ are regarded as strong support for a clade. Uncorrected pairwise distances (p) were calculated in PAUP*4.0b10.

Results

Molecular data and phylogenetic analyses

The final matrix consisted of 1011 bp aligned characters and the alignment contained no gaps. In total, 404 characters were found to be parsimony informative. MP analysis resulted in five most parsimonious trees having 1662 steps (CI = 0.41, RI = 0.72). Our tree topologies are very similar to those recovered by Guo et al. (2015) and Luu et al. (2018). The new species was recovered to be the sister species to a clade containing *L. multizonatus* + *L. liuchengchaoi*, with strong support in BI (PP = 96), but weak support in MP and ML ($BP_{MP} = 56$, $BP_{ML} = 69$) (Fig. 1). The new species has an uncorrected p -distance of at least 7.5% and 8.1% from *Lycodon liuchengchaoi* Zhang, Jang, Vogel & Rao, 2011 and *L. multizonatus* Zhao & Jiang, 1981, respectively.

Lycodon pictus sp. nov.

<http://zoobank.org/FEA7DFD1-BF41-4608-A477-93861FF13AD4>

Figs 2–6

Holotype. IEBR 4166 (field number CB 2012.97), adult male, collected on 18 April 2012 by TQN et al. (altitude 701 m a.s.l.), Trung Khanh District, Cao Bang Province.

Paratypes. ZFMK 93747, juvenile, collected on 15 October 2011 by TQN et al. (altitude 588 m a.s.l.), Ha Lang District, Cao Bang Province; ZFMK 93746, adult female, collected on 10 April 2012 by TQN et al., Ha Lang District, Cao Bang Province.

Diagnosis. *Lycodon pictus* sp. nov. can be differentiated from its congeners by the following morphological characters: dorsal scales in 17–17–15 rows, all smooth; supralabials usually eight (rarely nine); infralabials ten; one elongated loreal on each side, in contact with the eye; precloacal plate single; ventral scales 212–218 (plus one or two preventral scales); subcaudals 90 or 91; a total length of 597+ mm in males and 543 mm in females; tail / total length ratio 0.211–0.215; maxillary teeth 13 or 14; dorsal surface of body with 28 or 29 light body bands; dorsal surface of tail with 13 cream



Figure 2. Holotype of *Lycodon pictus* sp. nov. (IEBR 4166) in life. Photograph T. Lehmann.

bordering anterior temporals; anterior temporals 2/2, posterior temporals 3/3, upper ones thinner than lower ones. Left maxilla arched, with an angular apex, distinctly bent inwards anteriorly. A total of 13 maxillary teeth or teeth alveola, with the following formula: five small anterior teeth, with the last two ones being somewhat enlarged + two strongly enlarged teeth, thick, and not much curved + a wide gap, somewhat wider than the length of the largest teeth + four small teeth + a small gap + two enlarged posterior teeth.

Body elongate, SVL 488 mm; TaL > 109 mm (tail tip lost); prefrontal 1, ventrals 212, from behind neck region distinctly notched laterally; subcaudals > 54 (tail tip lost), paired; preloacal plate single; DSR 17-17-15, all smooth; the vertebral scales not enlarged; DSR reduction from 17 to 15 at the position of ventral 150.

Coloration in preservative. Head, neck, and dorsal surface of body brownish black; light body bands beginning after 1.5 times the head length behind the head, in total 29 transverse light bands on body and at least nine light bands on tail; the first four body bands yellowish cream, and distinctly widened towards the venter, increased in size posteriorly; a dark mottling in the vertebrate region more prominent posteriorly; the subsequent light body bands with two distinct indentations on each side, fused in the middle in the last third of the body. In dorsal view the light bands forming a distinct blotch in the vertebral region, with a dark centre and a lighter frame; laterally, the middle part of the light bands forming blotches, but wider and with an extended



Figure 3. Head views of *Lycodon pictus* sp. nov. (IEBR 4166) in preservative (scale bar refers to head in dorsal view). Photographs T. Ziegler (upper), C.T. Pham (lower).

dark centre, fused laterally in the last third part of the body; the lower and widest part of the light body bands with a dark small blotch in the centre in the anterior part of body; the light bands on the tail with a blotch like pattern in the vertebral region, but



Figure 4. Female paratype of *Lycodon pictus* sp. nov. (ZFMK 93746) in life. Photographs T.Q. Nguyen.

less pronounced than that on body, and one light blotch at the lateral side of tail, widened towards the venter, with a dark centre; ventral surface of head and neck yellowish cream, belly cream and greyish cream in the last third part of body and on lower tail



Figure 5. Juvenile paratype of *Lycodon pictus* sp. nov. (ZFMK 93747) in preservative (upper, dorsal view; lower, ventral view). Photographs T. Ziegler.

surface; the dark dorsal bands (28 on body and at least nine on tail) in part extending towards the venter (most prominent in the anterior five dark body bands), not forming complete dark bands around the body, but complete on the tail; lateral side of the head dark above and light below, with the lighter pattern beginning in the supralabial region; tip of lower jaw and infralabial region in part greyish; dorsal surface of the head and upper head sides a bit paler than the remaining head dorsum.

Hemipenis. Hemipenes elongated, not fully everted, not turgid. Truncus without spines. Spine ornamentation starting at truncus region with somewhat enlarged, medium sized spines. Apex with microspines. Sulcus stretches in the middle to apex. Apex not fully everted, ending somewhat widened with an oblique opening, with microspines inside, pointing to the not fully everted condition of the outer genital organ.

Variations. In the juvenile ZFMK 93747, the number of supralabials on the left side is nine, with fourth to sixth entering the orbit. The loreal does not touch the eye on the right side. The lower anterior temporal scale is not touching the postocular scale on the left side. In general, the coloration is more intense in the juvenile. The creamy pattern on the posterior third of the body sides is connected by a horizontal cream-colored stripe. It has a yellowish cream band on the head that reaches from SL 5 behind the jaws and distinctly lightens the posterior half of the head but does not touch the frontal. In the juvenile, the banded pattern is more simple, consisting of dark bands



Figure 6. Dorsal head and neck pattern of the juvenile paratype of *Lycodon pictus* sp. nov. (ZFMK 93747) in preservative. Photograph T. Ziegler.

which narrow towards the venter and light bands which widen towards the venter and bear a dark pattern and a more or less distinct dark blotch at the lower side (see Fig. 5).

In the female ZFMK 93746, the lower anterior temporal scale is not touching the postocular scale on the right side. For measurements and scalation data of the examined specimens see Table 1.

Dentition. Female ZFMK 93746 and juvenile ZFMK 93747: Left maxilla arched, with an angular apex, distinctly bent inwards anteriorly. A total of 13 (in female) or 14 (in juvenile) maxillary teeth or teeth alveola, with the following formula: five small anterior teeth, with the last two ones being somewhat enlarged + two strongly enlarged teeth, thick, and not much curved + a wide gap, somewhat wider than the length of the largest teeth + four small teeth + a small gap + two enlarged posterior teeth in the female and three posterior teeth in the juvenile, with the anterior two ones enlarged.

Comparisons. In our phylogenetic analysis, *Lycodon pictus* sp. nov. is most closely related to *L. liuchengchaoi* and *L. multizonatus*. From *L. liuchengchaoi*, the new species differs in terms of body scalation (all smooth in the new species vs. feebly keeled in several median rows in *L. liuchengchaoi*), head scalation (ten infralabials vs. 7–9) and dentition (13 or 14 maxillary teeth vs. 8 or 9). In addition, the new species differs from the latter in having 28 or 29 cream body bands (vs. 40 yellow rings on the body in *L. liuchengchaoi*) (Zhang et al. 2015).

Table 1. Sex, measurements (in mm), scalation data, and coloration pattern of *Lycodon pictus* sp. nov. For abbreviations see Materials and methods. Key: asterisk (*) lower Atem not touching PostOc; plus sign (+) tail tip lost.

	Holotype IEBR 4166	Paratype ZFMK 93746	Paratype ZFMK 93747
Sex	male	female	juvenile
TL	597	543	237
SVL	488	426	187
TaL	109+	117	50
TaL/TL	–	0.215	0.211
Teeth max	13	13	14
SL	8/8	8/8	9/8
SL/orbit	3–5	3–5	4–6/3–5
IL	10/10	10/10	10/10
PreOc	1/1	1/1	1/1
PostOc	2/2	2/2	2/2
Lor	1/1	1/1	1/1
Atem	2/2	2/2	2/2*
PTem	3/3	3/3	3/3
DSR	17-17-15	17-17-15	17-17-15
PreVen	1	2	1
Ven	212	216	218
Prec	single	single	single
Subc	54+	91	90
BodySc	smooth	smooth	smooth
Dark bands on body	28	29	28
Light bands on body	29	29	28
Dark bands on tail	9	13	13
Light bands on tail	9+	13	13

The new species differs from *L. multizonatus* by having more maxillary teeth (13 or 14 vs. 10 or 11 in *L. multizonatus*), more infralabials (10 vs. 8) and a single precloacal plate (vs. divided). In addition, the new species differs from the latter in terms of body scalation (minimum 212 ventrals and minimum 90 subcaudals vs. 190–195 ventrals and 68–75 subcaudals in *L. multizonatus*). Furthermore, *L. pictus* sp. nov. has fewer light body bands (28 or 29 vs. 55–73 in *L. multizonatus*) (Lei et al. 2014).

From its Vietnamese congeners, the new species can be differentiated as follows: *Lycodon pictus* sp. nov. differs from *L. capucinus* in having a single precloacal plate (vs. divided), a loreal touching the eye (vs. not in contact with the eye), in having more ventrals (minimum 212 vs. 182–211) and more subcaudals (90 or 91 vs. 59–74), and in terms of dorsal pattern (banded vs. reticulated) (Luu et al. 2019).

Lycodon pictus sp. nov. differs from *L. cardamomensis* in terms of dorsal scalation (17-17-15 smooth DSR vs. 19-17-15 weakly keeled DSR), in having a loreal in contact with the eye (vs. separated) and in having 28 or 29 light body bands (vs. 12-14 pinkish orange body bands) (Daltry and Wüster 2002, Do et al. 2017).

Lycodon pictus sp. nov. differs from *L. davisonii* in having 17 midbody dorsal scale rows (vs. 13 midbody dorsal scale rows), fewer ventral scales (maximum 218 vs. 235–265), more infralabials (10 vs. 8) and the absence of preocular (vs. present). In addition, the new species differs from the latter in having a different dorsal pattern

(28 or 29 cream bands on body vs. 36 white rings on the body) (Blanford 1878, Boulenger 1893).

Lycodon pictus sp. nov. differs from *L. fasciatus* in having smooth dorsal scales (vs. keeled) and more maxillary teeth (13 or 14 vs. 11). Additionally, the colour pattern of *Lycodon pictus* sp. nov. differs in being dark brownish black with light body bands turning into a marbling posteriorly, whereas *L. fasciatus* is black or purplish black above with yellowish cross-bars of irregular outline and has a dark median stippling (Pope 1928, Smith 1943). Werner (1922) described *Dinodon yunnanensis* from Yunnan Fu, now Kunming, Yunnan Province, southwestern China. This species was synonymized with *Lycodon fasciatus* by Pope (1935: 188), but according to Vogel and David (2010), this taxon might be a distinct species (see also Vogel and David 2019). *Lycodon pictus* sp. nov. differs from *Dinodon yunnanensis* Werner, 1922 in having more ventrals (minimum 212 vs. 193), more subcaudals (90 or 91 vs. 66), more infralabials (10 vs. 9) and more light body bands (28 or 29 vs. 23) (Werner 1922, Vogel and David 2010, Vogel and David 2019).

Lycodon pictus sp. nov. differs from *L. flavozonatus* in terms of dorsal scalation (smooth vs. keeled), in having more subcaudals (90 or 91 vs. 80–88), the loreal in contact with the eye in *Lycodon pictus* sp. nov. (vs. separated in *L. flavozonatus*) and in coloration pattern (brownish black with 28 or 29 cream body bands and 9–13 light bands on the tail vs. black with 68 yellow body bands and 21 on the tail) (Pope 1928, Vogt in Pope 1928).

Lycodon pictus sp. nov. differs from *L. futsingensis* in having more ventrals (minimum 212 vs. 193–208) and more subcaudals (minimum 90 vs. 72–87). Additionally, the loreal does not enter the orbit in *L. futsingensis*, whereas it enters the orbit in *Lycodon pictus* sp. nov. (Vogel et al. 2009).

Lycodon pictus sp. nov. differs from *L. laoensis* in having a single prelocaal plate (vs. divided), more ventral scales (minimum 212 vs. 163–192), more subcaudal scales (minimum 90 vs. 60–76), an elongated loreal scale in contact with the orbit (vs. separated) and cream body bands (vs. yellow) (Grismer et al. 2014, Neang et al. 2014).

Lycodon pictus sp. nov. differs from *L. meridionalis* in having smooth dorsals (vs. feebly keeled in 10–12 median rows), a lower ventral scale count (maximum 218 vs. 227–240) and fewer subcaudals (maximum 91 vs. 96–106). In addition, the new species differs in having cream body bands (vs. yellow thin crossbars) (Gawor et al. 2016 and examined ZFMK specimens, see Appendix 1).

Lycodon pictus sp. nov. differs from *L. namdongensis* in having more subcaudals (90 or 91 vs. 85) and the loreal in contact with the eye (vs. separated from the eye in *L. namdongensis*). The new species also differs in coloration pattern (brownish black with 28 or 29 light bands on the body vs. grey with 23 cream cross rings on the body in *L. namdongensis*), and in having irregular bands turning into a marbling posteriorly (vs. clearly demarcated cross bands on the body) (Luu et al. 2019).

Lycodon pictus sp. nov. differs from *L. paucifasciatus* in terms of dorsal scalation (17-17-15 smooth DSR vs. 19-(19-17)-15 DSR, the upper one or two plus vertebral

row distinctly keeled) and fewer ventral scales (maximum 218 vs. 219–222). In addition, the new species has a loreal entering the eye (vs. separated) and 28 or 29 light body bands (vs. 14–25 beige or dirty cream body bands) (Vogel et al. 2009).

Lycodon pictus sp. nov. differs from *L. rosozonatus* in having 17-17-15 smooth DSR (vs. 19-19- 15(17) keeled DSR), fewer ventral scales (maximum 218 vs. 221–234) and a loreal in contact with the eye (vs. separated). In addition, the new species has cream body bands (vs. pinkish red) (Hu et al. 1975, Neang et al. 2014).

Lycodon pictus sp. nov. differs from *L. rufozonatus* in having a loreal in contact with the eye (vs. separated), smooth dorsal scales (vs. feebly keeled in the posterior body part), and in coloration pattern (28 or 29 cream body bands vs. 44–52 light red body bands) (Zhao 2006, Luu et al 2018).

Lycodon pictus sp. nov. differs from *L. rubstrati abditus* in having smooth dorsals (vs. 7–8 dorsal scale (including vertebral) rows keeled), an elongated loreal in contact with the eye (vs. separated), and in having irregular bands turning into a marbling posteriorly (vs. clearly demarcated cross bands on the body) (Vogel et al. 2009).

Lycodon pictus sp. nov. differs from *L. septentrionalis* by its smooth dorsal scales (vs. 7–9 median rows feebly keeled), 10 infralabials (vs. 7 or 8), and the loreal entering the orbit (vs. separated in *L. septentrionalis*). In addition, the new species differs in having cream irregular bands on a brown body (vs. white narrow bands on a black body forming complete annuli) (Günther 1875, Boulenger 1893, Neang et al. 2014).

Lycodon pictus sp. nov. differs from *L. subcinctus* in having 10 infralabials (vs. 8 or 9), one preocular (vs. preocular absent), smooth dorsal scales (vs. feebly keeled) and 28 or 29 cream bands on the body and 9–13 on the tail (vs. 9–15 bands on the body and none on the tail) (Boulenger 1893, Neang et al. 2014).

Lycodon pictus sp. nov. differs from *L. ophiophagus*, a species from southern Thailand but with similar scalation, in having a loreal entering the eye (vs. separated) and in dorsal colour pattern (28 or 29 light bands on a brown body vs. 20 or 21 white bands on a dark body) as well as and in having irregular bands turning into a marbling posteriorly (vs. clearly demarcated cross bands on the body) (Vogel et al 2009).

For additional measurements, dentition, and scalation data see Tables 2–8.

Distribution. *Lycodon pictus* sp. nov. is currently known only from Ha Lang and Trung Khanh districts, Cao Bang Province, northern Vietnam (Fig. 7).

Etymology. The name of the species *pictus* means painted or decorated in Latin and refers to its unique dorsal colour pattern.

Natural history. *Lycodon pictus* sp. nov. seems to be closely associated with karst environment. Specimens were found at night between 19:00 and 23:00, on forest paths or on the ground near cave entrances. The surrounding habitat was secondary karst forest, consisting of medium and small hardwood trees mixed with shrubs and vines. Air temperature was 23.4–29.6°C and humidity was 66–79%. Other reptiles were also found at the site, including *Acanthosaura lepidogaster* (Cuvier, 1829), *Gekko adleri* Nguyen, Wang, Yang, Lehmann, Le, Ziegler & Bonkowski, 2013, *Goniurosaurus luii* Grismer, Viets & Boyle, 1999, *Lycodon futsingensis* (Pope, 1928), and *Protobothrops trungkhanhensis* Orlov, Ryabov & Nguyen, 2009 (Fig. 8).



Figure 7. Map showing the type locality of *Lycodon pictus* sp. nov. in Cao Bang Province.



Figure 8. Habitat of *Lycodon pictus* sp. nov.: the female paratype (ZFMK 93746) was found in Ha Lang District, Cao Bang Province.

Table 2. Measurements (in mm), dentition, and scalation data of *Lycodon* species from Vietnam. Data taken from Blanford (1878), Pope (1928), Smith (1943), Boulenger (1893), Daltry and Wüster (2002), Jackson and Fritts (2004), Vogel et al. (2009), Neang et al. (2014), Do et al. (2016), and Luu et al. (2019); distinguishing characters are marked in bold. For abbreviations see Materials and methods.

	<i>L. pictus</i> sp. nov.	<i>L. capucinus</i>	<i>L. cardamomensis</i>	<i>L. davisonii</i>	<i>L. fasciatus</i>	<i>L. flavozonatus</i>	<i>L. futsingensis</i>	<i>L. laeensis</i>
TL	597	816	896	920 ♂	894	1440 ♂, 1210 ♀	850 ♂, 773 ♀	470
Teeth max	13 or 14	15	10–12	11	11	13	12–15	
SL	8	9 or 10	8	7	8	8	8 (7)	9 or 10
SL/orbit	3–5	3–5	3–5	3–4	3–5	3–5	3–5 (4–5; 2–4; 4–6)	3–5
IL	10	9 or 10	10	8	9 (8, 10)	10	10 (9, 11)	10
PreOc	1	1	1	0	1	1	1	1
PostOc	2	2	2 or 3	1 or 2	2	2	2 (3)	2 (3)
Lor	1	1	1	1	1	1	1	1
Lor/eye	yes	no	no	yes	yes	no	no	no
Atem	2	2	2	1 or 2	2	2	2 (1)	2
P/Tem	3	3	2 or 3	2	2	2 or 3	3 (2)	3
DSR	17–17–15	17–17–15	19–17–15	13	17–17–15	17–17–15	17–17 (16)–15	17–17–15
Ven	212–218	182–211	215–228	233–265	182–225	211–221 ♂, 212–218 ♀	193–204 ♂, 198–208 ♀	163–192
Prec	single	divided	single	single	single	divided/ single	single	divided
Subc	90 or 91	59–74	87–93	90–108	65–94	81–88 ♂, 80–84 ♀	72–87 ♂, 78–85 ♀	60–76
BodySc	smooth	weakly keeled	weakly keeled	smooth	keeled	7 rows feebly keeled at midbody	smooth	smooth

Table 3. Measurements (in mm), dentition, and scalation data of *Lycodon* species from Vietnam (continuation of Table 2). Data from Günther (1875), Boulenger (1893), Hu et al. (1975), Zhao (2006), Vogel et al. (2009), Guo et al. (2013), Neang et al. (2016), Gawor et al. (2016), Luu et al. (2018), Luu et al. (2019), and based on examined specimens from ZFMK (see Appendix 1). Key: distinguishing characters are marked in bold; * Luu et al. (2019) mention 240 ventrals as maximum for *L. rufozonatus*; however, that is a transcription error from Bourret (1935) who gave 204 as the maximum number of ventrals. For abbreviations see Materials and methods.

	<i>L. meridionalis</i>	<i>L. namdongensis</i>	<i>L. paucifasciatus</i>	<i>L. rososonatus</i>	<i>L. rufozonatus</i>	<i>L. rubistrati abditus</i>	<i>L. septentrionalis</i>	<i>L. subincinctus</i>
TL	1139	723	763	1060	1234	964	1163	1000
Teeth max	11	12	11 or 12	12 or 13	11-13	11-13	7	8-14
SL	8	8	8	8	8	8	8	8
SL/orbit	3-5	3-5	3-5		3-5	3-5	3-5	3-5 (3-6)
IL	10	10	10	10 (9)	10 (9)	10 (9,11)	7 or 8	8 or 9
PreOc	1	2/1	1	1	1	1	1	0
PostOc	2	3	2	2	2	2	2	2 or 3
Lor	1	1	1	1	1	1	1	1
Lor/eye	no	no	no	no	no	no	no	yes
Atem	2	2	2	2	2	2 (1)	2	1
P'Tem	3	2	3	3	3	3 (2)	3	2
DSR	17-17-15	17-17-15	19- (19-17)-15	19-19- 15(17)	(19-17)-17-15	17-17-15	17-17-15	17-17-15
Ven	227-240	218	219-222	221-234	184-225*	197-229	202-224	192-230
Prec	divided	single	single	single	single	single	single	divided (rarely single)
Subc	96-106	85	90-92	53-98	90-103	90-103	83-104	60-91
Body/Sc	dorsals feebly keeled in 10-12	smooth	upper 1 or 2 dorsals scale row(s) plus vertebral row distinctly keeled	weakly keeled	feebly keeled	smooth (DSR 1-6), distinctly keeled (DSR 7-8 and vertebral row)	7 or 9 median rows feebly keeled	feebly keeled

Table 4. Measurements (in mm), dentition and scalation data of *Lycodon* species from China, Laos and Cambodia. Data taken from Zhao and Jiang (1981), Boulenger (1893), Vogel and David (2010) Vogel and Lua (2011), Zhang et al. (2011), Vogel et al. (2012), Lei et al. (2014), Neang et al. (2014), Zhang et al. (2015), Ganesh and Vogel (2018), and Luu et al. (2018). Key: plus sign (+) tail incomplete; distinguishing characters are marked in bold. For abbreviations see Materials and methods.

	<i>L. aulicus</i>	<i>L. banksi</i>	<i>L. davidi</i>	<i>L. gongshan</i>	<i>L. liuchengchaoi</i>	<i>L. multizonatus</i>	<i>L. synaptor</i>	<i>L. zoosivictoriae</i>
TL	719	465 +	389.5	963 ♂	676	505	487	520.7
Teeth max			11		8 or 9	10 or 11	10	9
SL	9 (8 or 10)	8	8	8	7 or 8	8 (rarely 7)	8	8
SL/orbit	3–5	3–5	3–5	3–5	3–5	3–5	3–5	3–5/4–5
IL	10 or 11	10	10	8	8 (7,9)	8 (7)	8	10
PreOc	1	1	1	1	1	0 or 1	1	1 or 2
PostOc	2	2	2	2	2	2	2	2
Lor	1	1	1	1	1	1	1	1
Lor/eye	no	yes	no	yes	yes	yes	no	no
Atem	2	2	2	2	1–3	2 (1)	2	2
PTem	3	3	2 or 3	2 or 3	1–3	3 (2)	2	2
DSR	17–17–15	17–17–15	17–17–15	17–17–15	17–17–15	17–17–15	15 or 17–17–15	17–17–15
Ven	180–215	241	224 ♂	210–216 ♂, 215 ♀	190–228	190–195	201–203 ♀	213 ♀
Prec	divided	single	single	single	divided	divided	single	single
Subc	57–78	26 +	99 ♂	95 or 96 ♂, 92 ♀	68–77	68–75	68 or 69 ♀	85 ♀
Body/Sc	smooth and glossy	smooth (six central DSR of posterior 1/3 feebly keeled)	middorsal scale rows slightly keeled, outermost rows entirely smooth	upper dorsal rows 6–12 and vertebral row keeled	feebly keeled in median rows	smooth	6–7 upper rows and vertebral row feebly keeled	weakly keeled

Table 5. Measurements (in mm), dentition, and scalation data of *Lycodon* species from Thailand and Myanmar. Data taken from Günther (1864), Boulenger (1893), Boulenger (1900), Smith (1943), Lanza (1999), Slowinski et al. (2001), Daltry and Wüster (2002), Vogel et al. (2009), Bahuguna and Bhuta (2010), Grismer et al. (2014), Luu et al. (2018), and Vogel and David (2019); distinguishing characters are marked in bold. For abbreviations see Materials and methods.

	<i>L. albofuscus</i>	<i>L. butleri</i>	<i>L. effraenis</i>	<i>L. gibsonae</i>	<i>L. gracilis</i>	<i>L. java</i>	<i>L. kundui</i>	<i>L. ophiophagus</i>	<i>L. subannulatus</i>	<i>L. zawi</i>
TL	1480	876	700	906	533	535 ♂, 550 ♀		909	684	480
Teeth max	12			13	9			11-13	8 or 10	12
SL	8	8 or 9	9	8	8	8 or 9	7	8	7	8 or 9
SL/orbit	3-5	3-5	3-5	3-4 and 3-5	3-4	3-5	3-4	3-5	3-4	3-5
IL		9 or 10	10 or 11	10				10	8	9 or 10
PreOc	1	1	1	1	2	1		1	1	1
PostOc	2	2	2-3	2	2	2	2	2	2	2 (1)
Lor	1	1	0	1	1 (united with lower PreOc)	1	1	1	1	1
Lor/eye	no	yes	no Lor	yes	yes	no	no	no	yes	no
Atem	2	2	2	2	2	1 or 2	1	2	2	2 (3)
P/Tem	2	2	2 or 3	3	3	2 or 3	2	3	2	3 (4)
DSR	17	19 (17 in Boulenger 1900)	17	17-17-15	15	17-17-15	15-15-15	17-17-15	15-15-15	17-17-15
Ven	241	220-227	215-228	223-226 ♂	234	167-188	186	211-212	225-244	179-194 ♂, 207 ♀
Prec	divided	single	single	single	single	divided	divided (entire in Lanza 1999)	single	single	divided
Subc	155-208	81-96	72-99	91-92 ♂	81-83	52-74	70	87-90	93-111	45-75 ♂
Body/Sc	keeled	keeled	smooth	upper 3 or 4 rows keeled	keeled	smooth	smooth	smooth	keeled	smooth

Table 6. Measurements (in mm), dentition and sculation data of *Lycodon* species from India. Data taken from Boulenger (1893), Wall (1906), Smith (1943), Taylor (1950), Captain (1999), Vijayakumar and David (2005), Mukherjee and Bhupathy (2007), Mistry et al. (2007), Vogel and Lou (2011), Vogel and Harikrishnan (2013), Ganesh and Vogel (2018), and Melvinsevan et al. (2018); distinguishing characters are marked in bold. For abbreviations see Materials and methods.

	<i>L. anamallensis</i>	<i>L. flavicollis</i>	<i>L. flavomaculatus</i>	<i>L. gammiti</i>	<i>L. hypsivinioides</i>	<i>L. mackinnoni</i>	<i>L. nympha</i>	<i>L. striatus</i>	<i>L. tinuarii</i>	<i>L. trauancoricus</i>
TL	522	543	520	1150	717 ♂, 563 ♀	365	574	432	790	600 ♂, 625 ♀
Teeth max							8–10			
SL	9	9	9	8 (7,9)	9	8 (7)	7 (8 or 6)	9		9
SL/orbit	3–5	3–5	3–5	3–5 (3–4)	3–5	3–5	3–4	3–5		3–5
IL	10 or 11	11	10		10	8		11		
PreOc	1	1	1	1	1	1	1 or 2	1		1
PostOc	2 or 3	2	2	2 (1)	2	2	2	2		2
Lor	1/1 (except Holotype 2/2)	1	1	1	1	1 (0 in Wall 1906)	1	1		1
Lor/eye		no	no	no	no	no	yes	no		no
Atem	2	2 (3)	2 (1)	2 or irregular	2	1 or 2	2	2 rarely 1		2 or 3
P/Tem	3+4	3 (rarely 2)	3 (rarely 2)	2 or irregular	3	2 or 3	2 or 3	3 rarely 2		3
DSR	17–17–15	17–17–15	17–17–15	17–17 (19)–15	17–17–15	17–17–15	13–13–13	17–17–15	?	17–17–15
Ven	174–186 ♂, 186–204 ♀	210–224	165–183	205–220	188–202 ♂, 199–210 ♀	163–187	200–243	153–178	218–237	176–206
Prec	divided (except holotype)	divided	divided	single	divided	divided	divided	divided	divided	single
Subc	63–73 ♂, 60–74 ♀	65–72	53–63	98–111	68–75 ♂, 61–68 ♀	48–56	65–88	42–66	61–102	64–76
BodySc	smooth	smooth with single apical pit	smooth	9 dorsal rows keeled, 5 rows at each side smooth	smooth	smooth	keeled	smooth	smooth	smooth

Table 8. Measurements (in mm), dentition and scalation data of *Lycodon* species from Sri Lanka, Malaysia, Japan and Indonesia. Data taken from Boulenger (1893), Stejneger (1907), Smith (1943), Vogel et al. (2009), Grismer et al. (2014), and Wöstl et al. (2017); distinguishing characters are marked in bold. For abbreviations see Materials and methods.

	<i>L. carinatus</i>	<i>L. caernicolus</i>	<i>L. multifasciatus</i>	<i>L. orientalis</i>	<i>L. semicarinatus</i>	<i>L. sidiki</i>	<i>L. stormi</i>	<i>L. tristrigatus</i>
TL	730	508.2	700	660	1100	715	597	360
Teeth max				10 or 11		7		8 or 10
SL	8 or 9	9 or 10		8	8	8	8	7
SL/orbit	3-5	4-6		3-5	3-5	3-5	3-4	3-4
IL		10 or 11				10/9		
PreOc	1	1		0	1	0	1	0
PostOc	2	2		2	2	2	2	2
Lor	1	1		1	1	1	1	1
Lor/eye	no	yes	no	yes	no	yes	no	yes
Atem	2	3 (2)		2	2	2	1	2
P'Tem	2 or 3	3 or 4		3	3	2	3	2 or 3
DSR	17 or 19-19-17	17-17-15	17-17-?	17	17	17-17-15	19	15
Ven	185-202	245 ♂, 232 ♀	232-237 ♂ 229-235 ♀	200-208	211-234	195	217	224
Prec	single	single		divided	single	divided	single	single
Subc	51-64	113 ♂, 92 ♀	115-119 ♂ 106- 117 ♀	68-74	65-105	85	75	86
Body/Sc	strongly keeled	the 8 medial rows weakly keeled	keeled	scales with a very faint keel along their anterior half	scales keeled along anterior half (4 outer rows smooth, other with a feeble though distinct keel on the basal half of each scale)	keeled	smooth	keeled

Discussion

Our phylogenetic analyses reveal *Lycodon pictus* sp. nov. to be the sister taxon to a clade containing *L. multizonatus* and *L. liuchengchaoi* from China, but only with strong statistical support in the BI. The new species differed from the latter by at least 7.5% in uncorrected pairwise sequence distance. There has been some taxonomic confusion in the genus *Lycodon*. Two of the *L. liuchengchaoi* sequences (KC733201, KC733202) in the phylogenetic tree had previously been identified as *L. fasciatus*, but the phylogenetic analysis by Guo et al. (2015) correctly assigned them to *L. liuchengchaoi*. *Lycodon* “*flavozonatus*”, on the other hand, appears to be paraphyletic with *Lycodon* “*meridionalis*” (MH669271, MH669268). Moreover, the *Lycodon subcinctus* species group is likely to contain cryptic diversity. In terms of uncorrected pairwise genetic distance of populations within this species group, two samples (GenBank numbers KX822581 and KX822582) are approximately 9.1–9.2% divergent from KC733203 and 6.3–6.5% from KC010384 and KC010385. The latter two clades differ by approximately 8.0% from each other. These issues need to be further investigated in future studies.

This new discovery increases the number of *Lycodon* known from Vietnam to 16, of which nine are confined to karst formations, underlining the importance of this habitat in promoting reptile speciation (Luu et al. 2018). Although Vietnam is located in the region with one of the most extensive limestone outcrops in the world (Day and Ulrich 2000) many of the areas are still poorly surveyed, and likely contain a high level of cryptic diversity. Recent studies show that this habitat harbours a significant portion of endemic diversity in the region and should be protected from anthropogenic threats (Clement et al. 2006, Nguyen et al. 2015, Luu et al. 2016).

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Appendix I

Comparative specimens examined

- Lycodon fasciatus*. Vietnam: Quang Binh Province (ZFMK 86448)
Lycodon fasciatus. Vietnam: Quang Binh Province (ZFMK 86449)
Lycodon fasciatus. Vietnam: Quang Binh Province (ZFMK 86450)
Lycodon futsingensis. Vietnam: Cao Bang (IEBR 4165)
Lycodon futsingensis. Vietnam: Cao Bang (IEBR 4170)
Lycodon futsingensis. Vietnam: Vinh Phuc (ZFMK 89385)
Lycodon laoensis. Cambodia: Phnom Penh (ZFMK 54886)
Lycodon laoensis. Vietnam: Dong Nai (ZFMK 88928)
Lycodon meridionalis. Vietnam: Quang Ninh (ZFMK 95193)
Lycodon meridionalis. Vietnam: Hai Phong (ZFMK 94906)
Lycodon meridionalis. Vietnam: Bac Giang (ZFMK 89389)
Lycodon meridionalis. Vietnam: Vinh Phuc (ZFMK 89225)
Lycodon paucifasciatus. Vietnam: Quang Binh (ZFMK 86452)
Lycodon paucifasciatus. Vietnam: Quang Binh (ZFMK 80661)
Lycodon paucifasciatus. Vietnam: Quang Binh (ZFMK 80662)
Lycodon subcinctus. Indonesia: Bali (ZFMK 95499)
Lycodon subcinctus. Vietnam: Dong Nai (ZFMK 91899)

Delineation of two new, highly similar species of Taiwanese *Cylindera* tiger beetles (Coleoptera, Carabidae, Cicindelinae) based on morphological and molecular evidence

Ming-Hsun Chou¹, Wen-Bin Yeh¹

¹ Department of Entomology, National Chung Hsing University, 250 Kuo Kuang Road, Taichung 40227, Taiwan

Corresponding author: Wen-Bin Yeh (wbyeh@nchu.edu.tw)

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Abstract

Tiger beetles have been recognized primarily based on morphological characters. However, the variations of elytral maculation and coloration sometimes lead to misjudgment in species classification and the overlooking of the existence of cryptic species. Recently, specimens of two endemic species of Taiwanese *Cylindera*, *C. sauteri* and *C. pseudocylindriformis*, exhibit morphologically recognizable forms, indicating that some undescribed species may exist. To clarify their taxonomic status, morphological characteristics including male genitalia were examined and two mitochondrial genes, COI and 16S rDNA, and one nuclear 28S rDNA were analyzed. Molecular phylogenetic inferences indicated that both forms in both species are reciprocally monophyletic. Moreover, molecular dating showed the forms diverged approximately 1.3 million years ago. Two new species, *Cylindera ooa* **sp. nov.** and *Cylindera autumnalis* **sp. nov.**, are thereby described. The main recognizable characteristics separating *C. ooa* **sp. nov.** from *C. sauteri* are the lack of a triangular spot at the middle edge of elytron and the elongated but not rounded subapical spot. For *C. autumnalis* **sp. nov.**, the apical lunula near the elytral suture is thickened but not linear and slender, and its elytra are more metallic brownish than those of *C. pseudocylindriformis*. Although their aedeagi characteristics are not distinctive, the body size of the proposed two new species is different. Field observation revealed that niche utilization would be relevant for differentiating these closely related species.

Keywords

COI, key, new species, taxonomy, 16S rDNA, 28S rDNA

Introduction

The subfamily Cicindelinae of Carabidae consists of approximately 2,600 species (Pearson and Cassola 2005). Among them, *Cylindera* Westwood, 1831 is a diverse genus and widely distributed throughout the world. In Taiwan, including offshore islands such as Lanyu and Kingman, there are ten known *Cylindera* species and subspecies in four subgenera, including *C. cylindriformis* (Horn, 1912), *C. pseudocylindriformis* (Horn, 1913), *C. redunculata* Lin, 2017, and *C. sauteri* (Horn, 1912) in the subgenus *Cylindera* s. str.; *C. kaleea kaleea* (Bates, 1866), *C. kaleea angulimaculata* (Mandl, 1955), and *C. psilica psilica* (Bates, 1866) in the subgenus *Ifasina*; *C. elisae reductelineata* (Horn, 1912) and *C. elisae formosana* (Minowa, 1932) in the subgenus *Eugrapha*; and *C. shirakii* (Horn, 1927) in the subgenus *Apterodela* (Wiesner 1992; Werner et al. 2002; Löbl and Smetana 2003; Lin 2017). Additionally, however, *Apterodela* is either elevated to a full genus (Pearson et al. 2015; Puchkov and Matalin 2017) or is a subgenus within *Cylindera* based on a molecular phylogeny study (Gough et al. 2018). Some taxonomic issues of Taiwanese *Cylindera* are open to debate. For instance, *C. elisae reductelineata*, which is endemic to Taiwan, was differentiated genetically from the widespread lineage composed of other *C. elisae* subspecies, including the endemic subspecies *C. elisae formosana* (Sota et al. 2011), which is worth discussing. Moreover, the *C. sauteri* described commonly is in fact different from its type specimen (Werner et al. 2002).

Cicindela sauteri and *C. cylindriformis* were described by Horn (1912), and then *Prothyma pseudocylindriformis* was also described by Horn (1913). Schilder (1953) transferred *C. sauteri* and *C. cylindriformis* to the subgenus *Jansenia* and *Thopeutica* in genus *Cylindera*, respectively. In 1961, Rivalier classified *Cylindera* as nine subgenera and transferred *C. sauteri* and *C. cylindriformis* to subgenus *Cylindera* s. str. with the aedeagus illustration of *C. sauteri*. Referring to Rivalier's opinion, Cassola (2002) transferred *P. pseudocylindriformis* to *Cylindera* s. str. based on the male genitalia characteristics. *Cylindera pseudocylindriformis* had been recorded in Vietnam (Horn 1929; Wiesner 1992; Cassola 2004), whereas Werner et al. (2002) considered it is endemic to Taiwan, and Wiesner et al. (2017) excluded it from the Cicindelinae checklist of Vietnam. Furthermore, one endemic new species, *C. redunculata* Lin, 2017, was described based on the elytral maculations compared with other *Cylindera* s. str. and *C. kaleea* (Lin 2017).

Recently, some specimens examined exhibit morphologically recognizable variations, which represents the possibility of undescribed *Cylindera* species in Taiwan. Field observation showed that *C. pseudocylindriformis*, inhabiting the soil slopes with gravels and litters near the forest, has a dark brownish body color and is seldom found on open ground. Several tiger beetles, however, collected from Pintung county, in southern Taiwan, are morphologically similar to *C. pseudocylindriformis* in elytral maculation pattern but have more obvious spots and lighter metallic coloration and inhabit the open forest trails. For *C. sauteri*, two forms were discovered in the specimens deposited in Museums für Naturkunde Berlin (MFNB): One is the commonly described

C. sauteri with three spots on each elytron, and the other was collected in Kosempo, southern Taiwan, has a smaller body size and only two visible spots on each elytron, which are incongruent with the original description of *C. sauteri* by Horn (1912). Here, the 'sauteri' group inclusive of *C. sauteri* and Kosempo form was defined, and the 'pseudocylindriformis' group was considered to include *C. pseudocylindriformis* and the Pintung form. This study will test whether Kosempo and Pintung forms are undescribed species.

Tiger beetles were determined and described mainly based on morphological characters (Duran et al. 2018), especially labral shape, labral setae, elytral maculation, and male genitalia (Pearson and Vogler 2001; Pearson et al. 2015). Rivalier (1961) described the subgenus *Cylindera* s. str. as the following: (1) body slender; (2) maculation reduced and with longitudinal tendency when existing; (3) elytra usually with punctures; (4) underside hairs sparse; (5) proepisternum hairless; (6) labrum with 6–8 setae on margin; and (7) several species flightless due to reduced hind wings. However, the varied elytral maculation and coloration of tiger beetles might misjudge species identification and classification (Kaulbars and Freitag 1993; Cardoso and Vogler 2005; Woodcock et al. 2007), and lack of morphologically distinguishable characters might also overlook the existence of cryptic species (López-López et al. 2012, 2016; Duran et al. 2018).

Molecular evidence has been helpful for systematic work in tiger beetles, such as the sequences of cytochrome oxidase I (COI), 16S rDNA, and 28S rDNA (Cardoso et al. 2003; Sota et al. 2011; López-López et al. 2012, 2013, 2015, 2016; Jaskuła et al. 2016). The barcoding fragment of COI has been commonly used for species identification and delimitation (Hebert et al. 2003a, 2003b, 2004a). In the present study, more samples of Taiwanese *Cylindera* were acquired to examine the morphological characteristics, including genital characteristics, and to analyze the sequences of the two mitochondrial genes COI and 16S rDNA and one nuclear 28S rDNA. Based on molecular and morphological evidence, two new species of the aforementioned Kosempo and Pintung forms are thereby documented and described.

Materials and methods

Sampling

Cylindera adults were collected by net around Taiwan. For the 'sauteri' group, 23 individuals of *C. sauteri* were sampled, and seven individuals of Kosempo form were collected in Jiaxian (Kosempo), Kaohsiung. As for the 'pseudocylindriformis' group, 11 individuals each of *C. pseudocylindriformis* and the Pintung form were collected. The sampling localities are shown in Fig. 1. Samples were preserved in 95% alcohol at -20 °C for morphology and DNA analysis. Some of them were processed as dry specimens for imaging after DNA extraction.

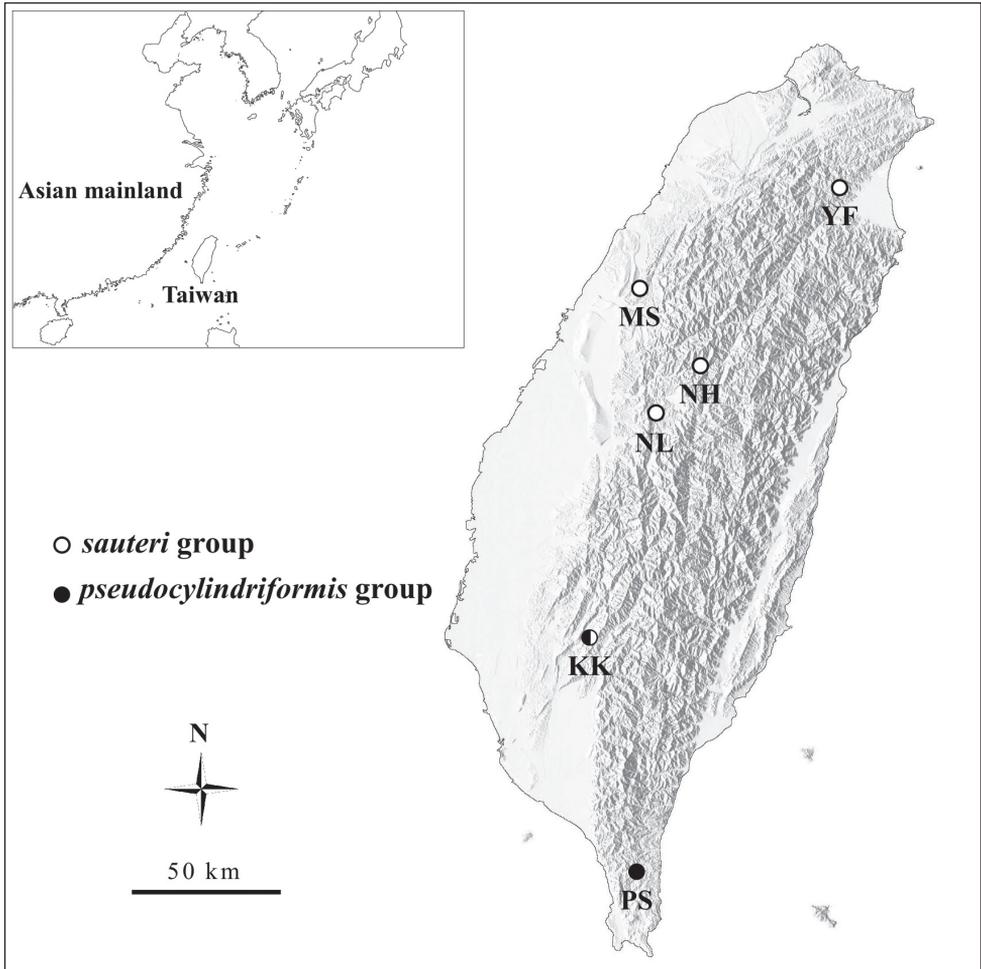


Figure 1. Sampling localities of the '*sauteri*' and '*pseudocylindriformis*' groups. Map was modified from the base map in website of Graduate Institute of Applied Geology of National Central University (<http://gis.geo.ncu.edu.tw/earth/shade/twshades.htm>).

Abbreviations

- NMNS** National Museum of Natural Science, Taichung, Taiwan
NCHU Department of Entomology of National Chung Hsing University, Taichung, Taiwan
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
MFNB Museum für Naturkunde, Berlin, Germany
KK Kosempo (Jiaxian), Kaohsiung, Taiwan
KD Daliao, Kaohsiung, Taiwan
MS Sanyi, Miaoli, Taiwan
NH Huisun Forest Area, Nantou, Taiwan

NL	Lianhuachi, Nantou, Taiwan
PS	Shuangliu Forest Recreation Area, Pintung, Taiwan
YF	Fushan, Yilan, Taiwan

DNA sequencing

Genomic DNA was extracted from the adult's thoracic or leg muscle. A piece of tissue was ground in 50- μ L solution of the QuickExtract DNA extraction kit (Epicentre Biotechnologies, Madison, WI), and then the sample solution was incubated at 65 °C for 10 min, followed by 98 °C for 2 min. After incubation, the sample solution was stored at -20 °C for polymerase chain reaction (PCR).

Primer pairs used to amplify COI, 16S rDNA, and 28S rDNA are listed in Table 1. PCR assay was performed in a 25- μ L volume under the following conditions: first denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 20 s, annealing at 45 °C or 50 °C for 40 s, and extension at 72 °C for 45 s. The final extension was at 72 °C for 10 min. The PCR products were purified by shrimp alkaline phosphatase/exonuclease I (USB Products, Affymetrix) treatment and then sequenced from both ends (COI) or single end (16S rDNA and 28S rDNA) by thermocycle sequencing using the BigDye terminator 3.1 sequencing kit (Applied Biosystems) following analyzed on an ABI 3730XL DNA Analyzer (Applied Biosystems). All sequence data were deposited in GenBank. Accession numbers for COI, 16S rDNA, and 28S rDNA are LC476849–LC476891, LC476978–LC477022, and LC477023–LC477066, respectively. Following Chakrabarty et al. (2013), the information on GenSeq and ranking of both '*sauteri*' and '*pseudocylindriiformis*' groups are listed in Suppl. material 1: Table S1.

Phylogenetic inference

DNA sequences were aligned using the ClustalW multiple alignment program and then edited in Bioedit 7.0 (Hall 1999). The pairwise genetic distances of three genes within both groups were calculated using Kimura 2-parameter model in MEGA 7.0

Table 1. The primer pairs used in PCR.

Genes	Primers	Sequences (5'–3')	References
COI	Col46 (+)	AACCATAAAGATATTGGAAC	Tsai et al. 2014
	Col731 (-)	CCAAAAATCAAAATAAATGTTG	Tsai et al. 2014
	LCO1490 (+)	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
	HCO2198 (-)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
16S rDNA	16SR21(+)	GCCTGTTTATCAAAAACAT	Yeh et al. 2004
	16S22 (-)	CCGGTCTGAACTCAGATCA	Yeh et al. 2004
28S rDNA	28Se (+)	TCCGTAACCTTCGGAACAAGGATT	Lin et al. 2003
	28Sf (-)	TGTACCGCCCCAGTCAAAC	Lin et al. 2003

(Kumar et al. 2016). Pairwise distances of COI were used to determine the barcoding gap between forms, which is helpful to delimit different species (Hebert et al. 2004b). In addition, the maximum intra-taxa COI sequence divergence and minimum inter-taxa COI sequence divergence were also applied (Meier et al. 2008).

Cylindera redunculata belonging to the same subgenus *Cylindera* s. str. was used as the phylogenetic outgroup. Sequences of COI, 16S rDNA, and 28S rDNA were used to perform phylogenetic analyses. The best-fit substitution models applied to different genes were inferred in jModelTest 2.1 (Darriba et al. 2012) using the Bayesian information criterion (BIC). The best-fit models for COI, 16S DNA, and 28S rDNA were TPM2uf+I, TPM1uf, and F81 for the ‘*sauteri*’ group and HKY+I, HKY, and F81 for the ‘*pseudocylindriiformis*’ group, respectively. Bayesian inference (BI) was conducted using MrBayes 3.2.6 (Ronquist et al. 2012). The partitioned analyses of the combined data (COI+16S rDNA+28S rDNA) were set up. Markov chain Monte Carlo (MCMC) methods were conducted for 1×10^6 generations, sampling every 1000 generations; then, the analyses were settled when the average standard deviation of split frequencies < 0.01 . The 25% trees were burn-in to obtain a consensus tree. The maximum likelihood (ML) analyses were performed on an online version of PhyML 3.0 (<http://www.atgc-montpellier.fr/phyml/>) (Guindon et al. 2010) with 1000 bootstrap replications, and the best-fit models were searched using BIC by Smart Model Selection (Lefort et al. 2017).

Divergence time estimation was performed in BEAST 2.5.1 (Bouckaert et al. 2018) using the combined data of COI, 16S rDNA, and 28S rDNA. The substitution models for partition were the same as BIs. Calibration rates of COI, 16S rDNA, and 28S rDNA were 3.34%, 0.76% (Pons et al. 2011), and 0.17% (Sota et al. 2011) per lineage per million years, respectively; and strict clock was applied. Parameters of the prior panel were set as the default. MCMC chain length was 1×10^8 generations sampling every 1000 steps. The output results were assessed in Tracer 1.6 to examine the effective sample sizes as optimal, i.e., > 200 , or not. The tree files were combined in LogCombiner 2.5.2 with the removal of 10% burnin, and then TreeAnnotator 2.5.1 was used to generate a maximum credibility tree with median node heights.

Morphology analyses

Body lengths were measured using Microsight 4.1.2 connected with a Canon EOS 800D camera (Tokyo, Japan); this equipment was also used for imaging aedeagi. Specimens images were taken using a Nikon Coolpix B700 camera (Tokyo, Japan) with a Raynox DCR-250 macrolens (Tokyo, Japan). To avoid influencing the measurement by head pose, lengths of the pronotum and elytron were applied as body length. R 3.4.3 (R Core Team 2017) was used to conduct two-sample Wilcoxon rank-sum tests to test whether the body lengths of the same sex between different forms of the two species group were different statistically. A two-tailed t-test and $p \leq 0.05$ was considered significant.

Male genitalia of both forms were dissected and dipped in 10% KOH solution at room temperature for 12 h. The treated genitalia were preserved in glycerol for imaging

and then described (Shi et al. 2013). The terminology of genital structures followed Freitag et al. (1985) and Acciavatti and Pearson (1989).

Results

Phylogenetic inferences

‘*sauteri*’ group. Twenty-five sequences of COI, 16S rDNA, and 28S rDNA with a length of 660 bp, 472–473 bp, and 850 bp, respectively, were obtained and aligned. The combined data indicated that Kosempo form and *C. sauteri* were reciprocally monophyletic groups with high support values (ML = 0.99, BI = 1 for each of them) (Fig. 2). ML trees of COI, 16S rDNA, and 28S rDNA are shown in Suppl. material 2: Figs S1, S2, and S3, respectively, and their topology resolutions show the reciprocal monophyly of Kosempo form and *C. sauteri*. These forms diverged approximately 1.36 million years ago (Mya) (Suppl. material 2: Fig. S4). The minimum COI distance between them was 0.083, and the maximum intra-form distance was 0.023 (Suppl. material 1: Table S2). The barcoding gap existed clearly (Fig. 3). Pairwise distances of 16S rDNA and 28S rDNA are shown in Suppl. material 1: Tables S3 and S4, respectively.

‘*pseudocylindriformis*’ group. There were 17, 19, and 18 sequences of COI, 16S rDNA, and 28S rDNA of lengths 661 bp, 471 bp, and 848 bp, respectively, that were obtained and aligned. The ML tree based on combined data showed the reciprocal monophyly of Pintung form and *C. pseudocylindriformis* with high support of values (ML = 0.96, BI = 1 for Pintung form; ML = 0.87, BI = 1 for *C. pseudocylindriformis*) (Fig. 5). Both ML trees of COI (Suppl. material 2: Fig. S5) and 16S rDNA (Suppl. material 2: Fig. S6) also showed that these forms were reciprocally monophyletic. However, the phylogenetic resolution inferred from 28S rDNA showed Pintung form monophyly only (Suppl. material 2: Fig. S7). Molecular dating placed the differentiation event between the two at approximately 1.26 Mya (Suppl. material 2: Fig. S8). The minimum inter-form and maximum intra-form distances of COI were 0.076 and 0.028, respectively (Suppl. material 1: Table S5), indicating existence of the barcoding gap (Fig. 4). Pairwise distances of 16S rDNA and 28S rDNA are shown in Suppl. material 1: Tables S6 and S7, respectively.

Morphology

Morphological and genital characteristics described for ‘*sauteri*’ and ‘*pseudocylindriformis*’ groups were as follows:

‘*sauteri*’ group. Body lengths (pronotum and elytron) of Kosempo form were 5.91–6.67 mm (mean = 6.44 mm, $n = 7$) for males and 6.95–7.53 mm (mean = 7.26 mm, $n = 8$) for females, and the lengths of *C. sauteri*, including the specimens borrowed from

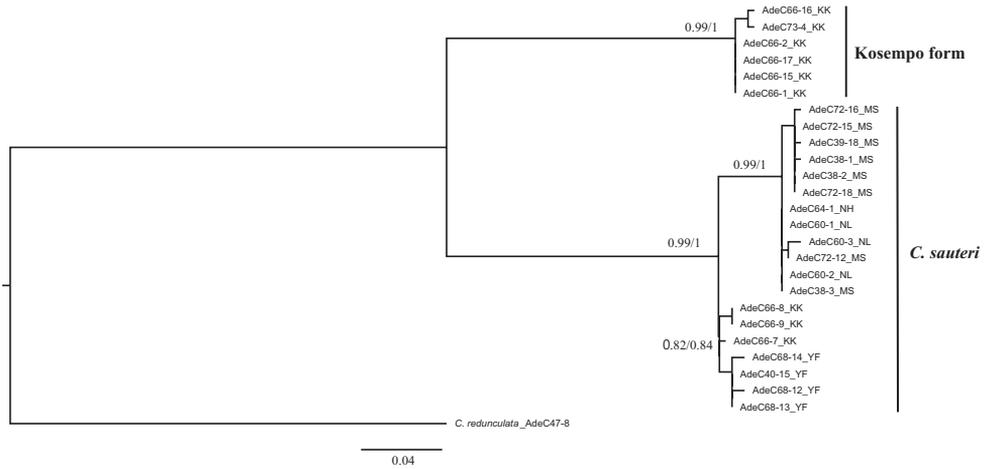
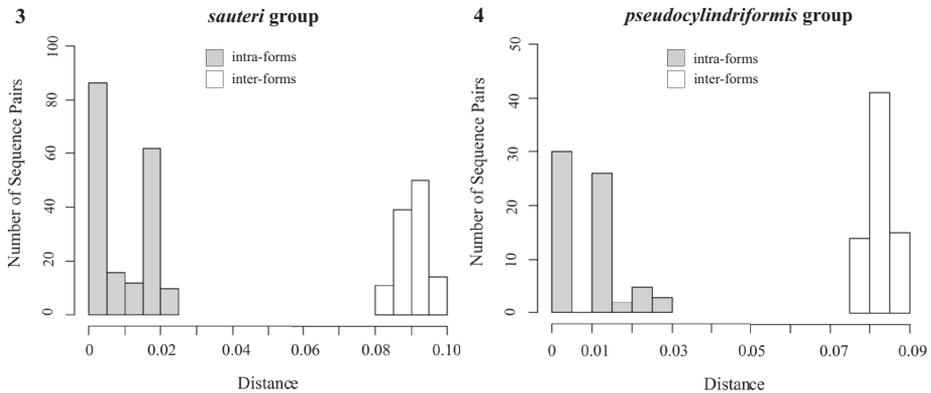


Figure 2. ML tree of the 'sauteri' group reconstructed based on the combined data of COI, 16S rDNA, and 28S rDNA with ML bootstrap values (left) and BI posterior probability (right) that are shown when > 0.5.



Figures 3, 4. Frequency distributions of COI pairwise distance of the 'sauteri' group (3) and the 'pseudocylindriformis' group (4), showing the barcoding gaps.

MFNB and our collections, were 7.23–8.19 mm (mean = 7.79 mm, n = 13) for males and 7.69–9.00 mm (mean = 8.35 mm, n = 15) for females (Fig. 6). In both sexes, body lengths of *C. sauteri* were significantly larger than those of Kosempo form ($p = 0.0004$ for males; $p = 0.000004$ for females).

Elytral maculation of Kosempo form mostly included two spots on each elytron: One spot near elytral suture (Fig. 7, a), and one subapical spot at subapical corner of elytron (Fig. 7, b). However, one of 15 individuals of Kosempo form possessed visible posthumeral spots. *Cylindera sauteri* possessing three spots on each elytron: one spot near suture (Fig. 8, c), one subapical spot at subapical corner (Fig. 8, d), and one spot at middle edge of elytron (Fig. 8, e). Spot near suture and spot at middle edge usually connected very weakly. Posthumeral spot absent or hardly visible in all 23 specimens of *C. sauteri*.

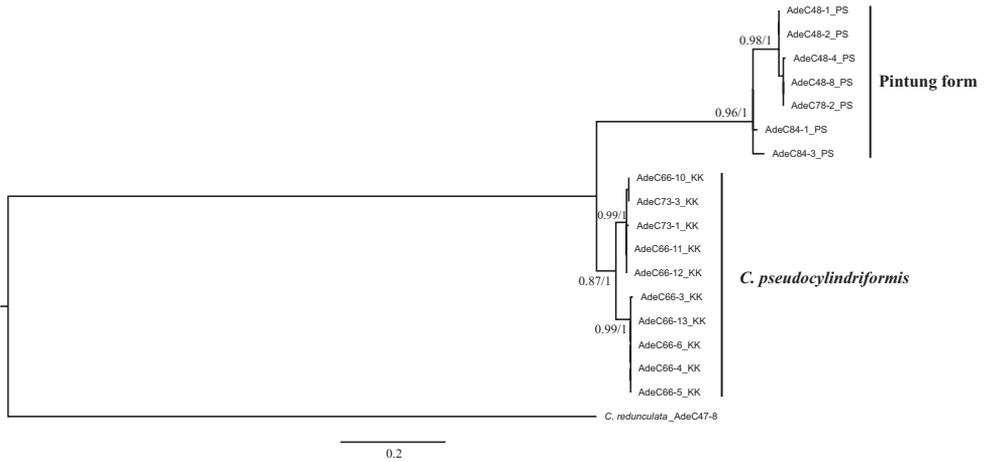


Figure 5. ML tree of the '*pseudocylindriformis*' group reconstructed based on the combined data of COI, 16S rDNA, and 28S rDNA with ML bootstrap values (left) and BI posterior probability (right) that are shown when > 0.5 .

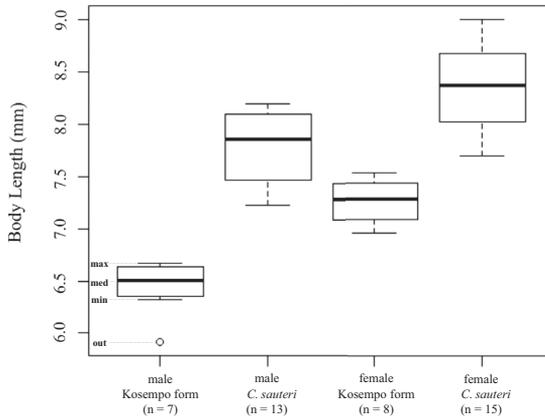
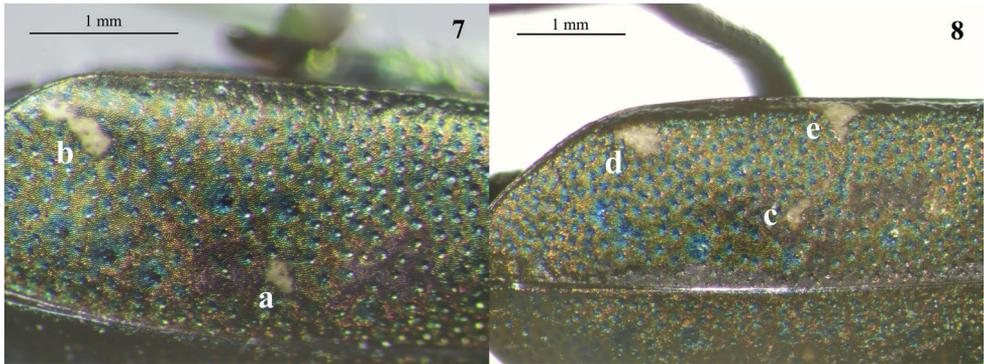


Figure 6. Body length (pronotum and elytron) of the '*sauteri*' group. Legends: **max** maximum; **med** median; **min** minimum; **out** outlier.

Male genitalia were very similar in external shape and inner sac between Kosempo form ($n = 3$) and *C. sauteri* ($n = 8$) but different in size (Figs 9, 10). Basal portion of aedeagus short and slightly bent, median portion widened, apical portion narrow gradually, apical top rounded. Paramere (*p*) slender, acanthoid. On the left view of aedeagus, base of flagellum (*f*) convoluted spirally; stiffening rib (*sr*) near base of flagellum with two upcurved ends; central plate (*cp*) irregular; medial tooth (*mt*) and arciform piece (*ap*) oblique near subapical apex and overlapping.

'*pseudocylindriformis*' group. Body lengths (pronotum and elytron) of Pintung form were 6.57–7.11 mm (mean = 6.79 mm, $n = 7$) for males and 7.14–7.72 mm (mean = 7.42 mm, $n = 4$) for females and of *C. pseudocylindriformis*, 5.77–6.43 mm (mean =



Figures 7, 8. The elytral maculations (left elytron). **7** Kosempo form lacks any spot on the middle elytral edge and has one spot near suture (**a**) and one subapical spot (**b**) **8** *Cylindera sauteri* has one spot near suture (**c**), one subapical spot (**d**), and one triangular spot on the elytral middle edge (**e**).

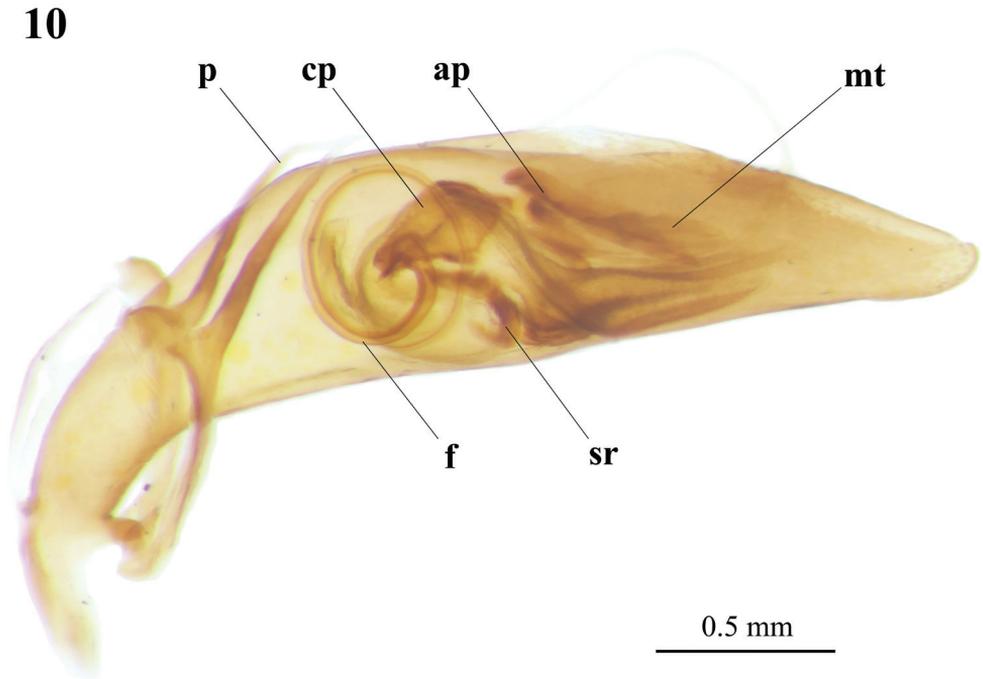
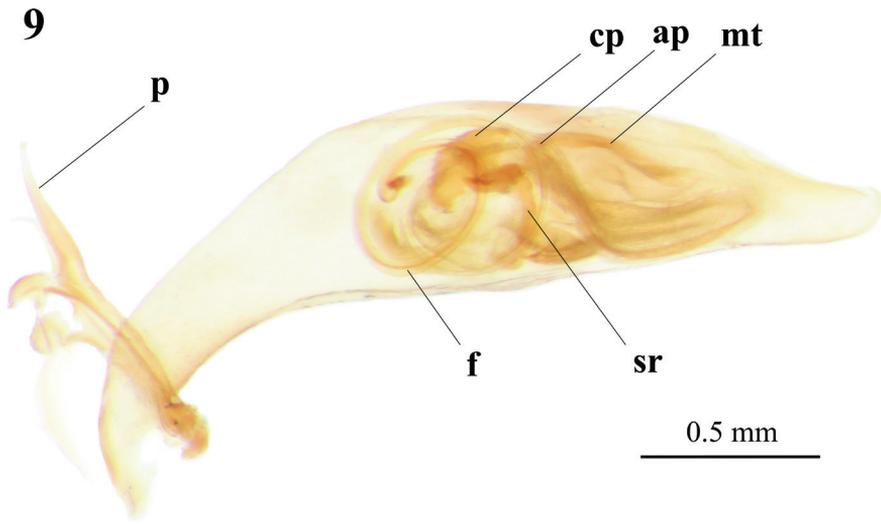
6.16 mm, $n = 6$) for males and 6.96–7.59 mm (mean = 7.16 mm, $n = 5$) for females (Fig. 11). Pintung form was significantly larger than *C. pseudocylindrifformis* in males ($p = 0.001166$) but not in females ($p = 0.14$).

The pattern of elytral maculation of Pintung form and *C. pseudocylindrifformis* almost identical (details provided below Figs 26–28). Humeral spot and posthumeral spot visible in both forms. Spot at middle edge connected to spot near suture very weakly but connected together in one *C. pseudocylindrifformis* and three Pintung form specimens. Apical lunula visible, and its subapical portion thickened in both forms, but apical end near suture thickened only in Pintung form.

Male genitalia similar in morphology between *C. pseudocylindrifformis* ($n = 5$) and Pintung form ($n = 4$) and even similar to ‘*sauteri*’ group. External shape slender, median portion widened, apical portion narrow gradually with a rounded apical top, basal portion slightly shorter in *C. pseudocylindrifformis* and slenderer in Pintung form. Paramere (p) slender, acanthoid. Structures of inner sac almost identical in both forms, base of flagellum (f) convoluted spirally on left view; stiffening rib (sr) near base of flagellum; central plate (cp) irregular; medial tooth (mt) and arciform piece (ap) oblique near subapical apex and overlap partially (Figs 12, 13).

Discussion

Phylogenetic trees inferred from molecular combined data show that both forms in ‘*sauteri*’ and ‘*pseudocylindrifformis*’ groups are monophyletic reciprocally with high support values (Figs 2, 5). The weak phylogenetic resolution inferred from the 28S rDNA fragments of Pintung form and *C. pseudocylindrifformis* might be due to the conserved property of 28S rDNA applying to resolve the relationship of closely related species (Guerra et al. 2016; Tsai and Yeh 2016). Phylogenetic inferences, molecular dating, and the deep barcoding gap indicate that the different forms are genetically distinct.



Figures 9, 10. Digital image of aedeagus in left view of Kosempo form (AdeC66-1) (**9**) and *Cylindera sauteri* (**10**). Abbreviations: **ap** arciform piece; **cp** central plate; **f** flagellum; **p** paramere; **mt** medial tooth; **sr** stiffening rib.

According to the original description of *C. sauteri* (Horn 1912), its elytron is garnished with two or three testaceous maculae: one is discoidal and very tiny near the middle suture, another triangular one is approximately at the middle edge (sometimes deficient), and the third is oblique on the subapical corner. This is the main

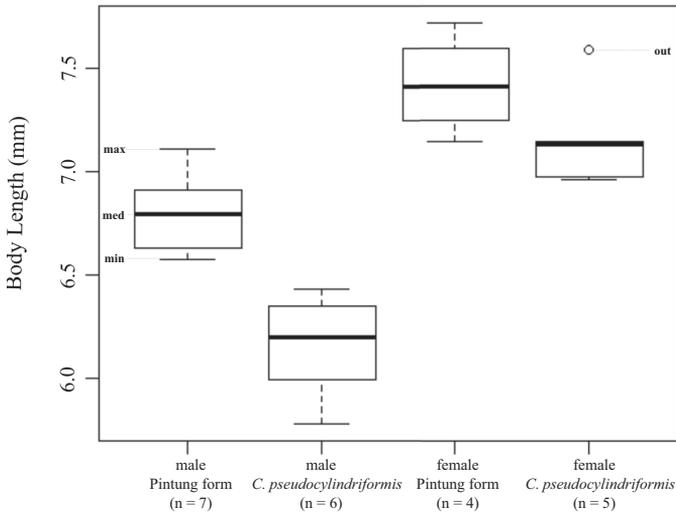
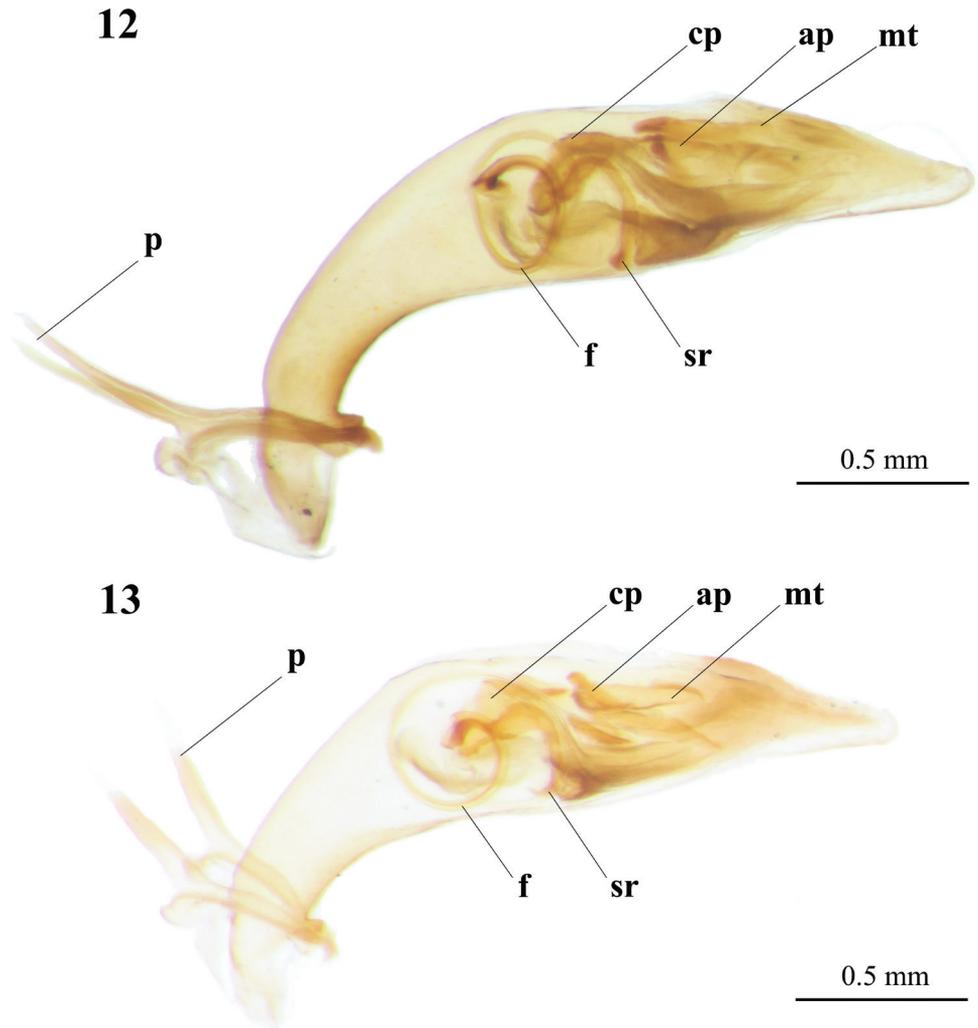


Figure 11. Body length (pronotum and elytron) of the ‘*pseudocylindrifformis*’ group. Abbreviations: **max** maximum; **med** median; **min** minimum; **out** outlier.

difference from the Kosempo form, which lacks the triangular spot at the middle edge of elytron and has an elongated subapical spot (Fig. 7b). The triangular spot and rounded subapical spot of *C. sauteri* were illustrated in the line drawing by Horn (1938). Some *C. sauteri* individuals have a very tiny or obscure triangular macula, but this spot does not disappear completely. As for ‘*pseudocylindrifformis*’ group, the elytral apical lunula of Pintung form is thickened in the apical portion near the elytral suture, but it stays linear and slender in *C. pseudocylindrifformis*. The line drawing of syntype of *C. pseudocylindrifformis* also shows this character of apical lunula (Cassola 2002). Moreover, Pintung form is more metallic brown than *C. pseudocylindrifformis*. Their aedeagi are poorly distinctive (Figs 12, 13); however, male genitalia of *C. sauteri* and *C. pseudocylindrifformis* are also nearly identical (Rivalier 1961; Cassola 2002), indicating morphologic conservation of male genitalia among closely related *Cylindera* species.

Based on the genetic distinction and stable morphological differences, Kosempo form and Pintung form could be recognized as two undescribed species. In the present study, Kosempo form of the ‘*sauteri*’ group is named *Cylindera ooa* sp. nov., and Pintung form of the ‘*pseudocylindrifformis*’ group is named *Cylindera autumnalis* sp. nov. Moreover, *C. ooa* sp. nov. seems to be confined to the Jiaxian region, but *C. sauteri* is widely distributed across the Taiwan Island. The type localities of *C. sauteri* are Kosempo (Jiaxian, Kaohsiung) and Taihorin (Dalin, Chiayi) (Horn 1912). Unfortunately, we could not examine the type specimens of *C. sauteri* because they were on loan till the time of writing this manuscript. It is necessary to clarify whether the type series of *C. sauteri* include *C. ooa* sp. nov. specimens. Even so, the recognizable morphological characters proposed in this study will be helpful in distinguishing them.



Figures 12, 13. Digital image of aedeagus in left view of Pintung form (**12**) and *Cylindera pseudocylindriformis* (**13**). Abbreviations: **ap** arciform piece; **cp** central plate; **f** flagellum; **p** paramere; **mt** medial tooth; **sr** stiffening rib.

Ecological niche differentiation in sympatric closely related species could be related to morphological divergence such as body size because of different resource utilization (Wilson 1975; Pearson and Stemberger 1980; Dangalle et al. 2013). *Cylindera autumnalis* sp. nov. inhabiting open forest trails might not overlap with *C. pseudocylindriformis* preferring soil slopes with more cover. However, *C. ooa* sp. nov. and *C. sauteri* occupy similar habitat types of soil slopes with some gravel and little vegetation, and both can be found in Jiashian area in the same season although a field survey did not observe the sympatric distribution of *C. sauteri* and *Cyl ooa* sp. nov. nor that of *C. autumnalis* sp. nov. and *C. pseudocylindriformis*. Notably, the body size is significantly

different in both proposed new species from their closely related species. The body size would be one of the characters shaped by the process of niche differentiation and speciation. In addition, physiological differences (Schultz and Hadley 1987), oviposition behaviors (Hoback et al. 2000, 2001), and thermoregulatory behaviors (Brosius and Higley 2013) are also relevant to niche differentiation of tiger beetles.

Moreover, the subgenus *Cylindera* s. str. of Taiwan possessing a comparatively longitudinally elongated labrum, thoracic proepisternum with hairs (*C. sauteri* and *C. ooa* sp. nov.), well developed hind wings for flight, and a more slender body seems morphologically distinct from the other members of the subgenus *Cylindera* s. str. Gough et al. (2018) showed the subgenus *Cylindera* s. str. was polyphyletic because the subgenus *Cylindera* s. str. of Palearctic and Oriental was a sister to the subgenus *Ifasina*, whereas its Nearctic fauna was nested with other genera.

Taxonomy

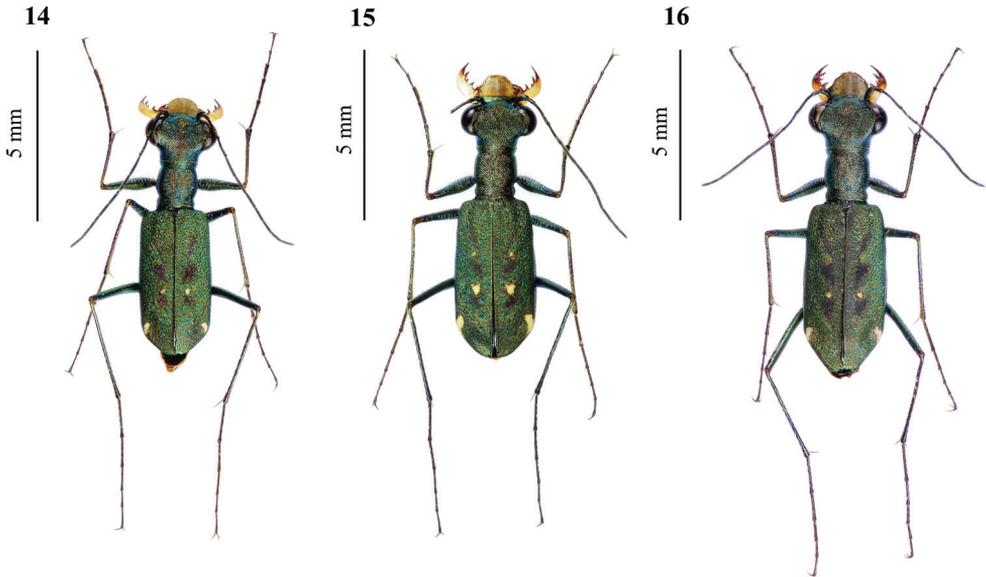
Cylindera (Cylindera) ooa sp. nov.

<http://zoobank.org/7D37BBD1-3BDA-4C13-9F2C-5C47412A21D9>

甲仙鏞虎甲

Type material. *Holotype*: male (Fig. 14; specimen code: AdeC66-1; dry pinned, with aedeagus in glycerol in a separated microvial labeled “AdeC66-1”): Taiwan, Kaohsiung, Jiaxian, Liuyi Mountain, altitude 400–500 m, 17 May 2018, Ming-Hsun Chou leg. Original label: “Locality: 高雄甲仙六義山 / Date: 2018.V.17 / Collector: 周明勳 / Code: AdeC66-1”; “NCHU 0011-0735”. Dry specimen and aedeagus of holotype deposited in NCHU. *Paratypes*: 1 male (Fig. 15; specimen code: AdeC66-15; dry pinned, with aedeagus in glycerol in a separated microvial) and 3 females (specimen code: AdeC66-2 (Fig. 16), AdeC66-16, and AdeC66-17, respectively; dry pinned, with genitalia in glycerol in a separated microvial, respectively): same collecting information as for holotype. 1 male (specimen code: AdeC73-4; dry pinned, with aedeagus in glycerol in a separated microvial): Taiwan, Kaohsiung, Jiaxian, Liuyi Mountain, altitude 400–500 m, 23 Jun. 2018, Ming-Hsun Chou leg. Above dry specimens and genitalia of paratypes deposited in NMNS. 3 females (dry pinned, labeled “Paratype-MFNB-01”, “Paratype-MFNB-02”, and “Paratype-MFNB-07”, respectively): Taiwan, Kaohsiung, Jiaxian, 9–17 May 1908, Sauter S.V. leg. 1 male (dry pinned, labeled “Paratype-MFNB-03”): Taiwan, Kaohsiung, Jiaxian, 17–23 May 1908, Sauter S.V. leg. 1 male (dry pinned, labeled “Paratype-MFNB-04”): Taiwan, Kaohsiung, Jiaxian, 2–14 May 1908, Sauter S.V. leg. 1 male (dry pinned, labeled “Paratype-MFNB-05”): Taiwan, Kaohsiung, Jiaxian, 1–5 May 1908, Sauter S.V. leg. 1 female (dry pinned, labeled “Paratype-MFNB-06”): Taiwan, Kaohsiung, Jiaxian, 1–5 May 1908, Sauter S.V. leg. Above dry specimens of paratypes deposited in MFNB. Original labels of paratypes see Table 2.

Type locality. Taiwan, Kaohsiung, Jiaxian, Liuyi Mountain.



Figures 14–16. Type specimens of *Cylindera ooa* sp. nov. **14** male holotype (AdeC66-1) **15** male paratype (AdeC66-15) exhibiting visible posthumeral spots **16** female paratype (AdeC66-2).

Diagnosis. *Cylindera ooa* sp. nov. can be recognized based on its elongated subapical spots and no any spot at the middle edges of elytra. This species is very similar to *C. sauteri* (Fig. 17) morphologically but can be distinguished from the latter by their elytral maculation, labrum, and body size. *Cylindera sauteri* has a nearly triangular spot at the middle margin of elytron, and its subapical spot is comparatively tiny or rounded. In contrast, the middle elytral margin of *C. ooa* sp. nov. does not have any spot, and its subapical spot is comparatively longer than that of *C. sauteri* (Figs 7, 8). The labrum of *C. ooa* sp. nov. is more straight laterally and has five or six preapical setae (Figs 18–21), but the labrum of *C. sauteri* is concave in lateral sides and has four or five preapical setae (Figs 22–25). Moreover, the body sizes of *C. sauteri*, as well as male genitalia, are usually larger than those of *C. ooa* sp. nov. (Figs 6, 9, 10).

Description. **Head** brownish patina with blue or green luster but more brownish when alive; vertex, frons, and genae almost glabrous except two setae on canthus and anterior portion of vertex, respectively; rugae longitudinal along frons, canthi, vertex, and lateral neck, and gradually becoming transverse on genae; frons and central vertex microsculptured; clypeus brownish patina and microsculptured. **Compound eyes** protruding and globular. **Antennae** long and filiform; scape with one apical seta; 1–4 antennomeres metallic bronze; 5–11 ones dark. **Mandibles** testaceous with dark teeth, exceeding labrum when closed. **Maxillary palps** dark testaceous with metallic luster, except last two palpomeres metallic dark green. **Labial palps** testaceous; last palpomere metallic dark green. **Labrum** testaceous; anterior portion narrow and tridentate; middle tooth longer than other two in female, shorter than or equivalent to others in male; margin with 5–6 preapical and two lateral setae (Figs 18–21). **Pronotum** cylindrical

Table 2. Original labels of type materials.

Species	Code	Type of type	Original label	In English
<i>Cylindera ooa</i>	AdeC66-1	Holotype	Locality: 高雄甲仙六義山 Date: 2018.V.17 Collector: 周明勳 Code: AdeC66-1	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.V.17 Collector: Ming-Hsun Chou Code: AdeC66-1
	AdeC66-2	Paratype	Locality: 高雄甲仙六義山 Date: 2018.V.17 Collector: 周明勳 Code: AdeC66-2	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.V.17 Collector: Ming-Hsun Chou Code: AdeC66-2
	AdeC66-15	Paratype	Locality: 高雄甲仙六義山 Date: 2018.V.18 Collector: 周明勳 Code: AdeC66-15	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.V.18 Collector: Ming-Hsun Chou Code: AdeC66-15
	AdeC66-16	Paratype	Locality: 高雄甲仙六義山 Date: 2018.V.18 Collector: 周明勳 Code: AdeC66-16	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.V.18 Collector: Ming-Hsun Chou Code: AdeC66-16
	AdeC66-17	Paratype	Locality: 高雄甲仙六義山 Date: 2018.V.18 Collector: 周明勳 Code: AdeC66-17	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.V.18 Collector: Ming-Hsun Chou Code: AdeC66-17
	AdeC73-4	Paratype	Locality: 高雄甲仙六義山 Date: 2018.VI.23 Collector: 周明勳 Code: AdeC73-4	Locality: Kaohsiung, Jiaxian, Liuyi Mountain Date: 2018.VI.23 Collector: Ming-Hsun Chou Code: AdeC73-4
	Paratype-MFNB-01	Paratype	“Formosa / Kosempo / Sauter S.V. / 9.–17. V. 08” “Zool. Mus. Berlin”	
	Paratype-MFNB-02	Paratype	“Formosa / Kosempo / Sauter S.V. / 9.–17. V. 08” Zool. Mus. Berlin	
	Paratype-MFNB-03	Paratype	“Formosa / Kosempo / Sauter S.V.” “17.–23. V. 08” “Zool. Mus. Berlin”	
	Paratype-MFNB-04	Paratype	“Formosa / Kosempo / Sauter S.V.” “2.–14. VI. 08” “Zool. Mus. Berlin”	
Paratype-MFNB-05	Paratype	“Formosa / Kosempo / Sauter S.V.” “1.–5. V. 08” “Zool. Mus. Berlin”		
Paratype-MFNB-06	Paratype	“Formosa / Kosempo / Sauter S.V.” “1.–5. V. 08” “Zool. Mus. Berlin”		
Paratype-MFNB-07	Paratype	“Formosa / Kosempo / Sauter S.V. / 9.–17. V. 08” “Zool. Mus. Berlin”		

Species	Code	Type of type	Original label	In English
<i>Cylindera autumnalis</i>	AdeC48-1	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2017.VIII.10 Collector: 周明勳 Code: AdeC48-1	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2017.VIII.10 Collector: Ming-Hsun Chou Code: AdeC48-1
	AdeC48-2	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2017.VIII.10 Collector: 周明勳 Code: AdeC48-2	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2017.VIII.10 Collector: Ming-Hsun Chou Code: AdeC48-2
	AdeC48-4	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2017.VIII.10 Collector: 周明勳 Code: AdeC48-4	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2017.VIII.10 Collector: Ming-Hsun Chou Code: AdeC48-4
	AdeC48-5	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2017.VIII.10 Collector: 周明勳 Code: AdeC48-5	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2017.VIII.10 Collector: Ming-Hsun Chou Code: AdeC48-5
	AdeC48-8	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2017.VIII.11 Collector: 周明勳 Code: AdeC48-8	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2017.VIII.11 Collector: Ming-Hsun Chou Code: AdeC48-8
	AdeC78-1	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2018.VII.21 Collector: 周明勳 Code: AdeC78-1	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2018.VII.21 Collector: Ming-Hsun Chou Code: AdeC78-1
	AdeC78-2	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2018.VII.21 Collector: 周明勳 Code: AdeC78-2	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2018.VII.21 Collector: Ming-Hsun Chou Code: AdeC78-2
	AdeC84-1	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2018.IX.03, Collector: 周明勳 Code: AdeC84-1	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2018.IX.03, Collector: Ming-Hsun Chou Code: AdeC84-1
	AdeC84-2	Paratype	Locality: 屏東雙流森林遊樂區 Date: 2018.IX.03, Collector: 周明勳 Code: AdeC84-2	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2018.IX.03, Collector: Ming-Hsun Chou Code: AdeC84-2
	AdeC84-3	Holotype	Locality: 屏東雙流森林遊樂區 Date: 2018.IX.03, Collector: 周明勳 Code: AdeC84-3	Locality: Pintung, Shuangliu Forest Recreation Area Date: 2018.IX.03, Collector: Ming-Hsun Chou Code: AdeC84-3

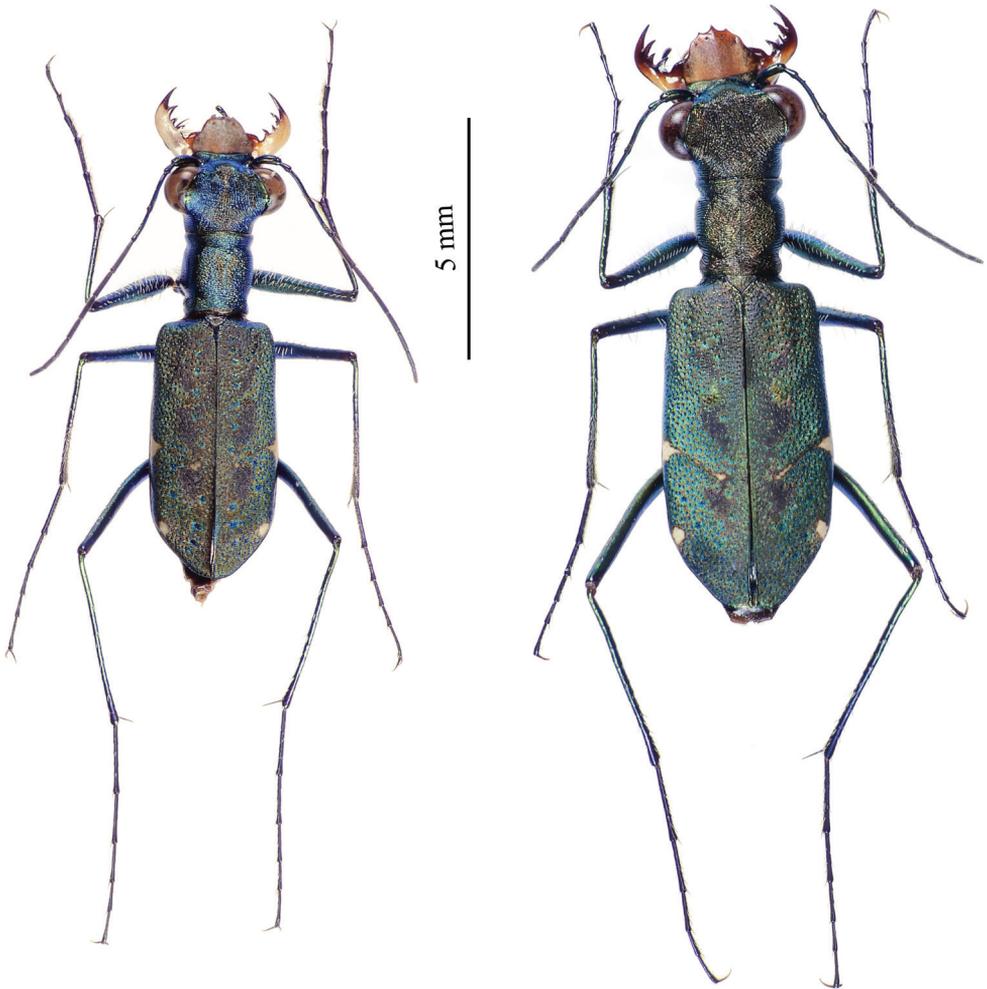
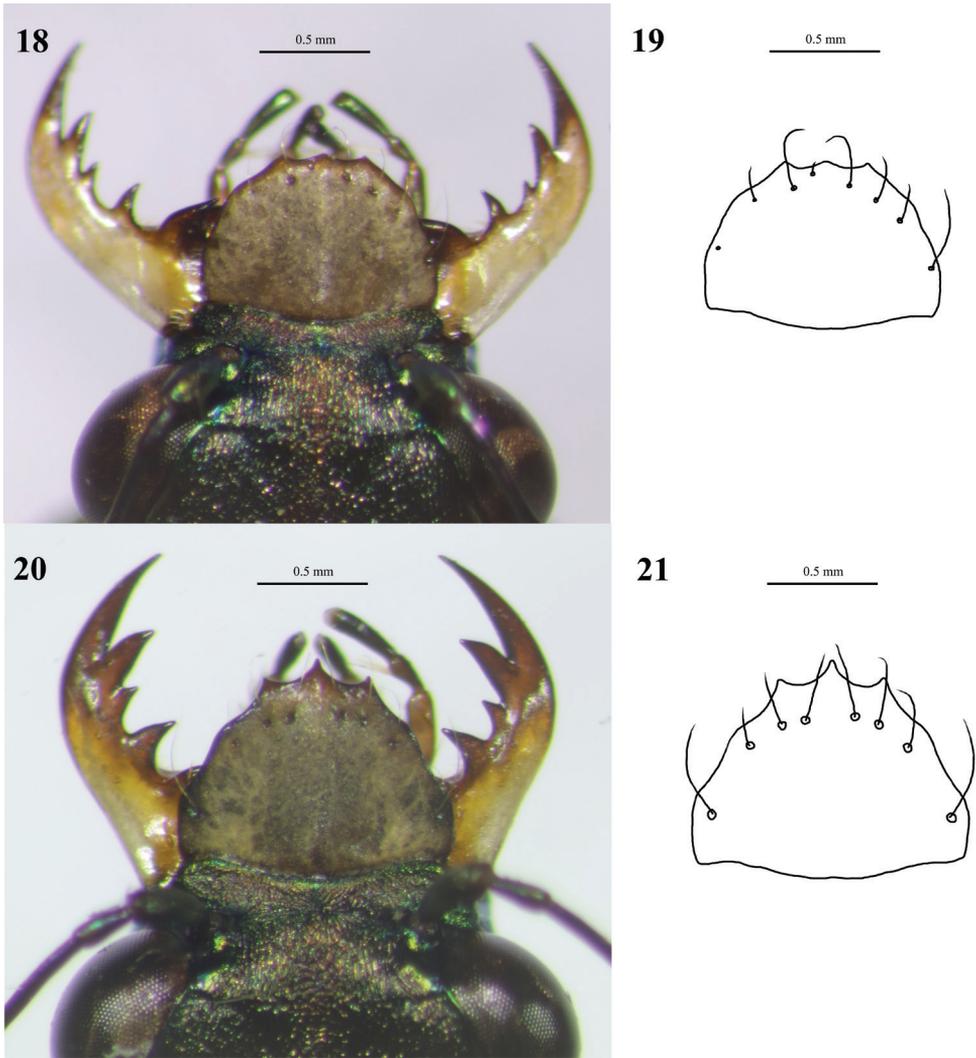


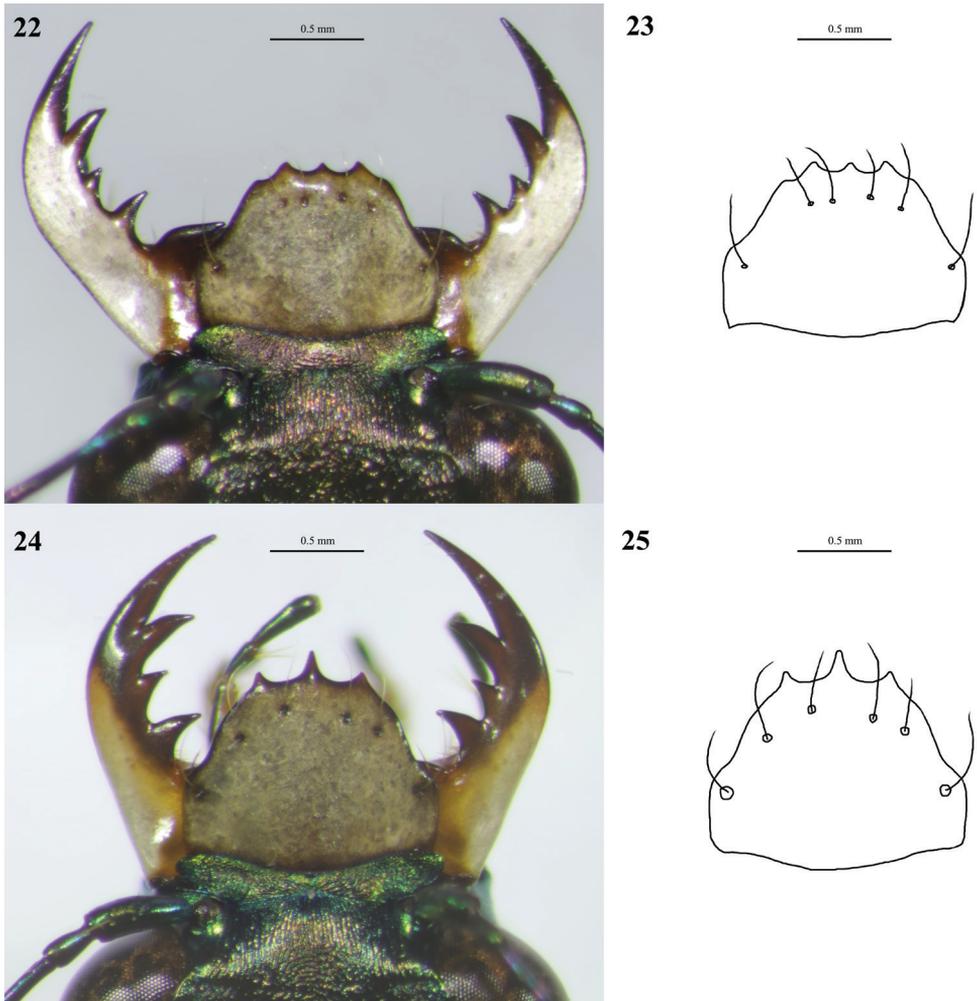
Figure 17. Dorsal habitus of *Cylindera sauteri* (left – male; right – female).

and brownish patina with blue or green luster but more brownish when alive; dorsum microsculptured and rugose transversely, with one transverse groove on each anterior and posterior portions connected with one longitudinal obscure groove; lateral sides little rounded. **Elytra** brownish patina but more brownish when alive, marked with many scattered punctures; three obscure brownish patches wiping longitudinally near suture; each elytron with usually two white or testaceous spots, one rounded or irregular near suture, one elongated a little and oblique on subapical corner; posthumeral spots usually absent or unobvious but visible in some individuals (Fig. 15). **Legs** long; trochanters brownish; coxae, femurs and tibiae metallic greenish bronze; tarsi dark greenish with purple luster, pro-tarsi sexually dimorphic, basal 1–3 tarsomeres with dense brush-like ventral setae and wider than last two tarsomeres in male, all pro-tarsomeres equivalent in width roughly and without brush-like ventral setae in female;



Figures 18–21. Digital images (left) and line drawings (right) of labra of *Cylindera ooa* sp. nov. **18, 19** male (holotype, AdeC66-1) **20, 21** female (paratype, AdeC66-2).

some white hairs on femurs and coxae, one long seta on pro-, mesocoxae, pro- and mesotrochanters. *Thoracic proepisternum* brownish patina with greenish luster, longitudinally rugose, with 2–4 hairs on lower portion. *Prosternum* brownish patina with greenish luster, transversally rugose, glabrous. *Mesoepisternum* brownish patina with greenish luster, longitudinally depressed and coarsely rugose, sometimes with rare hairs. *Mesosternum* brownish patina with greenish luster, transversally rugose, sometimes with rare hairs. *Metepisternum* brownish patina with greenish luster, coarsely sculptured, with a few hairs. *Metasternum* dark bronze with greenish luster, microsculptured, covered by many white hairs on both sides. *Abdomen sternum* dark green



Figures 22–25. Digital images (left) and line drawings (right) of labra of *Cylindera sauteri* **22, 23** male **24, 25** female.

with metallic greenish reflection and with scattered tiny hairs. *Aedeagus* of holotype shown in Fig. 8. Description same as Results.

Etymology. Jiaxian, the type locality, is famous for taro cultivation and products. The Taiwanese pronunciation of taro is ㄊㄠˊ-á, so it was applied as specific name.

Distribution. Only known from type locality.

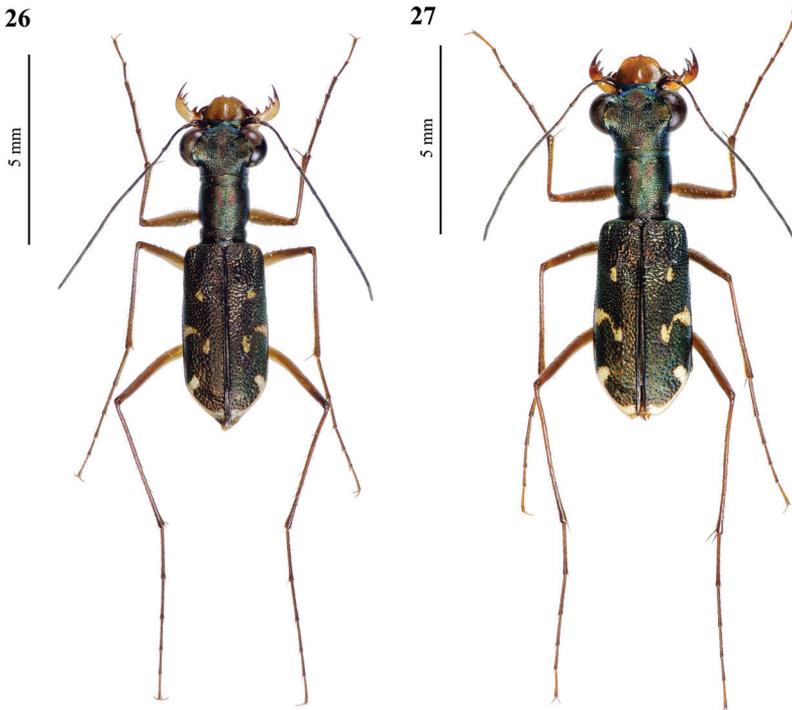
Ecology. Habitat of *C. ooa* sp. nov. is similar to *C. sauteri* that they inhabit soil slopes with some gravels and covered by a few vegetation in or near forest. *Cylindera sauteri* can also be found in Jiaxian, but we did not observe them in the same habitat. *Cylindera pseudocylindriformis* inhabits soil slopes as well and sometimes overlaps with *C. ooa* sp. nov.

***Cylindera (Cylindera) autumnalis* sp. nov.**

<http://zoobank.org/341884A9-BC65-4443-B269-A962E3472D0A>

金商虎甲

Type material. Holotype: male (Fig. 26; specimen code: AdeC84-3; dry pinned, with aedeagus in glycerol in a separated microvial labeled “AdeC84-3”): Taiwan, Pintung, Shuangliu Forest Recreation Area, 03 Sep. 2018, Ming-Hsun Chou leg. Original label: “Locality: 屏東雙流森林遊樂區 / Date: 2018.IX.03 / Collector: 周明勳 / Code: AdeC84-3”; “NCHU 0011-0736”. Dry specimen and aedeagus of holotype deposited in NCHU. **Paratypes:** 3 males (specimen code: AdeC48-4, AdeC48-5, and AdeC48-8, respectively; dry pinned, with aedeagus in glycerol in a separated microvial, respectively), 1 female (specimen code: AdeC48-1; dry pinned), and 1 female (specimen code: AdeC48-2; dry pinned, with genitalia preserved in glycerol in a separated microvial): Taiwan, Pintung, Shuangliu Forest Recreation Area, 10 Aug. 2017, Ming-Hsun Chou leg. 1 male (specimen code: AdeC78-1; dry pinned, with aedeagus in glycerol in a separated microvial) and 1 female (specimen code: AdeC78-2 (Fig. 27); dry pinned): Taiwan, Pintung, Shuangliu Forest Recreation Area, 21 Jul. 2018, Ming-Hsun Chou leg. 1 male (specimen code: AdeC84-1; dry pinned, with aedeagus in glycerol in a separated microvial) and 1 female (specimen code: AdeC84-2; dry pinned, with geni-



Figures 26–27. Type specimens of *Cylindera autumnalis* sp. nov. **26** male holotype (AdeC84-3) **27** female paratype (AdeC78-2).

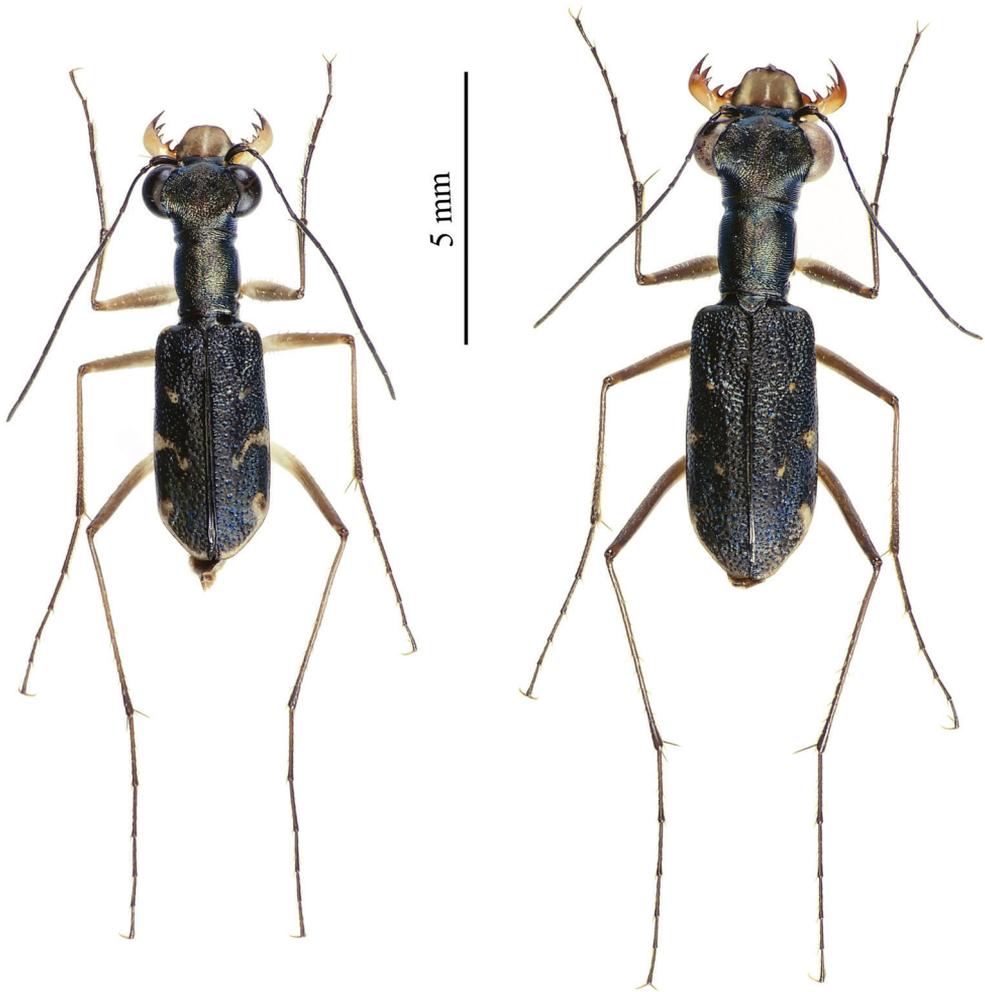
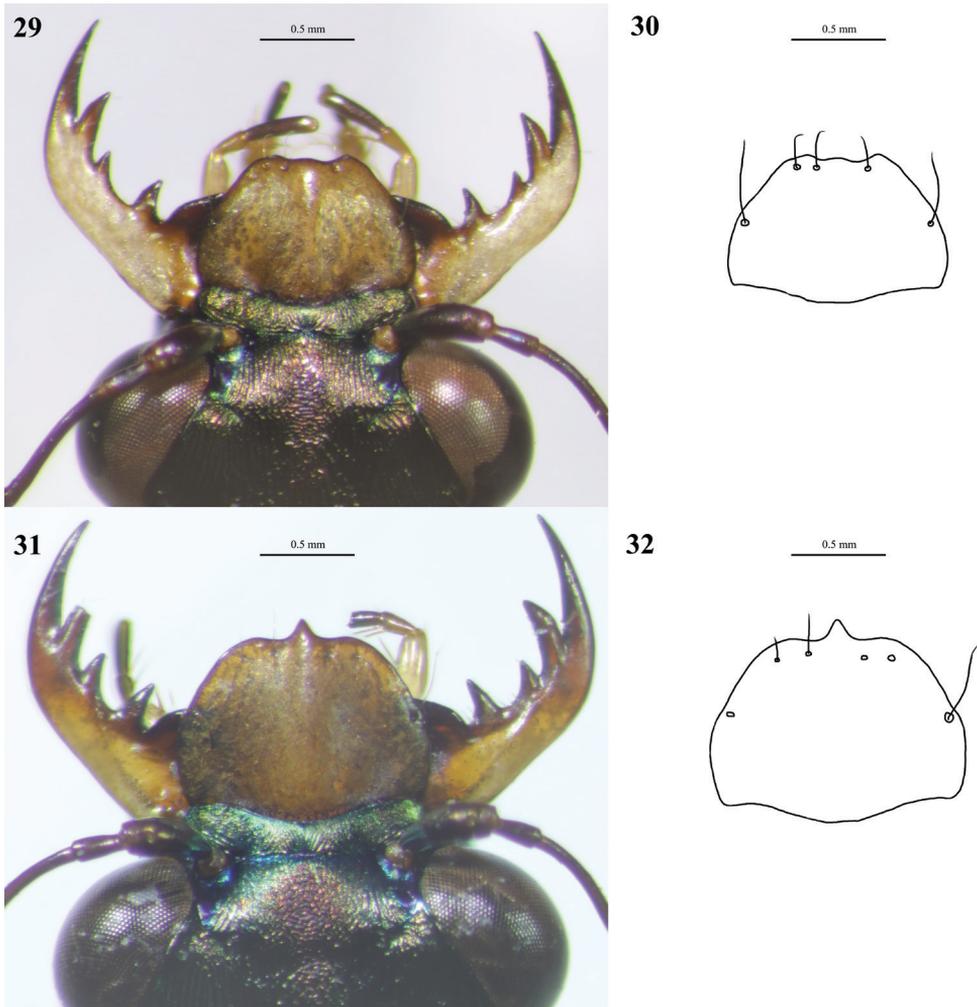


Figure 28. Dorsal habitus of *Cylindera pseudocylindriformis* (left – male; right – female).

talia in glycerol in a separated microvial): same collecting information as for holotype. Original labels of paratypes see Table 2. All dry specimens and genitalia of paratypes deposited in NMNS.

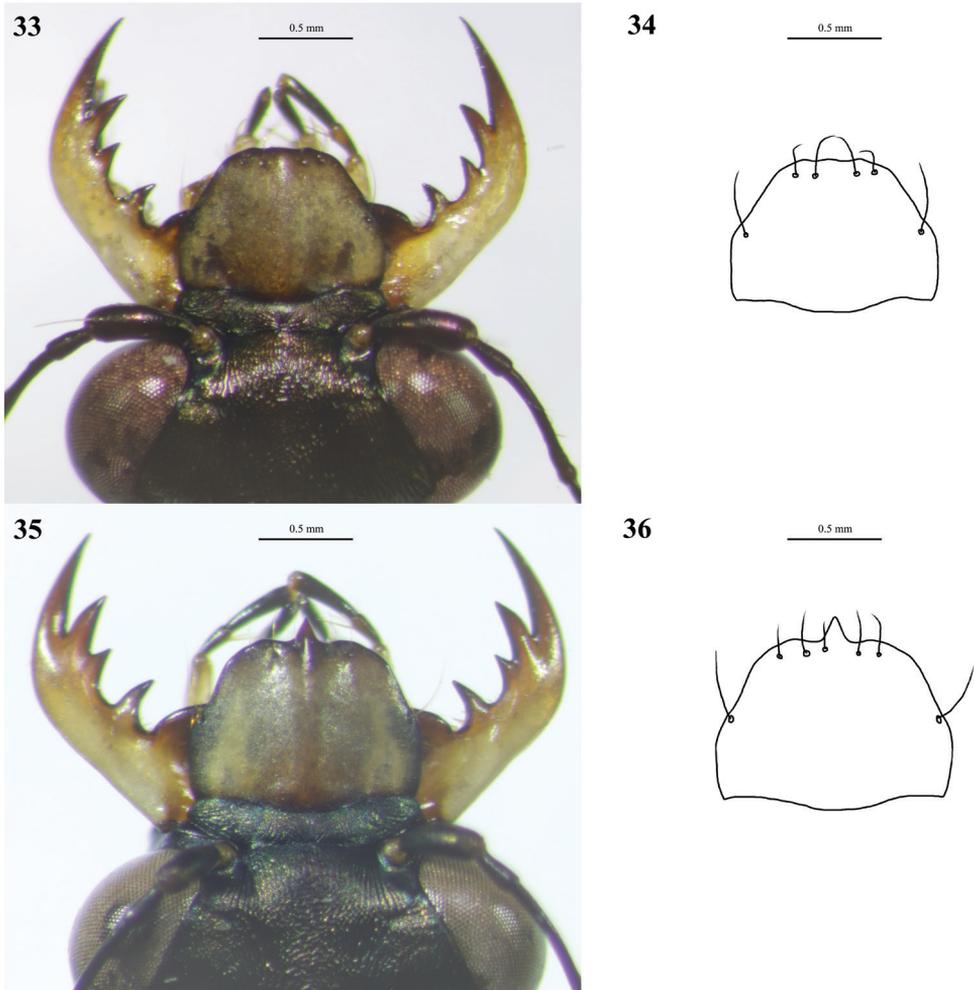
Type locality. Taiwan, Pintung, Shuangliu Forest Recreation Area.

Diagnosis. Elytra are metallic brownish and marked with obvious punctures. The apical lunula is thickened in both ends (subapical corner and apical end near suture). *Cylindera autumnnalis* sp. nov. has a different body coloration and more obvious elytral maculation than *C. pseudocylindriformis* (Fig. 28). The former has few hairs on mesoepisterna in male and on metepisterna in both genders, but the latter's mesoepisterna and metepisterna are glabrous in both genders. Body size of *C. autumnnalis* sp. nov. male was significantly larger than *C. pseudocylindriformis* although is not statistically significant in female. Their labrum (Figs 29–32, 33–36) and male genitalia (Figs 12, 13) might be poorly distinctive.



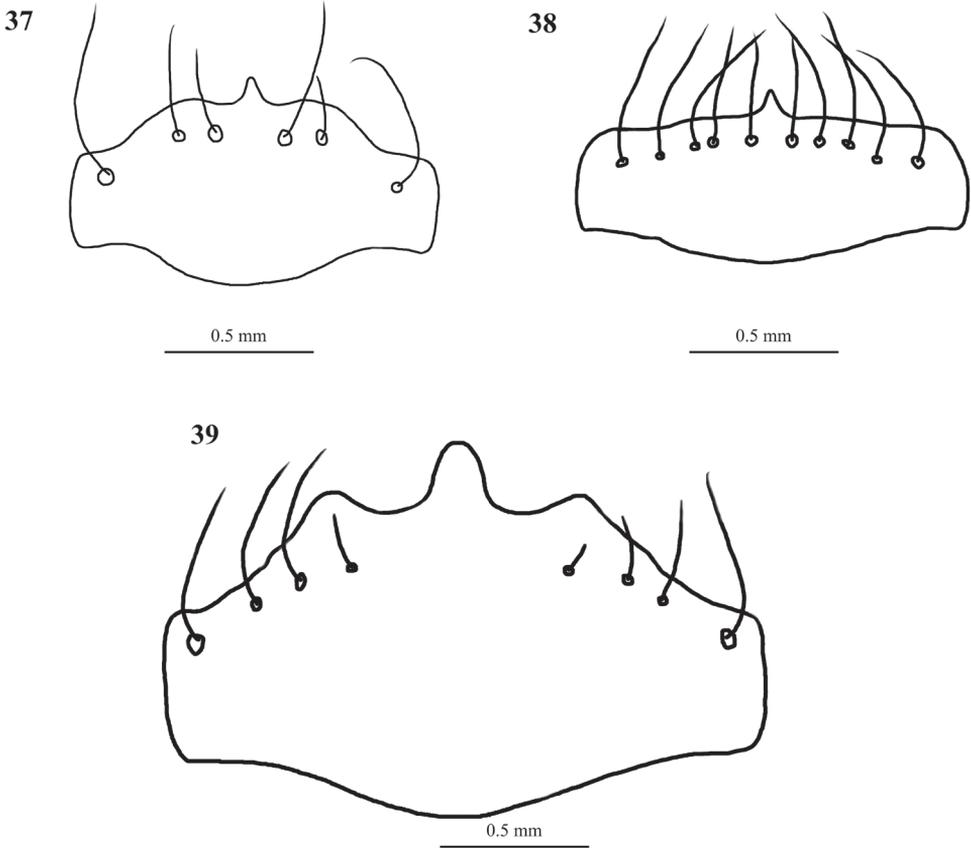
Figures 29–32. Digital images (left) and line drawings (right) of labra of *Cylindera autumnalis* sp. nov. **29, 30** male (holotype, AdeC84-3) **31, 32** female (paratype, AdeC78-2).

Description. *Head* metallic bronze with weak greenish luster; genae dark metallic green; canthus with one seta; rugae longitudinal along frons, canthi, vertex, and lateral neck, and becoming transverse on genae; clypeus patina and microsculptured. *Compound eyes* large and protruding. *Antennae* slender and filiform; scape with one apical seta; 1–4 antennomeres metallic dark brown; 5–11 ones darker. *Mandible* yellowish pale with darker teeth, exceeding labrum when closed. *Maxillary palps* yellowish; last palpomere metallic dark testaceous. *Labial palps* yellowish; last palpomere metallic dark testaceous. *Labrum* testaceous; anterior margin rounded and unidentate in female; anterior margin without noticeable tooth or even concaved in male; margin with three or four preapical and two lateral setae (Figs 29–32). *Pronotum* cylindrical and metallic bronze with little greenish luster; dorsum transversely rugose; one transverse groove on each anterior and posterior dorsum portions, connected with one shall-



Figures 33–36. Digital images (left) and line drawings (right) of labra of *Cyllindera pseudocylindrifformis* **33, 34** male **35, 36** female.

low longitudinal groove. **Elytra** bronze with metallic luster, slender, and marked with many obvious punctures; humeral spot present; posthumeral spot discoidal or irregular; one triangular spot on middle margin of elytron, connected with one clavate spot but disconnected in some individuals; apical lunula obvious, crescent; both subapical portion and apical end near suture of apical lunula thickened. **Legs** slender and testaceous, except metallic dark green coxae; some white hairs on coxae and femurs; pro-, mesocoxae, pro- and mesotrochanters with one long seta; pro-tarsi sexually dimorphic, basal 1–3 tarsomeres with short brush-like ventral setae and little wider than four or five tarsomeres in male, all pro-tarsomeres equivalent in width roughly and without brush-like ventral setae in female. **Thoracic proepisternum** dark metallic green, longitudinally rugose, and glabrous. **Prosternum** dark metallic green, transversally rugose, glabrous. **Mesoepisternum** dark metallic green, rugose and longitudinally depressed,



Figures 37–39. Line drawings of labra of Taiwanese *Cylindera* (female) **37** *C. kaleea* **38** *C. elisae reducte-lineata* **39** *C. shirakii*.

with two or three hairs in male but glabrous in female. **Mesosternum** dark metallic green, transversally rugose, glabrous. **Metepisternum** dark metallic green, coarsely sculptured, with few hairs. **Metasternum** dark metallic green, microsculptured, and almost glabrous. **Abdomen sternum** dark green with little metallic luster, almost hairless, except one pair of long hairs on 4–6 segments. **Aedeagus** of holotype shown in Fig. 10. Description same as Results.

Etymology. During the collection period in 2017 and 2018, this species was collected mostly in August to early September, especially in September. Many individuals could be found in early September when other tiger beetle adults disappeared mostly in that habitat. Thus, the specific name “*autumnalis*” means the autumnal tiger beetle.

Distribution. Only known from type locality.

Ecology. According to field observation, adults live in forest trails in late summer to autumn (late July to September). They crawl on the open ground and fly away for a short distance when being bothered, sometimes hiding in the grass or litters. The other two tiger beetle species which could be also found in the same habitat are *C. cylindriciformis* and *Therates alboobliquatus alboobliquatus* Horn, 1909. However, adults

of these three tiger beetles seem to appear in different seasons. *Cylindera cylindriformis* adults appear in early to mid-summer, and *T. a. alboobliquatus* was recorded mainly in mid-summer.

Key to *Cylindera* species in Taiwan

- 1 Labrum comparatively elongated (Figs 18–25, 29–36)..... **2**
- Labrum comparatively transverse (Figs 37–39) **7**
- 2 Labrum tridentate..... **3**
- Labrum unidentate; anterior portion of labrum without obvious teeth or even concaved in male (Figs 29–30, 33–34)..... **4**
- 3 Triangular spot on elytral middle edge present; subapical spot rounded or triangular *C. sauteri*
- Triangular spot on elytral middle edge absent; subapical spot elongated..... *C. ooa* sp. nov.
- 4 Labrum testaceous **5**
- Labrum not testaceous **6**
- 5 Apical lunula linear and slender in apical end near suture; metepisternum without hairs; body color dark brownish or dark iron gray; elytral maculation sometimes obscure *C. pseudocylindriformis*
- Apical lunula thickened in apical end near suture; metepisternum with few hairs; body color metallic brownish; elytral maculation obvious.... *C. autumnalis* sp. nov.
- 6 Middle spot triangular and about half elytral width long..... *C. cylindriformis*
- Middle spot bended downward and more than half elytral width long..... *C. redunculata*
- 7 Labrum tridentate (Fig. 39); posthumeral spot absent; body color brownish or iron gray *C. shirakii*
- Labrum unidentate (Figs 37, 38)..... **8**
- 8 Posthumeral spot absent; underside covered by dense and long white hairs; body color gray or dark gray; elytral maculation usually tiny.. *C. elisae reductelineata*
- Posthumeral spot present **9**
- 9 Body color brownish with green luster on head and pronotum; subapical spot oval or rounded and separated from apical spot; some individuals without apical spot..... *C. psilica*
- Not exactly fitting above description **10**
- 10 Middle spot long, slender and bended down; underside covered by dense and long white hairs..... *C. elisae formosana*
- Elytral maculation varied, middle spot and apical lunula present, posthumeral spot ranging from tiny to large; labrum extended a little in anterior portion and with a small tooth in the middle of the extended portion; body color usually black gray but sometimes dark brownish..... *C. kaleea*

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Supplementary material I

Tables S1–7

Authors: Ming-Hsun Chou, Wen-Bin Yeh

Data type: phylogenetic data

Explanation note: **Table S1.** GenSeq and accession number of vouchered and type specimens. **Table S2.** Pairwise distances of COI of ‘*sauteri*’ group. **Table S3.** Pairwise distances of 16S rDNA of ‘*sauteri*’ group. **Table S4.** Pairwise distances of 28S rDNA of ‘*sauteri*’ group. **Table S5.** Pairwise distances of COI of ‘*pseudocylindriformis*’ group. **Table S6.** Pairwise distances of 16S rDNA of ‘*pseudocylindriformis*’ group. **Table S7.** Pairwise distances of 28S rDNA of ‘*pseudocylindriformis*’ group.

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Supplementary material 2

Figures S1–8

Authors: Ming-Hsun Chou, Wen-Bin Yeh

Data type: phylogenetic data

Explanation note: **Figure S1.** ML tree inferred from COI of the '*sauteri*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S2.** ML tree inferred from 16S rDNA of the '*sauteri*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S3.** ML tree inferred from 28S rDNA of the '*sauteri*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S4.** Molecular clock inferred from the combined data of COI, 16S rDNA, and 28S rDNA of the '*sauteri*' group. **Figure S5.** ML tree inferred from COI of the '*pseudocylindriformis*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S6.** ML tree inferred from 16S rDNA of the '*pseudocylindriformis*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S7.** ML tree inferred from 28S rDNA of the '*pseudocylindriformis*' group with ML bootstrap values (left) and BI posterior probability (right). **Figure S8.** Molecular clock inferred from the combined data of COI, 16S rDNA, and 28S rDNA of the '*pseudocylindriformis*' group.

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The West Palaearctic genera of Nematinae (Hymenoptera, Tenthredinidae)

Marko Prous^{1,2}, Andrew Liston¹, Katja Kramp¹,
Henri Savina³, Hege Vårdal⁴, Andreas Taeger¹

1 Senckenberg Deutsches Entomologisches Institut, Eberswalder Str. 90, 15374 Müncheberg, Germany **2** Department of Zoology, Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, 51014 Tartu, Estonia **3** Parc Majorelle, 33 chemin du Ramelet-Moundi, bât. C, apt. 16, 31100 Toulouse, France **4** Swedish Museum of Natural History, Box 50007, SE-10405 Stockholm, Sweden

Corresponding author: Marko Prous (marko.prous@senckenberg.de)

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Abstract

Keys to adults and larvae of the genera of West Palaearctic nematine sawflies are presented. Species of some of the smaller genera are keyed, and their taxonomy, distribution, and host plants reviewed, with a geographic focus on north-western Europe, particularly Sweden. *Dinematus* Lacourt, 2006 is a new junior subjective synonym of *Pristiphora* Latreille, 1810, resulting in the new combination *Pristiphora krausi* (Lacourt, 2006) for the type species of *Dinematus*. *Hemichroa monticola* Ermolenko, 1960 is a new junior subjective synonym of *Hemichroa australis* (Serville, 1823). Lectotypes are designated for *Tenthredo opaca* Fabricius, 1775, *Mesoneura opaca* var. *nigerrima* Enslin, 1914, *Mesoneura opaca* var. *obscuriventris* Enslin, 1914, *Nematus hypogastricus* Hartig, 1837, *Nematus alnivorus* Hartig, 1840, *Leptopus rufipes* Förster, 1854, *Nematus protensus* Förster, 1854, and *Platycampus luridiventris* var. *pleuritica* Enslin, 1915. A phylogenetic analysis based on four genes (mitochondrial COI and nuclear NaK, POL2, and TPI) supports the current generic classification.

Keywords

Distribution, keys, lectotype designations, sawflies, Sweden, synonymy

Introduction

In 2012 a project funded by the Swedish Taxonomy Initiative was launched, with the main objective of improving our knowledge of the taxonomy and distribution of nematine sawflies in Fennoscandia, and Sweden in particular (STI Nematinae Group 2013). As a first step, the generic classification of the world Nematinae was revised by Prous et al. (2014), and the genera keyed. Here, we present a condensed version of that key, covering only the West Palaearctic genera, with which it should be possible to identify most specimens more easily. Included are treatments of the species of some smaller genera: *Hemichroa*, *Mesoneura*, *Neodineura*, *Platycampus*, and *Stauronematus*. The species of the other genera were either covered by Prous et al. (2017) and Liston et al. (2017, 2019a–c), or are to be dealt with in works currently in preparation. Geographic scope of the taxonomic treatments at genus / species group level varies between coverage of the whole West Palaearctic, to consideration only of the species which are known from Fennoscandia, or potentially present there. The differences in the size of regions covered for each genus / species group arise through the amount of material available for study, including fresh specimens suitable for genetic sequencing, and the perceived complexity of species-level taxonomy in the group. The present work thus represents an overview of all Nematinae known to occur in Fennoscandia, and in conjunction with the publications covering the remaining genera is intended to enable determination to species level of specimens of all nematine genera from north-west Europe.

Materials and methods

The Swedish Malaise Trap Project is abbreviated to **SMTP**. Abbreviations for the names of collections referred to in the text are as follows:

BMNH	Natural History Museum, London, United Kingdom
FMNH	Finnish Museum of Natural History, Helsinki, Finland
HNHM	Hungarian Natural History Museum, Budapest, Hungary
LSUK	Linnean Society, London, United Kingdom
MNHN	Muséum national d'Histoire naturelle, Paris, France
MZFN	Museo Zoologico dell'Università Federico II, Naples, Italy
MZLU	Lunds universitet, Entomology Collection, Lund, Sweden
NFVG	Niedersächsische Forstliche Versuchsanstalt, Göttingen, Germany
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden
NMPC	National Museum (Natural History), Prague, Czech Republic
RMNH	Naturalis Biodiversity Centre, Leiden, Netherlands
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
TUZ	Natural History Museum, Tartu, Estonia
ULQC	University of Laval, Quebec, Canada
USNM	National Museum of Natural History, Washington D. C., USA
ZMHB	Naturkundemuseum, Berlin, Germany

ZMUC Zoological Museum, University of Copenhagen, Copenhagen, Denmark
ZSM Zoologische Staatssammlung, Munich, Germany.

In the specimen data the dates are given as dd.mm.yyyy, and coordinates as positive (north or east) or negative (south or west) decimal degrees latitude and longitude.

Morphological terminology mostly follows Viitasaari (2002), but sawtooth is used instead of serrula (see Malagón-Aldana et al. 2017), and the large, ventrally situated, more or less triangular flange above each sawtooth is called a spurette (following Ross 1943; see Figs 108, 112 arrows). Images of complete imagines and morphological details were made at the SDEI with Leica cameras attached to a variety of microscopes. Composite images with an extended depth of field were created from stacks of images using the software CombineZP, and finally arranged and partly enhanced with Ulead PhotoImpact X3. Some of the figures were first published by Prous et al. (2014). Unless otherwise stated, photos of adults and larvae were made by AL, MP, HS, and AT.

First drafts of the key to larvae were based mainly on Lorenz and Kraus (1957), and subsequently modified to include the results of more recently published studies, and the examination of specimens available to us. The tree species known as Mountain Birch, which dominates large areas of vegetation in northern Fennoscandia, is referred to as *Betula pubescens* var. *pumila* (Zanoni ex Murray) Govaerts, following Plants of the World online (2017), which treats the formerly widely-used names *B. czerepanovii* N. I. Orlova and *B. tortuosa* Ledeb. as its synonyms.

DNA was extracted and purified with an EZNA Tissue DNA Kit (Omega Bio-tek) according to the manufacturer's protocol and stored at -20 °C for later use. Typically, one or two legs were used for DNA extraction, but for males the whole genital capsule was often additionally used to increase DNA yield and to free penis valves from muscles before photography. In some cases, the whole specimen was used for extraction. One mitochondrial and four nuclear regions were used in the phylogenetic analyses, although not all of these genes were obtained for all species. Primers used for amplification and sequencing are listed in Table 1. The mitochondrial region used is a large fragment (1078–1087 bp depending on the primer set) of the cytochrome oxidase subunit I gene (COI). The fragment includes the entire standard barcode region (658 bp) of the animal kingdom (Hebert et al. 2003). The nuclear markers used are fragments of sodium/potassium-transporting ATPase subunit alpha (NaK), triose-phosphate isomerase (TPI), DNA dependent RNA polymerase II subunit RPB1 (POL2), and transformation/transcription domain-associated protein (TRRAP). The NaK fragment used is a nearly complete sequence of its longest exon, 1654 bp. The TPI fragment used is the nearly complete gene region, containing 676 bp of three exons and two short introns (each around 50–100 bp) in Nematinae, altogether 788–842 bp. The POL2 fragment used is composed of two partial exons (together 2407–2623 bp depending on the primer set) and one short intron (67–86 bp). The TRRAP fragment used is a 3379 bp fragment of its longest exon (sequenced only for *Hoplocampa* and *Monocellicampa*). New POL2 and TRRAP primers were designed mainly based on four sawfly genomes (accessions AOFN02000108, AOFN02000124 [*Athalia rosae*], LGIB01000723, LGIB01000528 [*Neodiprion lecontei*], AMWH01002735,

Table 1. Primers used for PCR and sequencing (preferred primers in bold), with information provided on respective gene fragment, primer name, direction (forward, F or reverse, R), primer sequence, standard PCR annealing temperature, utilization (PCR/ sequencing), and reference. Primer annealing temperatures used for sequencing at Macrogen were usually 50 °C (47–50 °C).

Gene region	Primer name	F/R	Primer sequence 5'-3'	PCR annealing temperature (°C)	PCR/ Sequencing	Reference
COI	SymF1	F	TTTCAACWAATCATAAARAYATTGG	49	PCR, seq	(Prous et al. 2016)
COI	SymF4	F	AAATGATTATYTCWACWAATCAYAA	50	PCR, seq	This study
COI	sym-C1-J1718	F	GGAGGATTTTGGAAAYTGAYTAGTWCC	49	PCR, seq	(Nyman et al. 2006)
COI	symC1-J1751	F	GGAGCNCCTGATATAGCWTTYCC	47	seq	(Prous et al. 2016)
COI	SymR1	R	TAAACTTCWGGRTGCCAAARAATC	47	PCR, seq	(Prous et al. 2016)
COI	SymR2	R	TAAACTTCTGGRTGTCCAAARAATCA	47	PCR, seq	(Prous et al. 2016)
COI	A2590	R	GCTCCTATTGATARWACATARTGRAAATG	49	PCR, seq	(Normark et al. 1999)
NaK	NaK_263F	F	CTYAGCCAYGCRAARGCRAARGA	59	PCR, seq	(Prous et al. 2017)
NaK	NaK_809F	F	GCWTTYTTCTCNACSAAYGCSGTNGARGG	55	PCR, seq	(Prous et al. 2017)
NaK	NaK_907Ri	R	TGRATRAARTGRTGRATYTCYTTIGC	54	PCR, seq	(Prous et al. 2017)
NaK	NaK_910R	R	TGRATRAARTGRTGRATYTCYTT	50	PCR, seq	(Prous et al. 2017)
NaK	NaK_1250Fi	F	ATGTGGTTYGAYAAYCARATYATIGA	56	PCR, seq	(Prous et al. 2017)
NaK	NaK_1250Fv2	F	ATGTGGTTYGAYAAYCARATHATIGA	56	PCR, seq	This study
NaK	NaKRev475	R	TCGATRAITYTGRTTRTCRAACCACAT	56	seq	(Leppänen et al. 2012)
NaK	NaK_1498R	R	ACYTGRITAYTGTNGTNGARTTRAA	52	PCR, seq	(Prous et al. 2019)
NaK	NaK_1918R	R	GATTTGGCAATNGCTTTGGCAGTDAT	59	PCR, seq	(Prous et al. 2017)
POL2	POL2_104Fi	F	GYATGTCAGTYACNGATGGIGG	59	PCR, seq	(Prous et al. 2019)
POL2	POL2_104Fv2	F	CGNATGTCNGTNACNGAYGGIGG	60	PCR, seq	(Prous et al. 2019)
POL2	POL2_574R	R	TCYTCTRTNACRTGYTTCCAYTCNGC	59	seq	(Prous et al. 2019)
POL2	POL2_599F	F	GARTGGAARCAAYGTVAAAYGARGA	54	PCR, seq	(Prous et al. 2019)
POL2	POL2_797F	F	ATGTAYGGNTCNGCNAARAAYCARGA	58	PCR, seq	(Prous et al. 2019)
POL2	POL2_889R	R	TGRAAYTYGARCATYTTWATRTTYTC	52	PCR, seq	(Prous et al. 2019)
POL2	POL2_928R	R	GGCATNCCNGGCATRTCTRTCNAC	59	PCR, seq	(Prous et al. 2019)
POL2	POL2_1388F	F	CAYAARATGAGTATGATGGG	51	PCR, seq	(Prous et al. 2019)
POL2	POL2_1459R	R	TCATYTCRTNCCRTCRAARTC	52	PCR, seq	(Prous et al. 2019)
POL2	POL2_1706F	F	TGGGAYGGNAARATGCCNARCC	60	PCR, seq	(Prous et al. 2019)
POL2	POL2_1732R	R	GARAADATYTGTYTNCNGTCCA	55	PCR, seq	This study
POL2	POL2_1759R	R	ATCATRTTNACRTTNCNGGDATDAT	55	PCR, seq	(Prous et al. 2019)
POL2	POL2_1777Ri	R	GTRCTGTGTGTYCKDATCATRTT	55	PCR, seq	(Prous et al. 2019)
POL2	POL2 hym 3F	F	ACNCACAGYACNCAYCCN GAYGA	56	seq	(Malm and Nyman 2015)
POL2	POL2_2423F	F	CATTTYATHAARGAYGAYTAYGG	51	seq	(Prous et al. 2019)
POL2	POL2_2509R	R	TTNACRCGRGTATCRATNAGACCYTC	60	PCR, seq	(Prous et al. 2019)
POL2	POL2_2569R	R	TGNACCATNACNGAYTCCATAGCYTTDAT	60	PCR, seq	This study
POL2	POL2_2725R	R	GGATCRAAYTTTAAAYTTYTYTC	50	PCR, seq	(Prous et al. 2019)
TPI	TPI_29Fi	F	GAAAAITTYTYGTTGGNGGIAA	52	PCR, seq	(Prous et al. 2016)
TPI	TPI385Fi	F	GTRATYGCNTGYATYGGIGARA	52	seq	(Prous et al. 2016)
TPI	TPI_275Ri	R	GCCCANACNGGYTCRTAIGC	56	seq	(Malm and Nyman 2015)
TPI	TPI706R	R	ACNATYTGACRAARTCWGGYTT	52	PCR, seq	(Prous et al. 2016)
TRRAP	TRRAP_833F	F	AAYAARGARGTNTTYGTNGAYTTYATGGG	58	PCR, seq	This study
TRRAP	TRRAP_1658F	F	CARTCNAARCAATFYCARCCNAARGARAC	60	seq	This study
TRRAP	TRRAP_1702R	R	GGNGCCDATNGTRTARATRC	56	seq	This study
TRRAP	TRRAP_1831R	R	AADATYTCYTGRAANGTYTGNGGRITTCAT	59	seq	This study
TRRAP	TRRAP_2648Fi	F	ATGATGATHGARCCNCARAARYTNGAITA	58	PCR, seq	This study
TRRAP	TRRAP_3046R	R	TGNGCDATNGCNACCATNGTRTARTG	60	PCR, seq	This study
TRRAP	TRRAP_3482Fi	F	GTNTCNAAYGNGCHATHGAYATGGCIAA	62	seq	This study
TRRAP	TRRAP_3685Ri	R	ACYTCYTTTGTGNGGYTCCATNACYTCIGT	62	PCR, seq	This study
TRRAP	TRRAP_4086F	F	CARGARGCNGCNTTYGARTGYATG	59	seq	This study
TRRAP	TRRAP_4213Ri	R	CTRAANGTRCTNNGGRAANARYTGIGT	56	PCR, seq	This study

AMWH01006798 [*Cephus cinctus*], AZGP02002036, AZGP02002013 [*Orussus abietinus*]) and transcriptomes (Misof et al. 2014, Peters et al. 2017) available in GenBank. Numbers in the new POL2 and TRRAP primer names refer to the binding position of the 3' end of each primer in the coding region of *Athalia rosae* mRNA (accessions XM_012395805 and XM_012406083).

PCR reactions were carried out in a total volume of 15–35 μ l containing 1.0–2.5 μ l of extracted DNA, 1.5–3.5 μ l (5.0–15 pmol) of primers and 7.5–17.5 μ l of 2 \times Multiplex PCR Plus Master mix (QIAGEN). The PCR protocol consisted of an initial DNA polymerase (HotStar Taq) activation step at 95 °C for 5 min, followed by 38–40 cycles of 30 s at 95 °C, 90–120 s at 49–60 °C (depending on the primer set used), and 70–180 s (depending on the amplicon size) at 72 °C; the last cycle was followed by a final 30 min extension step at 68 °C. COI (primers symF4 [or symF1] + A2590), NaK (NaK_263F + 1918R) and TPI (TPI_29Fi + TPI706R) were in most cases amplified in one fragment, POL2 in one to three fragments, and TRRAP in two fragments (TRRAP_833F + 3046R and TRRAP_2648Fi + 4213Ri). Three μ l of PCR product was visualised on a 1.4% agarose gel and the remaining product was then purified with FastAP and Exonuclease I (Thermo Scientific). 1.0–2.2 U of both enzymes were added to 12–32 μ l of PCR solution and incubated for 15 min at 37 °C, followed by 15 min at 85 °C. 2–5 μ l of purified PCR product per primer in a total volume of 10 μ l (5–8 μ l of sequencing primer at concentration 5 pmol/ μ l) were sent to Macrogen Europe (Netherlands) for sequencing. Both sense and antisense strands were sequenced using the primers listed in Table 1. Ambiguous positions (i.e., double peaks in chromatograms of both strands) due to heterozygosity were coded using IUPAC symbols. Sequences reported here have been deposited in the GenBank (NCBI) database (accession numbers MK624656–MK624923 and MK720818–MK720821), although not all of them are analysed here (covered in further publications on some of the genera not treated here). Some of the sequences analysed here were originally published by Schmidt et al. (2017) and Prous et al. (2016, 2017). Alignment of COI, NaK, and TRRAP sequences was straightforward because of the lack of indels (insertions or deletions). Alignment of POL2 and TPI was also straightforward without introns, but these were retained in some analyses published elsewhere (Liston et al. 2019a) and aligned manually. To concatenate separate gene alignments, we used R (R Core Team 2018) package *apex* (Jombart et al. 2017). For phylogenetic analyses we used the maximum likelihood method (ML) implemented in IQ-TREE 1.5.6 (<http://www.iqtree.org/>) (Nguyen et al. 2015). By default, IQ-TREE runs ModelFinder (Kalyaanamoorthy et al. 2017) to find the best-fit substitution model and then reconstructs the tree using the model selected according to Bayesian information criterion (BIC). We complemented this default option with SH-like approximate likelihood ratio (SH-aLRT) test (Guindon et al. 2010) and ultrafast bootstrap (Hoang et al. 2017) with 1000 replicates to estimate robustness of reconstructed splits. Minimal p-distances between and maximal distances within BIN (Barcode Index Number) clusters were taken from BOLD (<http://www.boldsystems.org/>) BIN database. Some of the COI barcode sequences used here were obtained from BOLD (<http://www.boldsystems.org/>). In this case, DNA extraction, PCR amplification, and sequencing were conducted at the Canadian Centre for DNA

Barcoding (CCDB) in Guelph, Canada, using standardised high-throughput protocols (Ivanova et al. 2006, deWaard et al. 2008), available online under www.ccdb.ca/resources.php. DNA aliquots of SDEI vouchers are deposited in the DNA storage facility of the SDEI (including those that were originally extracted in CCDB).

Results

Previous taxonomic publications have mostly recognised several tribes within the Nematinae. For example, Vikberg (1982) allocated the North European genera to six tribes, of which his Nematini was further divided into three sub-tribes. Subsequently, additional tribes were erected, often for species-poor lineages with more or less distinctive morphological and biological characters, e.g., Pristicampini (Zinovjev 1993), Stauronematini, and Bacconematini (Lacourt 1998). The circumscription of the tribes, and even of the Nematinae itself, has varied considerably between authors. Lacourt (1998), for example, removed *Cladius*, *Hoplocampa*, and *Susana* from the Nematinae, and treated each of these as a separate subfamily of Tenthredinidae. A clearer and more objective assessment of suprageneric classification was first achieved with the application of genetic data by Nyman et al. (2006). A second analysis in Prous et al. (2014), based on extended taxon sampling and more genes, yielded essentially similar results. A further refinement based on mitochondrial COI and three nuclear genes (NaK, POL2, TPI), with stronger support for some clades, is presented in Fig. 1. Noteworthy is that Nyman et al. (2006), Prous et al. (2014), and Malm and Nyman (2015) all recovered the Nematinae as monophyletic and indicated that *Cladius* (missing in Malm and Nyman 2015), *Hoplocampa*, and *Susana* do belong to the subfamily. Because monophyly of Nematinae is unambiguously supported based on previous analyses using the same genes, we did not test this here further. Our analyses of the subfamily without outgroups supports the previous generic classification as proposed in Prous et al. (2014). Because of limited sampling, Prous et al. (2014) were unable to state whether the three subgenera of *Cladius* are monophyletic, but based on expanded sampling, we now find that the largest subgenus *Priophorus* is not (Fig. 1). Because the delimitation of the subgenera of *Cladius* is problematic also morphologically, we propose here to abandon subgeneric classification until better evidence justifies it. Whether the various tribal names which have been proposed for single genera have much practical value is questionable. *Hoplocampa*, *Stauronematus*, and *Susana*, for example, although apparently phylogenetically isolated from other genera, are more clearly referred to by using their generic names. This will remain so at least until genetic data become available for a number of morphologically distinctive genus-series taxa. In the West Palaearctic, genetic data are still lacking for *Armenocampus*, *Neodineura*, and *Nescianeura*. On the other hand, to simplify discussions on phylogeny and biodiversity, use of the tribal names Nematini (equivalent to the “higher Nematinae” of Prous et al. 2014), Dineurini, and Pseudodineurini seems justified and useful. Support for Nematini and

Dineurini (Pseudodineurini could not be tested because of the lack of sampling) in our molecular phylogeny is unambiguous (Fig. 1). Formally, the West Palaearctic genera belong to the following tribes:

Dineurini: *Anoplonyx*, *Dineura*, *Hemichroa*, *Nematinus*, *Platycampus* [and *Neodineura*?]

Nematini: *Euura*, *Mesoneura*, *Nematus*, *Pristiphora* [and *Nescianura*?]

Pseudodineurini: *Endophytus*, *Pseudodineura*

Cladiini: *Cladius*

Hoplocampini: *Hoplocampa*

Stauronematini: *Stauronematus*

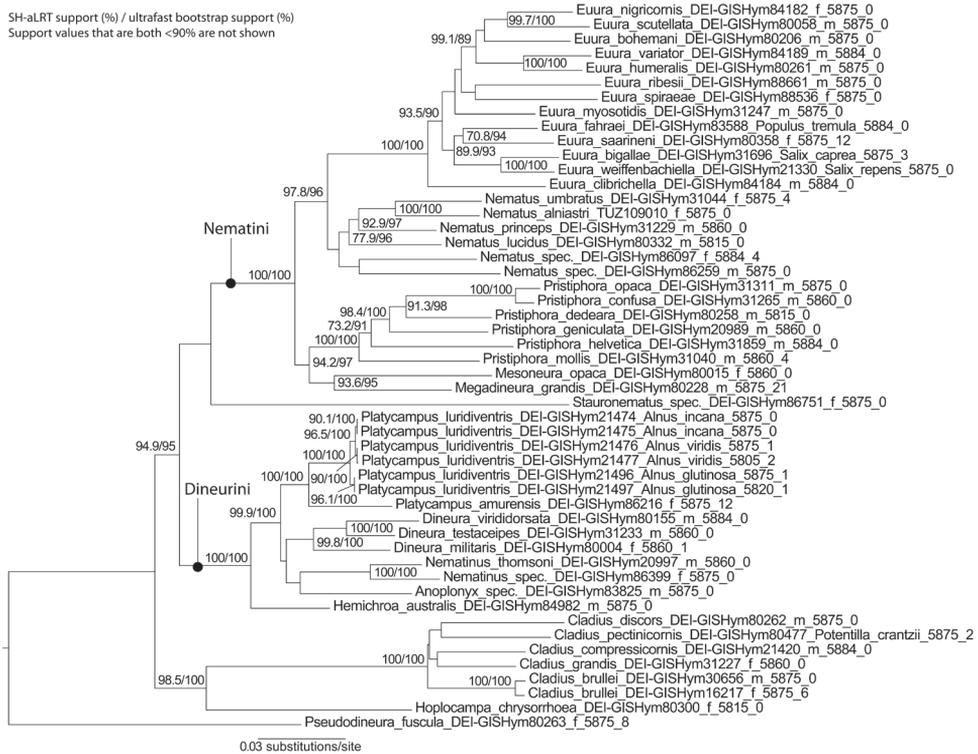


Figure 1. Maximum likelihood tree of Nematinae based on four genes (COI, NaK, POL2, TPI). Only specimens sequenced for all four genes were included. Short introns from POL2 and TPI were excluded. The best-fit model chosen according to Bayesian information criterion was GTR+R4. Numbers at branches show SH-aLRT support (%) / ultrafast bootstrap support (%) values. Support values for weakly supported branches (<90) are not shown. Letters “f” and “m” stand for “female” and “male”, and are not given for larvae. Numbers at the end of the tip labels refer to the length of the sequence and the number of ambiguous positions (e.g., heterozygosities). The number of ambiguous positions given for two males are due to variation in mitochondrial COI because of possible heteroplasmy. The tree was rooted as in Prous et al. (2014). The scale bar shows the number of estimated substitutions per nucleotide position.

Key to the West Palaearctic genera and selected species of Nematinae (imagines)

Genera and species represented in Fennoscandia are marked with an asterisk (*). Species numbers are for the West Palaearctic realm, followed by Fennoscandia.

- 1 **a** Fore wing normal, veins normally developed (Figs 2–3) **12**
 – **aa** Fore wing shortened, apex usually not reaching to the tip of the abdomen, veins often strongly aberrant (Figs 4–5) [some females of one arctic-alpine species] ****Euura abnormis* (Holmgren, 1883)** ♀
- 2(1) **a** Vein 2A of hind wing complete, cell A closed (Fig. 5); **b** Body length 2–12 mm; **c** Vein 2r-rs frequently absent (Fig. 8) (ca. 600 species) **3**
 – **aa** Vein 2A of hind wing incomplete, cell A open distally (Fig. 6); **bb** Body length 2–6 mm; **cc** Vein 2r-rs usually present (compare Fig. 9) (7 species) **12**
- 3(2) **a** Vein 2r-rs absent (Fig. 8) (more than 550 species) **4**
 – **aa** Vein 2r-rs present (Fig. 9) (less than 30 species) **13**
- 4(3) **a** Base of vein 2A+3A incomplete and straight, cell PA open distally (Fig. 10) (more than 500 species) **5**
 – **aa** Base of vein 2A+3A complete and curved up to 1A, cell PA closed (Fig. 11) (ca. 25 / 15* species) **9**
- 5(4,18) **a** Apex of vein C of fore wing swollen; at the point of origin of vein Rs+M from R, cell c usually only approx. as wide as R (Fig. 12); **b** Clypeus more or less truncate, at most slightly emarginate (Fig. 14); **c** Claws usually with subapical tooth (cf. Figs 18, 19), sometimes bifid or simple (Fig. 17), but never with basal lobe; **d** Valvula 3 frequently distinctly emarginate apically in dorsal view (Fig. 21); **e** Tangium of lancet with campaniform sensilla (“pores”) (Fig. 25), rarely absent (see Prous et al. 2017); **f** Tergum 8 in males of most species without distinct apical projection (Fig. 23), see Prous et al. (2017); **g** Valvispina of penis valve in many species at ventral margin (Fig. 27; see also Prous et al. 2017) (ca. 120 / 90* species) ****Pristiphora Latreille, 1810***
 – **aa** Apex of vein C of fore wing often less swollen; at the point of origin of vein Rs+M from R, cell c approx. twice as wide as R or wider (Fig. 13); **bb** Clypeus usually at least one third deep emarginate (Fig. 15); exceptionally, truncate; **cc** Claws of various shape, but frequently bifid (cf. Fig. 20), rarely with basal lobe (Fig. 16); **dd** Valvula 3 only exceptionally emarginate apically in dorsal view (Fig. 22); **ee** Tangium of lancet without campaniform sensilla (Fig. 26); **ff** Tergum 8 in males often with distinct apical projection (Fig. 24); **gg** Valvispina of penis valve often distinctly removed from ventral margin (Fig. 28) **6**
- 6(5) **a** Claws with basal lobe in addition to subapical tooth, subapical tooth erect and well separated from apical tooth, longer than apical tooth (Fig. 16); **b** Clypeus more or less truncate (2 / 1* species) ****Stauronematus Benson, 1953***
 – **aa** Claws without basal lobe (Figs 17–20), subapical tooth usually shorter than apical tooth (Figs 18–19), sometimes claws simple (Fig. 17); **bb** Clypeus usually at least emarginate to one third depth; exceptionally, truncate **7**

- 7(6) **a** Vein Sc before point of origin of vein M from R (Fig. 29) (most species)....**8**
 – **aa** Vein Sc beyond point of origin of vein M from R (Fig. 30) (few species)....**16**
 8(7) **a** In female, abdominal tergum 9 in lateral view more than 3 times as long as tergum 8 (Fig. 31); **b** In male, pseudoceps apically strongly narrowed, often forming distinct filament (Figs 33–34, figs 7–11 in Lindqvist 1957, <http://doi.org/10.6084/m9.figshare.5100877>); **c** Left mandible in lateral view tapered evenly towards apex (Figs 36–37) (8 / 7* species)....***Nematinus Rohwer, 1911**
 – **aa** In female, abdominal tergum 9 in lateral view usually less than 2 times as long as tergum 8 (Fig. 32); **bb** In male, penis valve without distinct filament (Fig. 35); **cc** Left mandible in lateral view usually markedly constricted near middle (Fig. 38). Two genera which are currently only separated genetically, not morphologically; exceptionally, specimens of *Pristiphora* might also run here (ca. 440 / *number of Fennoscandian species still unclear)
 ***Euura Newman, 1837** and (13 / 10* species) ***Nematus Panzer, 1801**

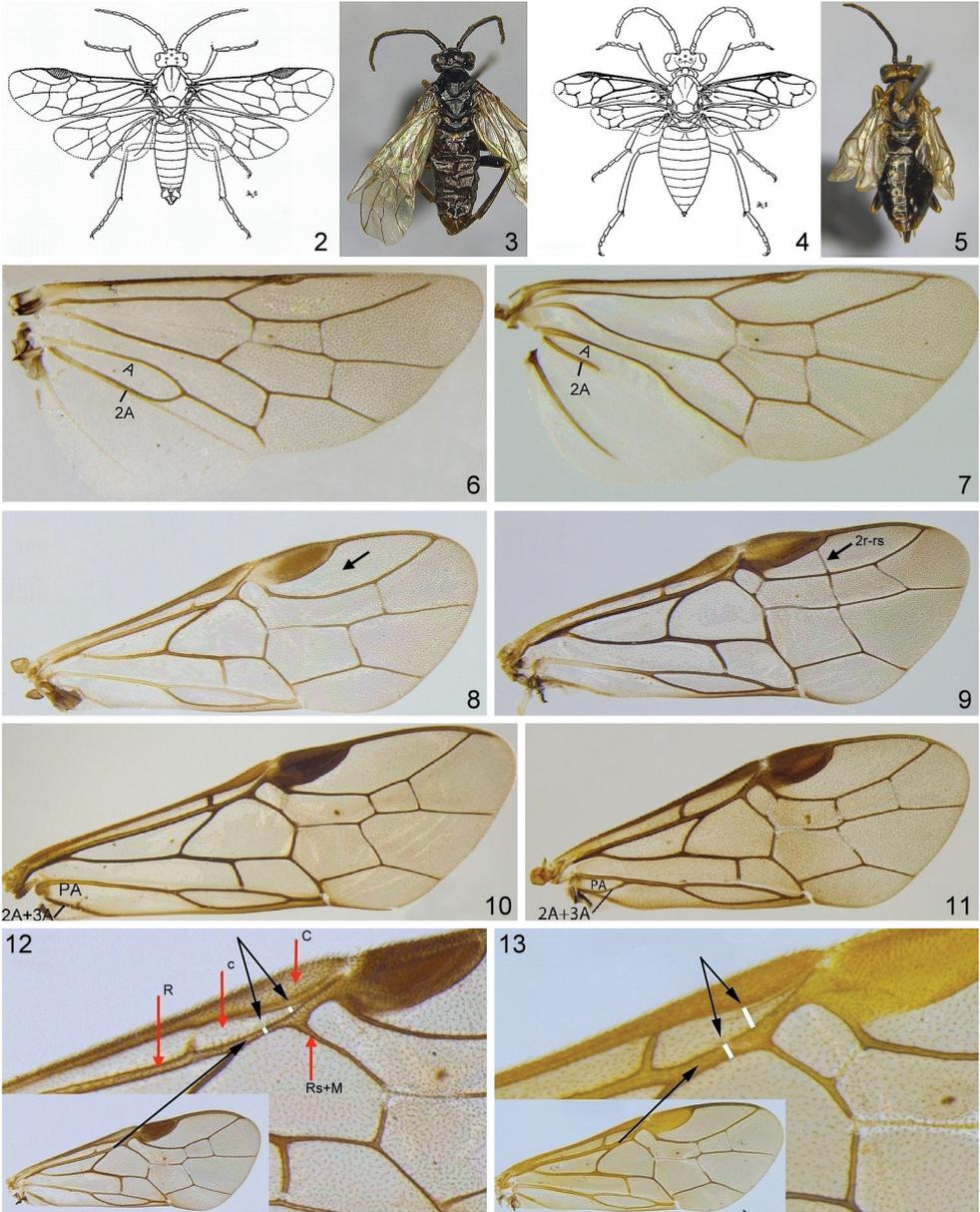
Preliminarily, the European *Nematus* species may be separated morphologically from *Euura* as follows:

- A (a) 1st metatarsomere 2.0–3.0 times as wide as width of 2nd metatarsomere (Fig. 39) (formerly *Craesus*) (6 / 3* species) ***Nematus septentrionalis group**
 – (b) 1st metatarsomere only slightly wider than width of 2nd metatarsomere (Fig. 40)..... **B**
 B(A) (a) Pterostigma dark brown to black (Figs 41–43, 56–58); (b) Antennae black (Figs 41–43); (c) Pronotal angles and tegulae reddish or yellowish (Figs 41–43) **C**
 – (aa)–(cc) Characters not in the combination of (a)–(c): (aa) Pterostigma often mainly pale; (bb) Antennae frequently (especially ventrally) pale; (cc) Pronotal angles and / or tegulae may be black **F**
 C(B) (a) Mesepisternum densely sculptured, ± matt; (b) Terga (1–)2–3(–6), femora, tibiae, and tarsi of fore and middle legs reddish (Figs 41–42); (c) Body 7–11 mm, torpedo-shaped (Figs 41–42) ***Nematus lucidus (Panzer, 1801)**
 – (aa) Mesepisternum shiny, at most weakly sculptured; (bb) Coloration different (Figs 43, 56–58); (cc) Body 5–10.5 mm, usually not torpedo-shaped **D**
 D(C) (a) Abdomen black (Fig. 43); (b) Thorax black (except for tegulae and pronotum); (c) Legs largely pale (hind tibia with basal half pale, apical half black or reddish with black apex) (Fig. 43); (d) Valvula 3 in dorsal view narrowing towards the apex, apically broadly rounded (Fig. 44); (e) Paravalva of penis valve roughly oval-shaped and distinctly longer than valvula, valvispina distinctly removed from ventral margin and paravalva with a small lobe at base of valvispina (Fig. 50). Larva on *Lonicera* (formerly *Paranematus*). (5 / 5* species)..... ***Nematus wahlbergi group**
 – (aa) Abdomen usually at least partly yellowish or reddish (Fig. 56); (bb) Thorax often at least laterally ± yellowish (Fig. 56); (cc)–(ee) Characters often different..... **E**

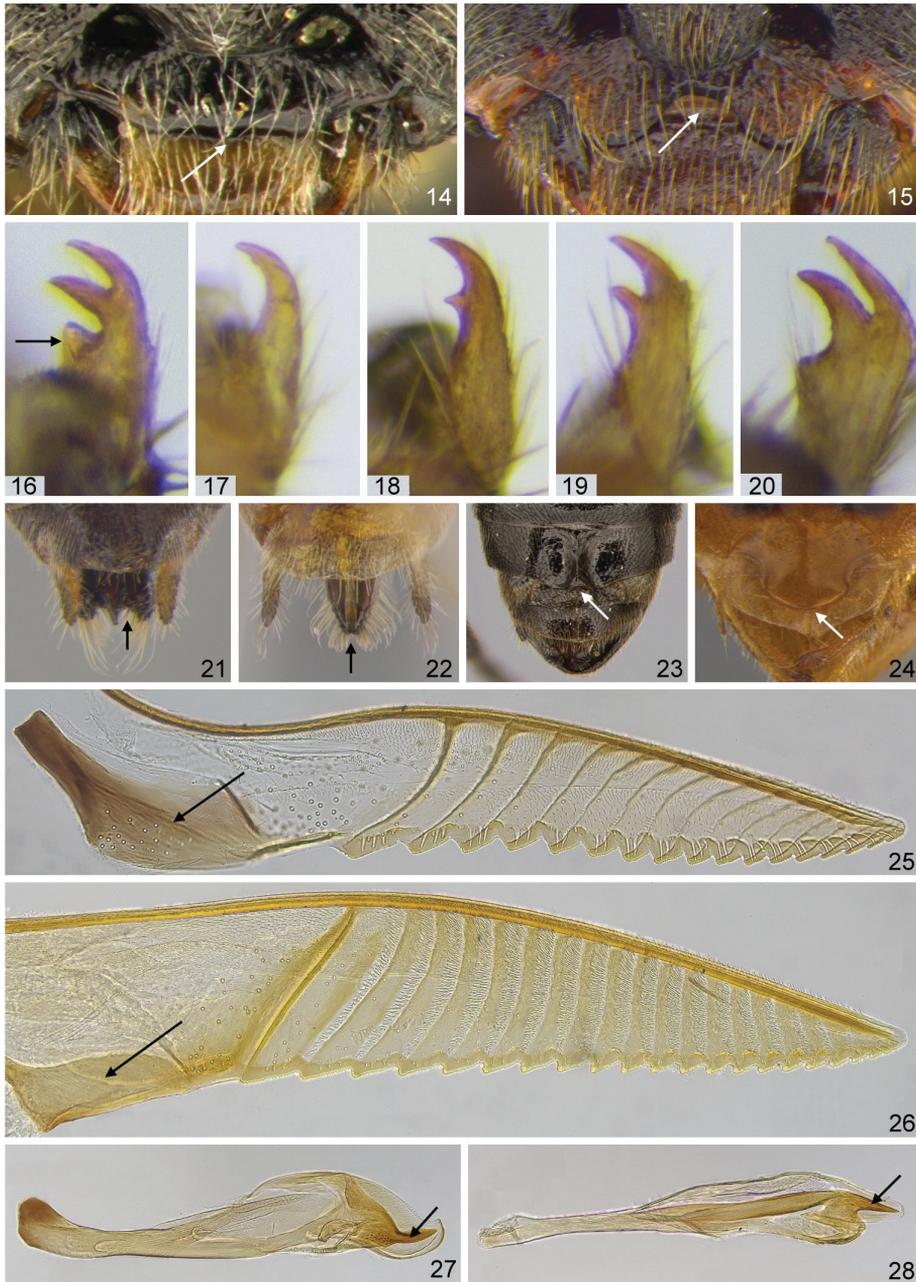
- E(D) (a) Valvula 3 in dorsal view hardly tapering towards apex, and visible parts approx. as long as broad (Fig. 45); bases of longest setae on each valvula nearly parallel (Fig. 45); (b) Straight and gradually narrowing valvispina of penis valve roughly in the middle of paravalva, paravalva excluding valvispina distinctly shorter than pseudoceps, ventroapical lobe of paravalva extending ca. 1/3 of length of valvispina, basal third or half of valvar strut more or less at the ventral margin of paravalva (Fig. 51).....***Nematus umbratus Thomson, 1871**
- (aa) Valvula 3 in dorsal view tapering towards apex, and visible parts *often* longer than broad (Fig. 48); bases of longest setae on each valvula 3 *often* strongly divergent from each other (Figs 46–47, 49); (bb) Penis valve different (Figs 52–54) ...
... **Euura part. (*melanocephalus, *bohemani, *ribesii species group, *salicis)**
- F(B) (a) Pronotal angles black (Figs 57–58); (b) Body 8–12 mm, torpedo-shaped (Fig. 57); (c) Abdomen black with 3rd and 4th segment ± pale (alive: green) (Fig. 58) or sometimes completely black in males; (d) Valvispina of penis valve roughly in the middle of paravalva and with a distinct hook; dorsal part of anterior margin of paravalva at base of valvispina more basal than ventral part, but both margins roughly perpendicular to valvispina; basal third of valvar strut more or less at the ventral margin of paravalva (Fig. 55).....***Nematus princeps Zaddach, 1876**
- (aa) Pronotal angles often pale marked; (bb) Body length frequently less than 8 mm, usually not torpedo-shaped; (cc) Abdomen coloured differently (dd) Penis valve different **Euura part**

- 9(4) a Vein 2m-cu running into cell 2Rs (Fig. 59) (in few aberrant specimens into cell 1Rs, very slightly distal to 2r-m, or vein 2r-m absent); b Length of vein R in the fore wing between junctions with veins M and Rs+M usually not longer than first sector of Rs (Fig. 59) **10**
- aa Vein 2m-cu running into cell 1Rs (Fig. 60); bb Length of vein R in the fore wing between junctions with veins M and Rs+M clearly longer than first sector of Rs (Fig. 60)..... **11**
- 10(9) a Claw usually with large or small inner tooth; exceptionally, simple; b Scape and pedicellus together much shorter than the first flagellomere, sometimes in male the latter with basal projection (Fig. 61) (11 / 8* species)
.....* **Cladius Illiger, 1807**
- aa Claw simple; bb Scape and pedicellus together approx. as long as the first flagellomere, the latter without projection (Fig. 62) (Only one rare species from Armenia, *A. necopinus* (Zhelochovtsev, 1941); not examined)
..... [**Armenocampus Zinovjev, 2000**]
- 11(9) a Claw simple, without subapical tooth; b Apex of vein C of fore wing swollen; at the point of origin of vein Rs+M from R, cell c usually only approx. as wide as R (cf. Fig. 65) (5 / 4* species)***Anoplonyx Marlatt, 1896**

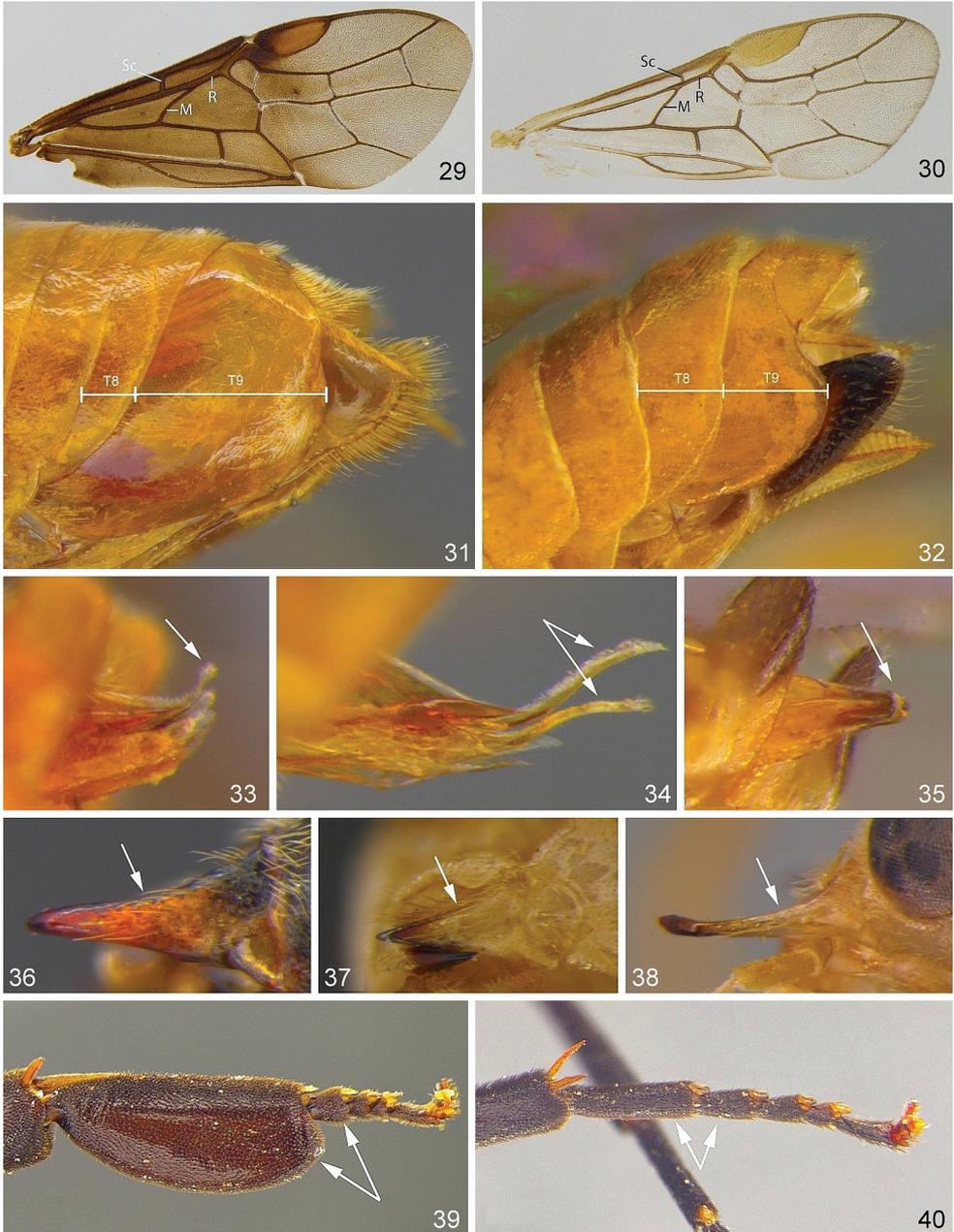
- **aa** Claw with subapical tooth; **bb** Apex of vein C of fore wing less swollen; at the point of origin of vein Rs+M from R, cell c approx. twice as wide as R or wider (cf. Fig. 66) (2 / 1* species) ***Platycampus Schiödte, 1839**
- 12(2) **a** Base of vein 2A+3A incomplete and straight (Fig. 63); **b** Vein 2r-m usually present (Fig. 63); **c** Vein 2m-cu present (Fig. 63) (6 / 3* species; see key in Liston et al. 2019b)..... ***Pseudodineura Konow, 1885**
- **aa** Base of vein 2A+3A more or less complete and curved up to 1A (Fig. 64); **bb** Vein 2r-m of fore wing often absent (Fig. 64); **cc** Vein 2m-cu absent or present (Only *E. anemones* (Hering, 1924)*)..... ***Endophytus Hering, 1934**
- 13(3) **a** Base of vein 2A+3A complete and curved up to 1A (Fig. 64) **14**
- **aa** Base of vein 2A+3A incomplete and straight (Fig. 63) **15**
- 14(13) **a** Vein 2m-cu running into cell 2Rs (Fig. 65); **b** Apex of vein C of fore wing swollen; at the point of origin of vein Rs+M from R, cell c usually only approx. as wide as R (in pale specimens may be hardly visible) (Fig. 65); **c** Body length 3–7 mm, frequently less than 5 mm (14 / 9* species; see key in Liston et al. 2019c)..... ***Hoplocampa Hartig, 1837**
- **aa** Vein 2m-cu running into cell 1Rs (Fig. 66); **bb** Apex of vein C of fore wing less swollen; at the point of origin of vein Rs+M from R, cell c approx. twice as wide as R or wider (Fig. 66); **cc** Body length 5–8 mm (2 / 2* species).....
..... ***Hemichroa Stephens, 1835**
- 15(13) **a** Vein Sc before point of origin of vein M from R (cf. Fig. 29) **17**
- **aa** Vein Sc beyond point of origin of vein M from R (Fig. 30)
..... ***Dineura Dahlbom, 1835**
- 16(7) **a** Left mandible in lateral view markedly constricted near middle (cf. Fig. 38); **b** Head, legs, thorax ventrally, valvifer 2 and valvula 3 black; abdomen and mesonotum yellow or orange (Figs 123–126) (one very rare species: *N. noblecourtii* Lacourt, 2006) **Nescianeura Lacourt, 2006**
- **aa** Left mandible in lateral view tapered regularly towards apex (Figs 36–37); **bb** Coloured differently (4 / 4* species; see key in Liston et al. 2019a).....
..... ***Dineura Dahlbom, 1835**
- 17(15) **a** Clypeus long (Fig. 67); **b** Labrum short, apically emarginate (Fig. 67); **c** Left mandible in lateral view tapered regularly towards apex (Figs 36–37) (One very rare species: *N. arquata* (Klug, 1816)) . **Neodineura Taeger, 1989**
- **aa** Clypeus short (Fig. 68); **bb** Labrum normal, apically rounded (Fig. 68); **cc** Left mandible in lateral view markedly constricted near middle (cf. Fig. 38) **18**
- 18(17) **a** Antenna rather short, ca. 1.5 times as long as width of head; **b** Claw with large inner tooth (2 / 1* species) ***Mesoneura Hartig, 1837**
- **aa** Antenna longer, ca. 2–3 times as long as width of head; **bb** Claw simple or with small inner tooth (few specimens of *Pristiphora*; see key in Prous et al. 2017) **5**



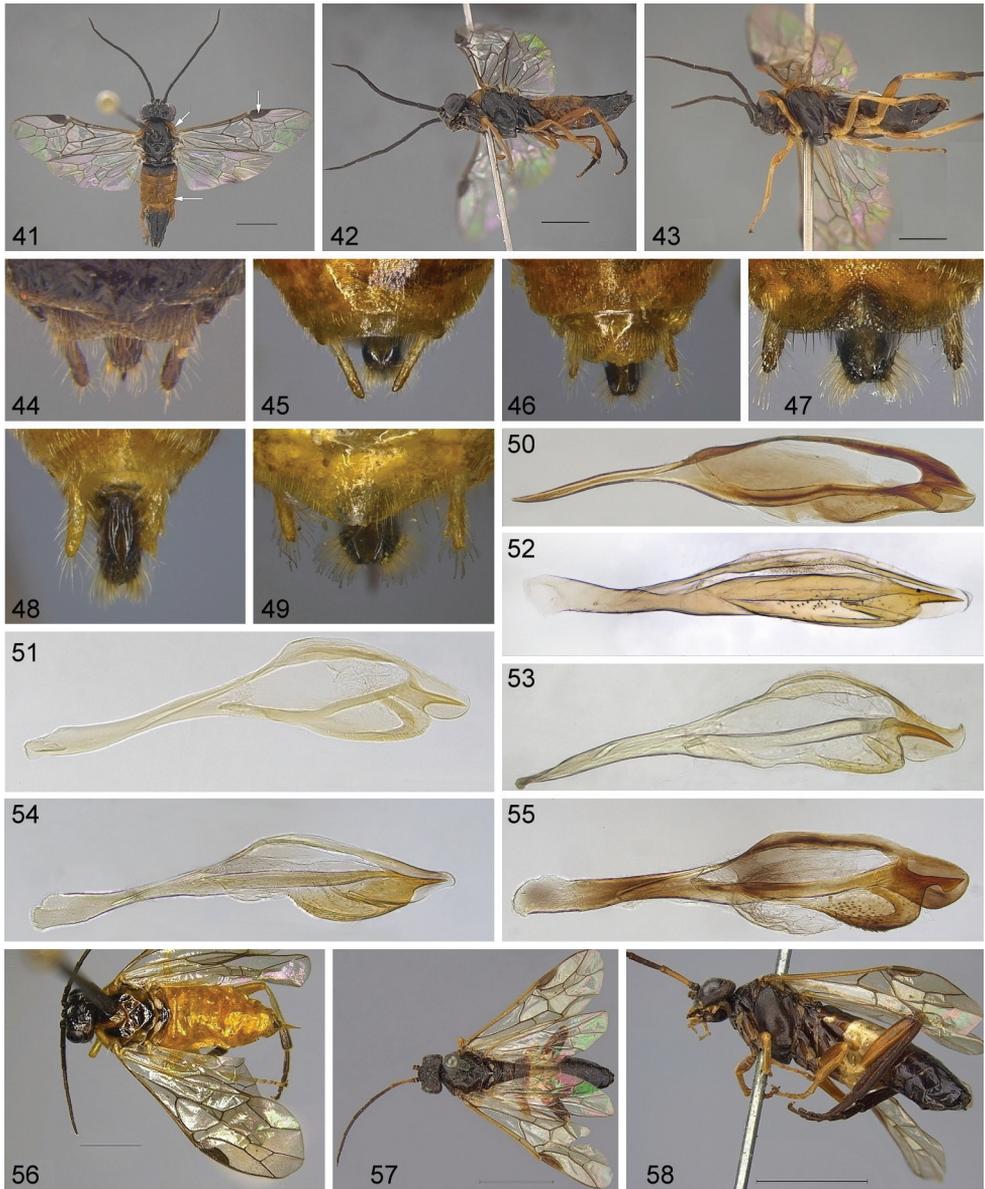
Figures 2–13. Generic characters of Nematinae **2–3** *Euura abnormis* ♂ **4,5** *Euura abnormis* ♀ (drawings after Benson 1958) **6** *Hoplocampa chrysorrhoea* rear wing **7** *Pseudodineura enlini* rear wing **8** *Euura mucronata* fore wing **9** *Mesoneura opaca* fore wing **10** *Nematus lucidus* fore wing **11** *Platycampus luridiventris* fore wing **12** *Pristiphora pallidiventris* fore wing **13** *Euura annulata* fore wing.



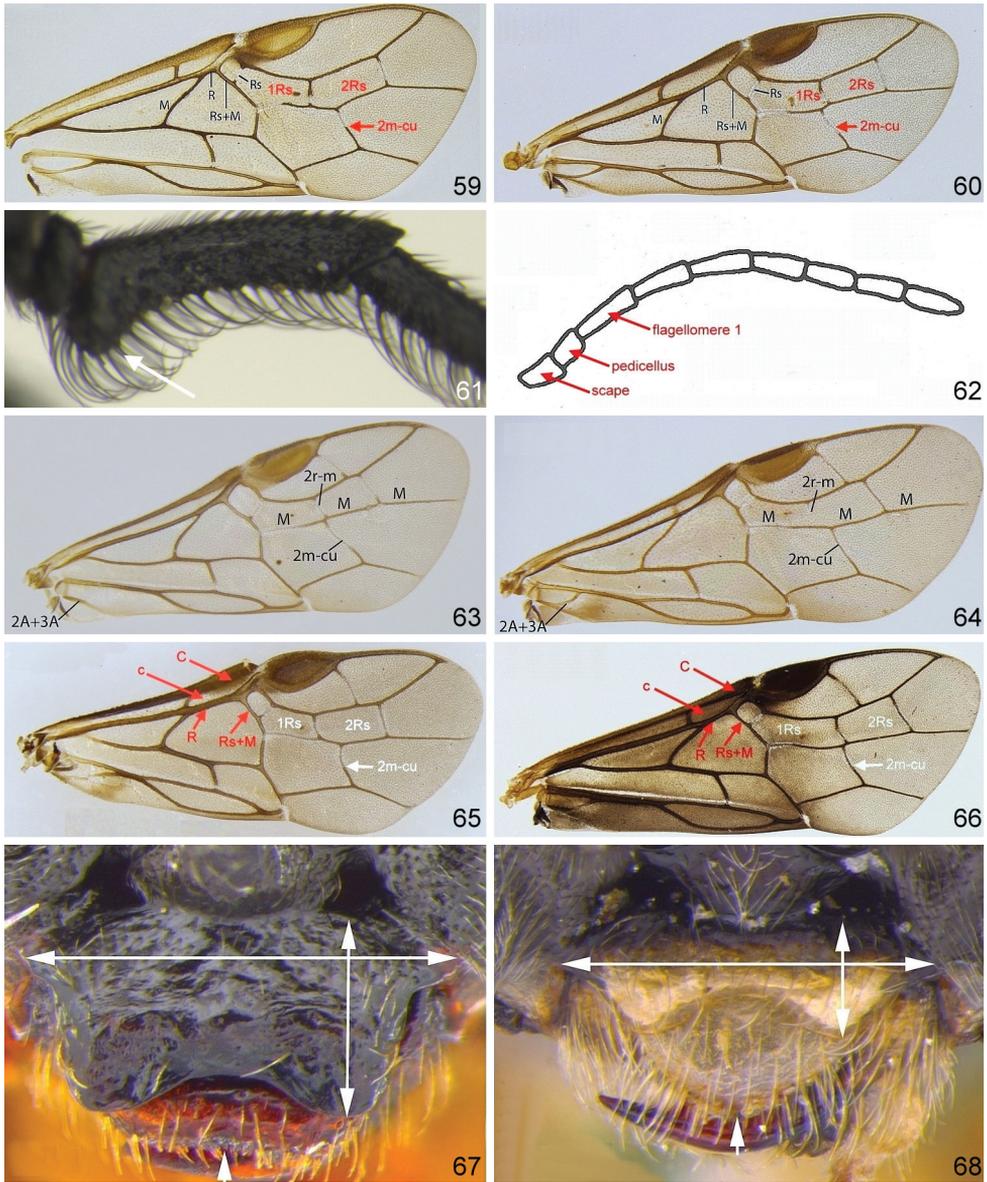
Figures 14–28. Generic characters of Nematinae **14** *Pristiphora dedeara* clypeus **15** *Nematus septentrionalis* clypeus **16** *Stauronematus platycerus* claw (arrow: basal lobe) **17** *Euura pumilio* claw **18** *E. clitellata* claw **19** *Nematus lucidus* claw **20** *E. ribesii* claw **21** *Pristiphora pallidiventris* valvula 3 (arrow: emargination) **22** *Euura reticulata* valvula 3 (arrow: not emarginate) **23** *Pristiphora subopaca* tergum 8 **24** *Euura ribesii* **25** *Pristiphora astragali* lancet (arrow: campaniform sensilla on tangium) **26** *Euura bertilpoppii* lancet (arrow: no campaniform sensilla on tangium) **27** *Pristiphora pseudodecipiens* penis valve (arrow: valvispina) **28** *Euura jugicola* penis valve (arrow: valvispina).



Figures 29–40. Generic characters of Nematinae **29** *Nematinus fuscipennis* fore wing **30** *Dineura virididorsata* fore wing **31** *Nematinus fuscipennis* abdomen tip **32** *Euura vesicator* abdomen tip **33** *Nematinus fuscipennis* penis valve **34** *Nematinus bilineatus* penis valve **35** *Euura vesicator* penis valve **36** *Nematinus fuscipennis* left mandible **37** *Dineura virididorsata* left mandible **38** *Pristiphora krausi* left mandible **39** *Nematus septentrionalis* metatarsus **40** *Euura caeruleocarpus* metatarsus.



Figures 41–58. Generic characters of Nematinae **41–42** *Nematus lucidus* ♀ **43** *N. wahlbergi* ♀ **44** *N. wahlbergi* valvula 3 **45** *N. umbratus* valvula 3 **46** *Euura melanocephalus* valvula 3 **47** *E. bohemani* valvula 3 **48** *E. ribesii* valvula 3 **49** *E. salicis* valvula 3 **50** *Nematus wahlbergi* penis valve **51** *N. umbratus* penis valve **52** *Euura salicis* penis valve **53** *E. ribesii* penis valve **54** *E. bohemani* penis valve **55** *Nematus princeps* penis valve **56** *Nematus umbratus* ♀ **57–58** *Nematus princeps* ♀. Scale bars: 2 mm (**41–43, 56**), 5 mm (**57–58**)



Figures 59–68. Generic characters of Nematinae **59** *Cladius compressicornis* fore wing **60** *Platycampus luridiventris* fore wing **61** *Cladius ulmi* ♂ flagellomere 1 **62** *Armenocampus necopinus* antenna (after Zinovjev 2000) **63** *Pseudodineura enslini* fore wing **64** *Endophytus anemones* fore wing **65** *Hoplocampa chrysorrhoea* fore wing **66** *Hemichroa australis* fore wing **67** *Neodineura arquata* clypeus **68** *Mesoneura opaca* clypeus.

Key to the West Palaearctic genera and selected species of Nematinae (larvae)

Numbers of setae on dorsal annulets are for only one side of the body, as in Lorenz and Kraus (1957). The best results should be possible with full-grown larvae, but before these undertake a final “extra moult”, in the groups where this applies. Presence or absence of the extra moult is a useful additional taxonomic and identification character in itself (Kontuniemi 1965), but can usually only be scored if the larvae are reared. Larvae of many species which perform an extra moult differ greatly in appearance after this moult from preceding instars: colour pattern and ground-colour frequently change, and setation can be much reduced. Even in species which have no extra moult, pronounced colour differences between instars are often noticeable. Larvae of the monotypic genera *Armenocampus*, *Neodineura*, and *Nescianeura* are unknown, as well as the larvae of many species of *Euura* and *Pristiphora*, particularly the northern species. Even in the less speciose genera, larvae of some species are undescribed, while several others are insufficiently described, or existing descriptions are partly contradictory, e.g., for *Cladius compressicornis* and *brullei*. Because high interspecific morphological variability is already evident in *Euura* larvae, it would not be surprising if larvae were found which have combinations of characters not included in the key. Only the two species of the *Nematus wahlbergi* group known in Sweden are included. Descriptions of larvae of some of the other species of this group may be found in Zinovjev (1979). We have seen no specimens or images of larvae of *Nematus brischkei*: the characters used below to distinguish it are taken from the descriptions by Zaddach (1876) and Chambers (1950). In view of the incomplete and imperfect nature of the available data, the key is highly provisional. Unless otherwise stated, the larvae are exophytic, and feed mostly on leaves. The numbers of species refer to Fennoscandia.

- 1 **a** Prolegs present on abdominal segments 2–8 and 10 (Fig. 69), or when (rarely) on 2–7 and 10, then antenna more or less conic, and comprising a single antennomere; **b** Antenna with 1–5 antennomeres, never completely flat; **c** Abdominal segment 3 with 2–6 annulets **2**
- **aa** Prolegs present on abdominal segments 2–7 and 10 (Fig. 74); **bb** Antenna with 3–5 antennomeres, sometimes completely flat; **cc** Abdominal segment 3 with 3–6 annulets **3**
- 2(1) **a** Prolegs normally developed on segment 8; **b** Antenna with 1–5 antennomeres; **c** Abdominal segment 3 with 2–6 annulets [**not Nematinae**]
- **aa** Prolegs on segment 8 reduced to protuberances much smaller than prolegs on segment 7 (Fig. 69); **bb** Antenna with 3 antennomeres; **cc** Abdominal segment 3 with 6 annulets [*Quercus*] *Mesoneura opaca*
- 3(1) **a** Leaf-miners of Ranunculaceae; **b** Prosternum with median dark fleck and pair of lateral flecks (Fig. 70); dorsum of thorax without any markings (Fig. 71) [Antennae with 3 antennomeres, flat; abdomen segment 3 with

- 4 dorsal annulets, 2 of which with setae] ***Pseudodineura*** [3 species] **and** ***Endophytus anemones*** [1 species]
- **aa** Exophytic on leaves of many plant families, or in galls on *Salix*, fruits of *Ribes* or Rosaceae, or catkins of *Salix*; **bb** Prosternum without dark markings, or only with a median fleck; dorsum of thorax often with markings..... **4**
- 4(3) **a** Abdominal segment 3 with less than 6 dorsal annulets..... **5**
- **aa** Abdominal segment 3 with 6 dorsal annulets **24**
- 5(4) **a** Abdominal segment 3 with 3–4 dorsal annulets **6**
- **aa** Abdominal segment 3 with 5 dorsal annulets **15**
- 6(5) **a** Body flat, woodlouse-shaped (Figs 72–73); **b** Upper anterior head with saddle-shaped indentation (Fig. 73) [*Alnus*] ***Platycampus*** [1 species]
- **aa** Body at most slightly flattened; **bb** Upper head normal..... **7**
- 7(6) **a** Supra-anal lobe with pseudocerci (cf. Figs 90–92)..... ***Euura*** [part: ca. 50 species of *Salix* gall-makers of former *Pontania*, *Phyllocolpa*, *Tubpontania*, and also some exophytic species; overview of galls and larvae of gall-makers in Liston et al. (2017)]
- **aa** Supra-anal lobe without pseudocerci **8**
- 8(7) **a** Setae on dorsal body annulets arising singly and not from warts (Fig. 74) **9**
- **aa** Setae on dorsal body annulets arising from warts, singly or partly in groups (Figs 75–77) ***Cladius*, 10**
- 9(8) **a** Dorsal body annulets with some very long setae: as long as length of head (Fig. 74); **b** Abdomen segments with 3 dorsal annulets [*Potentilla fruticosa*, *Dryas octopetala*] ***Pristiphora dasiphorae* and *malaisei*** [former *Pristicampus*]
- **aa** Dorsal body annulets with short setae: longest much shorter than length of head; **bb** Abdomen segments with 4 dorsal annulets ***Euura*** [part: approx. 16 *Salix* gall-makers of *atra* group; overview of galls and larvae in Liston et al. (2017). Some exophytic species, on various plant genera]
- 10(8) **a** Setae on dorsal annulets 2 and 3 of abdominal segment 3 arise in groups from large, pale warts..... **11**
- **aa** Setae on dorsal annulets 2 and 3 of abdominal segment 3 arise singly on small warts which are close to each other (Fig. 75) ***Cladius brullei*, *C. compressicornis***
- 11(10) **a** Annulet 1 of abdominal segment 3 with 5–8 setae of which 3–4 arise together from a single wart; **b** Head without black markings (Fig. 76) [Rosaceae: particularly *Rosa*, *Fragaria*, and *Potentilla*] ***Cladius pectinicornis***
- **aa** Annulet 1 of abdominal segment 3 with 2–5 setae each arising singly from a small wart; **bb** Head at least partly black (Fig. 77) [*Populus*, *Salix*, or *Ulmus*] **12**
- 12(11) **a** Head black (Fig. 77); **b** Surpedal lobe *sometimes* with small black fleck; **c** Anal lobe with large black fleck (Fig. 77) [*Populus* or *Salix*] **13**
- **aa** Head green to reddish-yellow with small black flecks; **bb** Surpedal lobe without black markings; **cc** Anal lobe without black fleck [*Ulmus*] **14**
- 13(12) **a** Surpedal lobe with small black fleck; **b** Body of younger instars yellow-green, apart from yellow-orange caudal and distal parts [mature: entirely

- yellow-orange] [*Populus*, rarely *Salix*]
 *Cladius grandis*
- **aa** Surpedal lobe without small black fleck; **bb** Body of younger instars whitish, apart from yellow-orange caudal and distal parts [*Salix* spp.] *Cladius aeneus*
- 14(12) **a** A black fleck only medially on upper head *Cladius rufipes*
- **aa** A black fleck medially on upper head, a pair of black flecks around stemmata, and a black frontal fleck *Cladius ulmi*
- 15(5) **a** Tips of setae on dorsal annulets modified: spatulate or slightly cleft [*Betula*, *Prunus padus*, *Crataegus*, or *Sorbus*: known larvae keyed by Macek (2015)] ...
 *Dineura* [4 species]
- **aa** Tips of setae not modified **16**
- 16(15) **a** In female catkins of *Salix* species; **b** Antenna completely flat, comprising several incompletely formed antennomeres (Fig. 78) [Setae on body sparse, very short] *Euura* [part: ca. 6 species of former *Pontopristia*]
- **aa** Exophytic on leaves, or endophytic in fruits of Rosaceae; **bb** Antenna completely flat, or at least apical antennomere clearly conic **17**
- 17(16) **a** Body somewhat dorso-ventrally flattened (Figs 79–81); **b** Supra-anal lobe with longitudinal keel; **c** Dorsal annulets 1–4 of abdominal segment 3 with setae; **d** Small head can be withdrawn into prothorax [*Alnus*, *Betula*, or (rarely) *Corylus*] [*Nematinus*, 6 species], **18**
- **aa** Body cylindrical (cf. Figs 82–87); **bb** Supra-anal lobe without longitudinal keel; **cc** Dorsal annulets [1–4], or [1, 2 and 4], or [2 and 3] of abdominal segment 3 with setae; **dd** Head normal **22**
- 18(17) **a** Dorsum of body sooty-black; with rows of white warts [*Betula*]
 *Nematinus caledonicus*
- **aa** Dorsum of body green; with or without white warts **19**
- 19(18) **a** Dorsum of body without white warts (Fig. 79) [*Betula*, rarely *Corylus*]
 *Nematinus acuminatus*
- **aa** Dorsum of body with white warts (Figs 80–81) **20**
- 20(19) **a** Top of head with pair of dark brown flecks, one each side of coronal suture (Figs 80–81) **21**
- **aa** Top of head without dark brown flecks [*Alnus* spp.] *Nematinus fuscipennis*
- 21(20) **a** Dark brown around orbits, particularly towards temples and rear of head (Fig. 80); **b** Supra-anal lobe dorsally at caudal end with two large dark-brown flecks, often half-moon shaped and partly confluent (Fig. 80) [*Alnus* spp., rarely on *Corylus avellana*] *Nematinus luteus*
- **aa** Not dark brown around orbits (Fig. 81); **bb** Supra-anal lobe dorsally without dark-brown flecks (Fig. 81) [*Alnus* spp.] *Nematinus steini*
- 22(17) **a** Dorsum of body with extensive dark pattern of brown patches, or grey longitudinal stripes (Figs 82–83); **b** Dorsal annulets [1, 2 and 4] of abdominal segment 3 with minute setae [On *Larix*] *Anoplonyx*
- **aa** Dorsum of body at most with small, separate dark markings on abdomen; **bb** Dorsal annulets [2 and 3] or [1–4] of abdominal segment 3 with setae....
 **23**

23(22) **a** Dorsal annulets [2 and 3] of abdominal segment 3 with setae; **b** Body without colour pattern except for dark dorsum of abdomen apex (Fig. 84) [In fruits of tree and shrub Rosaceae]..... *Hoplocampa* [9 species]
– **aa** Dorsal annulets [1–4] of abdominal segment 3 with setae; **bb** Body usually with different colour pattern [Exophytic on leaves, mostly *Salix*]
..... *Euura* [part: some former *Amauronematus*]
24(4) **a** Supra-anal lobe without pseudocerci or protuberances **25**
– **aa** Supra-anal lobe with pseudocerci or protuberances **33**
25(24) **a** Stipes of maxilla with 0–1 setae..... **26**
– **aa** Stipes of maxilla with 2–3 setae **29**
26(25) **a** 3 dorsal annulets [1, 2 and 4] of abdominal segment 3 with setae (Fig. 86)....**27**
– **aa** 2 dorsal annulets [2 and 4] of abdominal segment 3 with setae **28**
27(26) **a** Setae on surpedal and substigmal lobes approx. twice as long as those on body dorsum; **b** All antennomeres incomplete; antenna completely flat [*Populus*, sometimes *Salix*: leaf around larva usually surrounded by pillars of dried white secretion: Fig. 85]..... *Stauronematus platycerus*
– **aa** Setae on surpedal and substigmal lobes not longer than setae on body dorsum (Fig. 86); **bb** Apical 2 antennomeres completely developed; most apical one conic [*Potentilla fruticosa*]
..... *Pristiphora malaisei* [see taxon commentary under that name, below]
28(26) **a** Stipes without setae. If with one seta, then supra-anal lobe in the middle with conspicuous protuberance [coniferous trees, or diverse dicot plants]
..... *Pristiphora* [larger part: ca. 90 species]
– **aa** Stipes with one seta. Supra-anal lobe dorsally with brown-marked depressions [grasses and sedges] *Euura clitellata* group
29(25) **a** Two dorsal annulets [2 and 4] of abdominal segment 3 with setae.....
..... *Euura* [part: *E. spiraeae*, some former *Pachynematus*]
– **aa** More than 2 dorsal annulets of abdominal segment 3 with setae **30**
30(29) **a** Four dorsal annulets [1–4] of abdominal segment 3 with setae.....
..... *Euura* [part: some former *Amauronematus*]
– **aa** Three dorsal annulets [1, 2 and 4] of abdominal segment 3 with setae.. **31**
31(30) **a** Annulet 1 of abdominal segment 3 with only one seta, annulet 2 without warts bearing several setae *Euura* [part: some former *Pachynematus*]
– **aa** Annulet 1 of abdominal segment 3 with two setae, if not, then annulet 2 with 2 warts each bearing several setae **32**
32(31) **a** Body somewhat dorso-ventrally flattened; **b** Annulet 2 of abdominal segment 3 with 4 setae [*Salix*]..... *Euura flavescens*
– **aa** Body cylindrical; **bb** Annulet 2 of abdominal segment 3 with more than 4 setae..... *Euura* [part: some former *Amauronematus*]
33(24) **a** Caudal margin of supra-anal lobe with 10–12 blunt-conic protuberances; **b** Antenna with 5 antennomeres **34**
– **aa** Supra-anal lobe with 2 pseudocerci, and without blunt-conic protuberances; **bb** Antenna with 4 antennomeres..... **35**

- 34(33) **a** Each body side with three longitudinal black stripes (Fig. 87); **b** Head black [*Alnus*, *Betula*, *Corylus*] *Hemichroa crocea*
 – **aa** Body without black stripes (Fig. 88); **bb** Head brown (younger larvae), to mainly yellowish-green (older larvae) [*Betula*, *Alnus*].... *Hemichroa australis*
- 35(33) **a** Three dorsal annulets [1, 2 and 4] of abdominal segment 3 with setae ... **36**
 – **aa** Two dorsal annulets [2 and 4] of abdominal segment 3 with setae..... **40**
- 36(35) **a** Dorsal annulet 1 of abdominal segment 3 with 1 seta; annulet 2 with 6–7 setae [Surpedal lobe with 8–9 setae; *Picea*] *Euura insignis*
 – **aa** Dorsal annulet 1 of abdominal segment 3 with 2–6 setae..... **37**
- 37(36) **a** All antennomeres incomplete and flat [Dorsal annulet 1 of abdominal segment 3 with 2 large and 1 small setae; setae arise from dark flecks]
 *Euura* [part: some former *Amauronematus*]
 – **aa** At least antennomere 4 button-, peg- or cone-shaped..... **38**
- 38(37) **a** Exophytic on *Lonicera*, rarely on *Symphoricarpos*; **b** Pseudocerci in dorsal view very close to each other, near median line of abdomen (Fig. 90) **39**
 – **aa** Exophytic on many plant genera, but not *Lonicera* or *Symphoricarpos*; **bb** Pseudocerci in dorsal view much further apart, near lateral edges of tergum (Fig. 92)..... *Euura* [part: former *Pteronidea*]
- 39(38) **a** Whole upper head darkened (Fig. 89); **b** A row of dark flecks above the abdominal prolegs (Fig. 89) *Nematus loniceræ*
 – **aa** Head pale with rather narrow median stripe (Fig. 90); **bb** No row of dark flecks above the abdominal prolegs (Fig. 90) *Nematus wahlbergi*
- 40(35) **a** Substigmatal lobe with at least 8 setae..... **41**
 – **aa** Substigmatal lobe with no more than 6 setae..... **42**
- 41(40) **a** Pseudocerci apically blunt, and widening towards apex (Fig. 91); distance between them at most 2 × the length of one pseudocercus [*Crataegus*, *Prunus* spp., especially *P. spinosa*] *Nematus lucidus*
 – **aa** Pseudocerci apically pointed, and cone-shaped; distance between them 3–4 × the length of one pseudocercus [*Salix*, *Rumex*, rarely *Betula*]
 *Euura vicina*
- 42(40) **a** Abdominal segments ventrally between the prolegs with large black flecks, or body except for more or less pale 1st and last 3 segments nearly completely brown-black (Fig. 93), or abdominal segments with 4 black markings sub- and suprastigmatal, and one or more surpedal markings (Figs 95–96)
 **43** [*Nematus* part: former *Craesus*]
 – **aa** Abdominal segments without large black flecks ventrally, body markings different [if with black markings, these as more complicated pattern of small flecks: cf. Fig. 92]..... **46**
- 43(42) **a** Either nearly whole dorsum black (Fig. 93), or each black fleck of uppermost row on body at least as long as half the length of an abdomen segment (Fig. 94); **b** Head nearly entirely black (Figs 93–94) **44**
 – **aa** Dorsum largely green, more or less with black flecks on sides of body, but individual black flecks much smaller than half the length of an abdomen

- segment (Figs 95–96); **bb** Head entirely pale: green, to pale brown (Figs 95–96)..... **45**
- 44(43) **a** At least dorsum of body broadly black, except at most for prothorax and tip of abdomen (Fig. 93) [*Betula*, and *Alnus viridis* in C. Europe]..... *Nematus latipes*
- **aa** Dorsal midline of body entirely without black markings (Fig. 94) [*Betula*, *Alnus*, *Corylus*, *Sorbus aucuparia*, *Carpinus betulus*] *Nematus septentrionalis*
- 45(43) **a** Abdominal prolegs yellow; **b** Coxae entirely pale [*Carpinus betulus*, *Corylus avellana*] *Nematus brischkei*
- **aa** Abdominal prolegs green (Fig. 95); **bb** Coxae dark-marked [*Alnus* spp.]... *Nematus alniastri*
- 46(42) **a** Pseudocerci visible in dorsal view; subparallel or diverging, and more or less symmetrical [Various plant genera] *Euura* [part: former *Pteronidea*]
- **aa** Pseudocerci not visible in dorsal view; directed inwards, and curved [*Betula*. Body entirely green, except for dark marks on coxae, and small flecks at bases of the more ventral setae: Fig. 97] *Nematus princeps*

Taxon commentaries

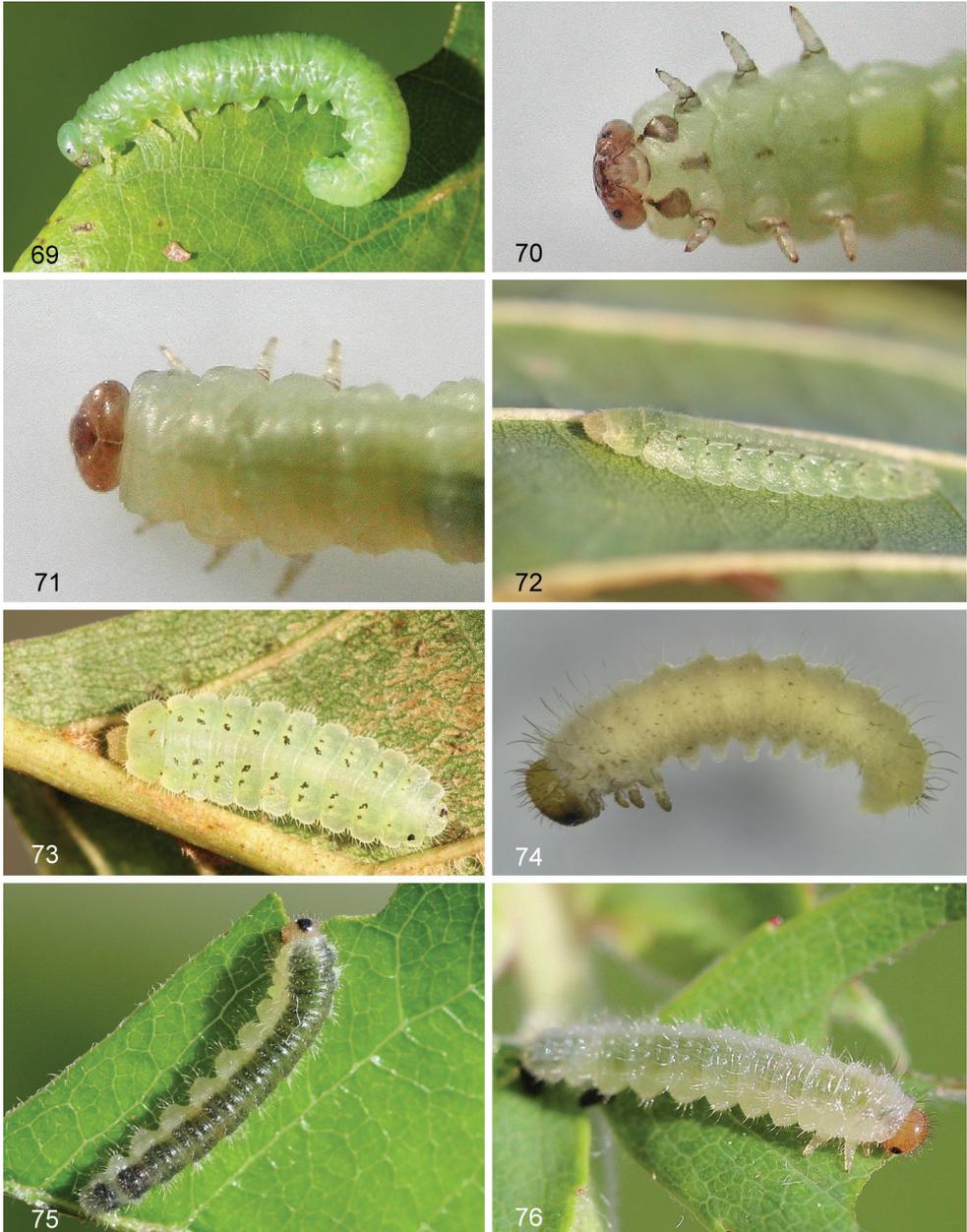
Synonymy of genus-group names was given by Prous et al. (2014) and is not repeated here, except for *Euura* and *Nematus*, where the synonymy proposed in the former work is extensive, and probably not yet familiar to many users. The known nomina nuda and names for aberrations (unavailable names following International Commission on Zoological Nomenclature (1999)) for the listed species were given by Taeger et al. (2010). Taxa are dealt with in alphabetical order.

Anoplonyx Marlatt, 1896

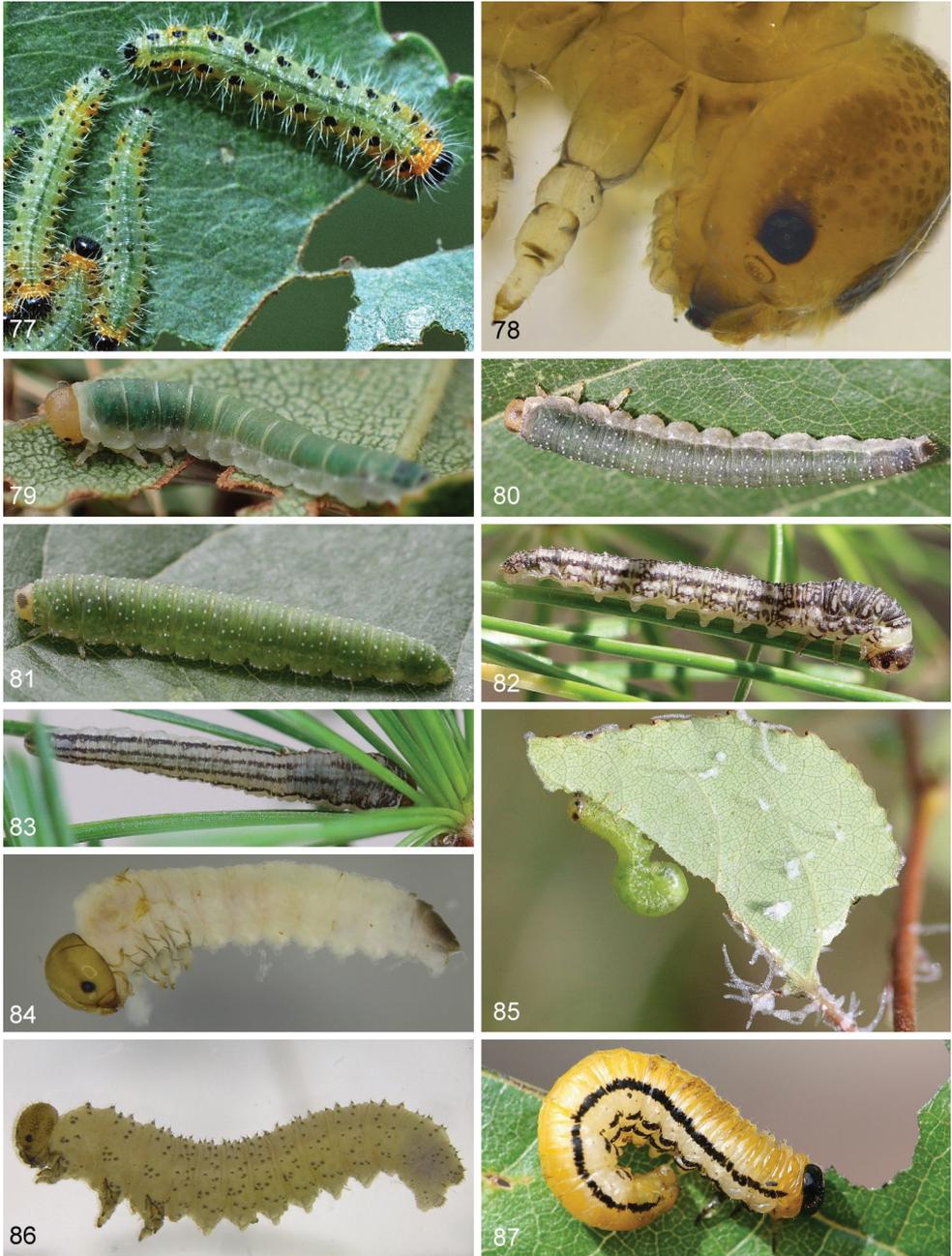
No reliable key or species treatments are available to date.

Armenocampus Zinovjev, 2000

This genus was erected for a single species, *Armenocampus necopinus* (Zhelochovtsev, 1941), originally described as *Caulocampus necopinus*, known only from the small type series of both sexes collected in Armenia. Nothing is known about its biology.



Figures 69–76. Larvae of Nematinae **69** *Mesoneura opaca* **70–71** *Pseudodineura clematidis*; ventral, dorsal **72–73** *Platycampus luridiventris* **74** *Pristiphora malaisei* from *Dryas octopetala* **75** *Cladius compressicornis* **76** *Cladius pectinicornis*.



Figures 77–87. Larvae of Nematinae **77** *Cladius grandis* **78** *Euura* sp. *amentorum* group **79** *Nematinus acuminatus* **80** *Nematinus luteus* **81** *Nematinus steini* **82–83** *Anoplonyx albitarsis* **84** *Hoplocampa crataegi* **85** *Stauronematus platycerus* **86** *Pristiphora malaisei* from *Potentilla fruticosa* **87** *Hemichroa crocea*.



Figures 88–97. Larvae of Nematinae **88** *Hemichroa australis* **89** *Nematus loniceræ* (photo E. Altenhofer) **90** *Nematus wahlbergi* **91** *Nematus lucidus* **92** *Euura melanocephalus* **93** *Nematus latipes* **94** *Nematus septentrionalis* **95–96** *Nematus alniastri* **97** *Nematus princeps* (photo V. Vikberg).

***Cladius* Illiger, 1807**

No reliable key or species treatments are available to date.

***Dineura* Dahlbom, 1835**

See key and species treatments in Liston et al. (2019a).

***Endophytus* Hering, 1934**

See species treatment in Liston et al. (2019b).

***Euura* Newman, 1837**

Prous et al. (2014) treated a large number of genus-group names as synonyms of *Euura*. A complete list of these is contained therein. The synonyms listed below have been recently used as valid for West Palaearctic taxa. Nearly all species formerly included in these genera, and the majority of species previously placed by many authors in *Nematus*, now belong to *Euura*. The north-west European gall-making species of *Euura* were recently revised by Liston et al. (2017).

Pontania Costa, 1852

Amauronematus Konow, 1890

Pachynematus Konow, 1890

Pteronidea Rohwer, 1911

Pontopristia Malaise, 1921 (Malaise 1921a)

Brachycoluma Strand, 1929

Decanematus Malaise, 1931 (Malaise 1931a)

Pikonema Ross, 1937

Phyllocolpa Benson, 1960 (Benson 1960a)

Eitelius Kontuniemi, 1966

Gemmura E.L.Smith, 1968

Eupontania Zinovyev, 1985

Larinematus Zhelochovtsev, 1988

Polynematus Zhelochovtsev, 1988

Bacconematus Zhelochovtsev, 1988

Alpinematus Lacourt, 1996

Epicenematus Lacourt, 1998

Kontuniemiana Lacourt, 1998

Lindqvistia Lacourt, 1998

Tubpontania Vikberg, 2010

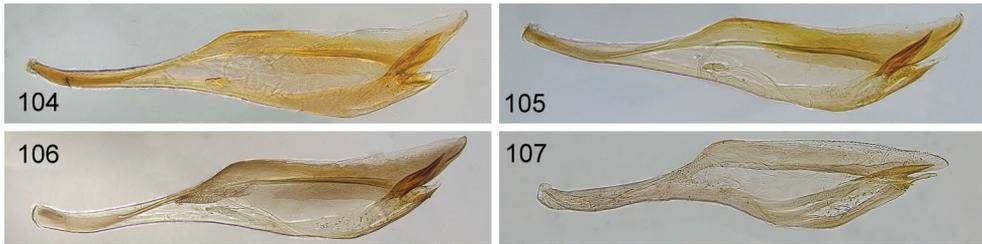
Hemichroa* Stephens, 1835*Key to the European species**

- 1 **a** Female **2**
 – **aa** Male..... **3**
 2 **a** Abdomen yellow or orange except for black valvula 3 and more or less tergum 1 (Figs 98, 100); **b** Upper mesepisternum yellow, lower part black (Fig. 100)..... ***Hemichroa crocea (Geoffroy, 1785)♀**

- **aa** Abdomen black except for more or less red terga 8, 9, 10 and hypopygial area (Figs 99, 101); **bb** Whole mesepisternum black (Fig. 101).....
 **Hemichroa australis* (Serville, 1823) ♀
- 3 **a** Penis valve: upper edge of pseudoceps convex, distal part more evenly tapering; distal projections small (Fig. 107); **b** Parts of abdominal terga and sterna *sometimes* pale (Fig. 102)..... **Hemichroa crocea* (Geoffroy, 1785) ♂
- **aa** Penis valve: upper edge of pseudoceps concave, distal part more abruptly tapering; distal projections larger (Figs 104–106); **bb** Abdomen entirely black, except for harpes and more or less distal edge of sternum 9 (Fig. 103)
 **Hemichroa australis* (Serville, 1823) ♂



Figures 98–103. *Hemichroa* **98–100** *crocea* DEI-GISHym19402 ♀, Germany, Mecklenburg-Vorpommern **99, 101** *australis* DEI-GISHym15401 ♀, Sweden, Torne Lappmark **102** *crocea* DEI-GISHym31838 ♂, Germany, Mecklenburg-Vorpommern **103** *australis* DEI-GISHym20618 ♂, Sweden, Torne Lappmark, fore wing. Scale bar: 2 mm.



Figures 104–107. *Hemichroa*, penis valves **104** *australis* DEI-GISHym15392 Germany, Saxony **105** *australis* DEI-GISHym20618, Sweden, Kiruna **106** *australis* DEI-GISHym84982, Japan, Honshu **107** *crocea* DEI-GISHym31838, Germany, Mecklenburg-Vorpommern.

Hemichroa australis (Serville, 1823)

Tenthredo alni Linné, 1767: 925. Lectotype ♀, designated by Malaise and Benson (1934: 8), not examined, in LSUK (images: <http://linnean-online.org/16581/>). Type locality: Sweden. Primary homonym of *Tenthredo alni* Linné, 1758 (*Nematus septentrionalis* (Linné, 1758)).

Tenthredo luctuosa Hill, 1773: 5–6, pl. 1. Syntype(s) ♀, lost. Type locality: Uxbridge (United Kingdom). Treated as nomen oblitum and synonymised with *australis* by Blank et al. (2009: 32).

Tenthredo australis Serville, 1823: 16. Syntype(s) ♀, lost. Type locality: Midi (France). Nomen protectum, as stated by Blank et al. (2009: 32).

Tenthredo australis Lepeletier, 1823:71. Syntype(s) ♀, lost. Type locality: Midi (France). Primary homonym of *Tenthredo australis* Serville, 1823.

Hemichroa monticola Ermolenko, 1960: 208–210. Holotype ♀ (Schmalhausen Institute, Kiev: not examined) and 4 female paratypes (one examined). Type locality: Ukraine, Lvovskoj oblasti, Slavekogo rajona, Tuhovalskom perevale. **Syn. nov.**

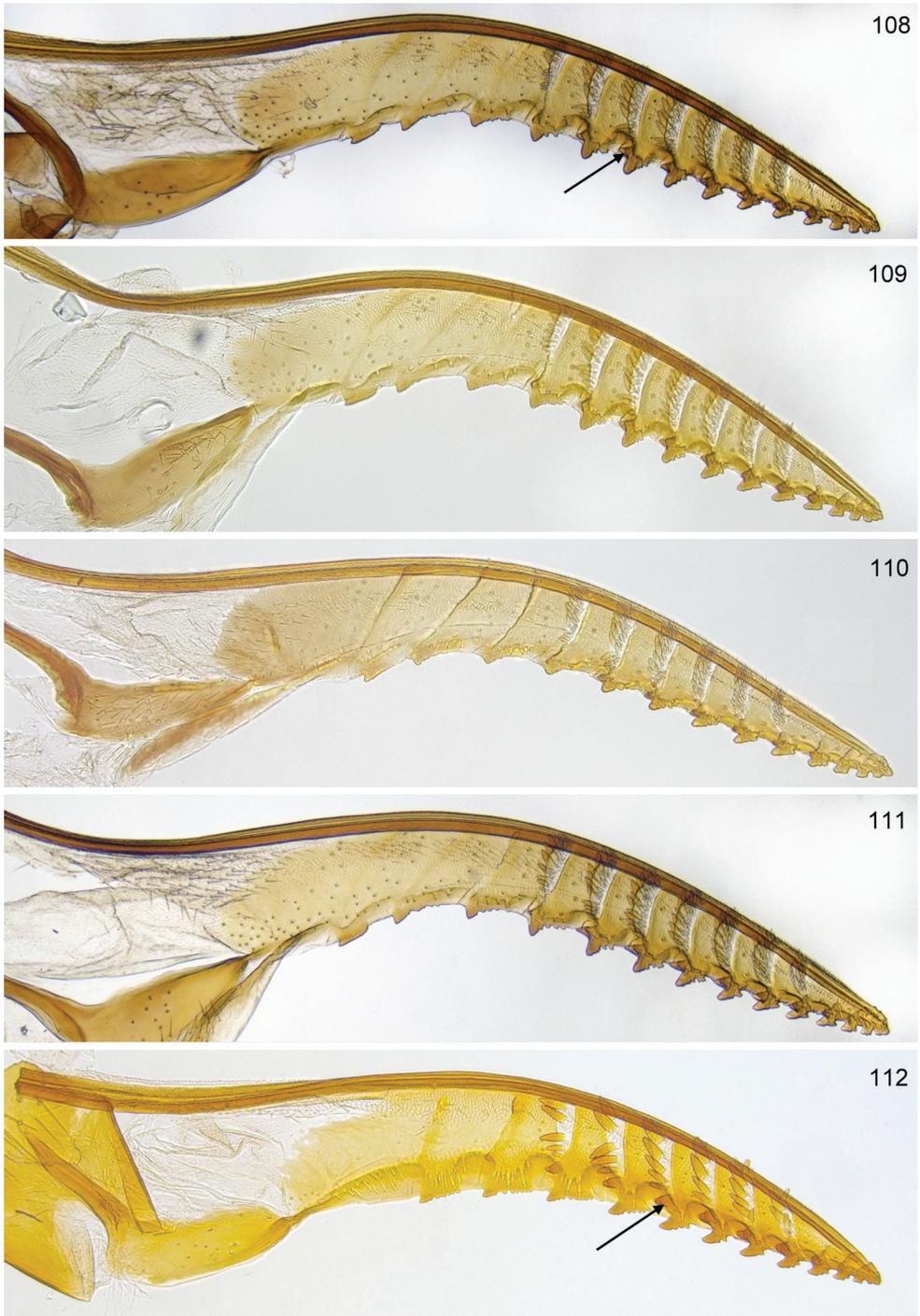
Taxonomy. Ermolenko (1960) stated that *australis* differs from *monticola* in the following characters [character state for *monticola* in brackets]:

- lower surface of antenna noticeably paler than the upper [uniformly dark]
- medial emargination of clypeus deep, usually exceeding half of its length [reaching half of its length]
- intercostal and lanceolate cells of the fore wing and main half of the hind wing are clearly darkened [wings nearly completely hyaline]
- the 2nd anal cell of the posterior wing is almost equal to the length of the median cells [2nd anal cell of the posterior wing noticeably shorter than median one]
- 9th tergum predominantly dark [9th tergum red]
- cerci yellow [cerci basally yellow, apically fuscous]
- valvula 3 of ovipositor on lower margin noticeably convex in lateral view [only slightly convex]
- teeth of the proximal half of the ovipositor have two or more smaller additional denticles at the base [these teeth with only one small additional tooth]

Only a single paratype of *monticola* was available for examination, but we also examined four females (HNHM) which have the combination of colour characters described for *monticola* and were collected at subalpine levels in the Ukrainian Carpathians, as was the type series of *monticola*. We did not observe any significant difference in the depth of the clypeal emargination between Carpathian specimens and *australis* from other parts of Europe. The other characters used to distinguish *monticola* are either extremely weak, such as the slightly darkened tips of the cerci and the degree of curvature of the lower edge of valvula 3, or are variable among studied *australis* females, such as the length of the hind wing anal cell and the presence or absence of denticles on the more basal serrulae of the lancet (Figs 108–111). The shape of sawteeth and the number of serrulae can even vary between the left and right lancets of the same individual (Figs 108–109), possibly as a result of wear (see Schmidt and Walter 1995). Ermolenko considered *H. monticola* to be a neo-endemic element of the Carpathian subalpine fauna, associated with *Alnus viridis*, but several of the characters which he gave as distinguishing it from *australis* occur apparently independently of each other in the *australis* females which we have examined from many parts of the West Palaearctic. For example, tergum 9 mainly pale, but whole wing-membrane blackish from base of fore wing up to approximately the level of the pterostigma [Germany, Berlin], or antennae entirely black, and wing membrane nearly entirely hyaline, but 9th tergum black [Sweden, Lapland]. In our opinion, Ermolenko underestimated the range of variability in *australis*, and *monticola* falls within this range. Therefore, we treat the taxa as conspecific. Nevertheless, comparison of relevant genetic data should still be undertaken.

Previously published descriptions of the male of *Hemichroa australis*, and the colour characters which are claimed to distinguish it from that of *crocea*, are partly contradictory, and may not be reliable. Enslin (1915: 317) wrote [translated from German]: “According to Cameron, the male of *H. crocea* Geoffr. is just like that of *H. alni* [*australis*]; Cameron (Monograph Brit. Phyt. Hym. II p. 7) saw some males of *crocea* reared by Fletcher and could not distinguish them from *H. alni*. Because nothing further on this subject is reported in the literature and it was not possible for us to obtain males of *H. crocea* for examination, the separation of the males of these species must remain unresolved until a later date”. Benson (1958) stated that the male of *australis* “Differs from *crocea* ♂ in that the antenna is at least red below [*crocea*: antenna entirely black] and the stigma of the wing is piceous [*crocea*: pterostigma brown in the middle]”. Smith (1975), in his key to World *Hemichroa* species, wrote that he did not know the male of *australis*, and repeated the characters given by Benson (1958). But in the text under *H. crocea*, Smith (1975) wrote “It may be separated from other species by the presence of the radial crossvein [2r-rs] in the fore wing and characters of the genitalia (figs 3, 4)”. The first character state was surely mentioned in error: all *Hemichroa* species usually possess vein 2r-rs, except for the taxon treated by Smith (1975) as *H. militaris* (Cresson, 1880), which is currently placed in *Dineura* (Fig. 1, Prous et al. 2014). See below under *crocea* for additional discussion of diagnostic characters of males of *australis* and *crocea*.

Description. Body length: female 6.5–8.5 mm, male 6.0–6.5 mm. Wing colour highly variable in both sexes, from nearly entirely hyaline, to entire hind wing and



Figures 108–112. *Hemichroa*, lancets **108–109** *australis* DEI-GISHym15387, Sweden, Torne Lappmark; arrow, spurette **110** *australis* DEI-GISHym31836, Ukraine, Carpathians **111** *australis* DEI-GISHym31837, Russian Federation, Baskiria **112** *crocea* DEI-GISHym19401, Germany, Brandenburg; arrow, spurette.

basal fore wing up to about pterostigma conspicuously darkened. Female (Figs 99, 101): Black. Red are head, except more or less for labrum and antenna; pronotum, tegula, mesoscutum, more or less mesoscutellar appendage; more or less the apex of abdomen. Legs black, except for more or less brownish fore legs. Lancet: Figs 106–109. Male (Fig. 103): Head and body entirely black, except more or less for underside of antennae, tegulae, extreme upper posterior edge of pronotum, and subgenital plate. Legs entirely red, except for black coxa and more or less trochanters and trochantelli. One male (DEI-GISHym20617), presumably atypical, has the thorax red and black patterned, exactly as in females. Penis valve: Figs 104–106; note the variability in shape of the distal projections.

Our characterisation of the male of *australis* is based primarily on three specimens from Germany (BC ZSM HYM 04094), Lapland (DEI-GISHym20618), and Japan (DEI-GISHym84982), with identity confirmed by barcoding. Fore wing basally darkened or mostly subhyaline, the antennae black with reddish undersides (or nearly completely pale in the Japanese specimen), and the stigma uniformly dark. The body is completely black, except for the slightly brown tegulae, harpes, and distal edge of sternum 9; and all tibiae completely pale. One further male from Torne Lappmark in the SDEI, and the long series of males from Ukraine, have the same coloration except for mostly subhyaline fore wing. The latter exhibit little variability, except that the tegulae and upper posterior edges of the pronotum may be completely black, or more or less brown, and the antennae usually extensively reddish, but occasionally nearly completely black. The wing veins of the males from Lapland, including the fore wing pterostigma, are, however, darker than the Ukrainian specimens.

Similar species. See key, and notes on male (above, and under *crocea*, below). Compared with *crocea* (Fig. 112), the most obvious differences in the lancet of *australis* (Figs 108–111) are the greater number and smaller size of ctenidia on the annular sutures, smaller distance between each basal and median sawtooth and its spurette, and its less hooked median sawteeth.

Life history. Host plants (in Europe): *Betula pendula*, *pubescens* (Kontuniemi 1960), *pubescens* var. *pumila* (see Specimens examined), *utilis* (Schedl 2010), *Alnus glutinosa*, *incana*, and *viridis* (Kontuniemi 1960, Pschorn-Walcher and Altenhofer 2000), and further *Alnus* species in the East Palaearctic. Larvae solitary, and cryptic (Fig. 88). Boevé (2015) compared the defensive strategy of *australis* and *crocea* larvae. Two overlapping generations in the lowlands. Although males of both European *Hemichroa* species have generally been considered to be rare (e.g., Benson 1958, Smith 1975), males of *australis* are, at least regionally, evidently rather abundant. In a series of 104 specimens collected by Ermolenko in the montane zone of the Ukrainian Carpathians, 92 are males, and 2 of 5 specimens recently collected in the Torne Träsk Region are males. Malaise (1921b) also noted that although males of *australis* are usually extremely rare, three of six specimens which he collected in the Torne Träsk area were males. Perhaps males are more frequent in areas with a cooler climate, which would represent an interesting departure from the usual pattern in Tenthredinoidea of a higher female to male ratio in warmer areas (Benson 1950: 126).

Distribution. Trans-palaearctic from the British Isles, through north and central Europe (Taeger et al. 2006) to Yakutia (Sundukov 2017) and Japan (Smith 1975; see also Specimens examined).

Occurrence in Sweden. Published records: Skåne (Andersson 1962), “this species seems to be widespread throughout Sweden” (Thomson 1871). Material was examined from Skåne, Småland, Östergötland, Bohuslän, Uppland, Västmanland, Jämtland, Lycksele Lappmark, Torne Lappmark.

Specimens examined. Czech Republic: 1 ♀ (ZSM). France: Gironde: 1 ♂ (DEI-GISHym20617), Saucats, 44.65000N, 0.60000W, 16.08.2012, leg. H. Chevin (SDEI). Germany: 17 ♀ (SDEI, ZSM, ZMHB). 1 ♂ (DEI-GISHym31923), Bayern, Dingolfing, Stadtwald, 06.06.1992, leg. Liston (SDEI). 1 ♂ (DEI-GISHym15392), Sachsen, Erzgebirge, Altenberg Umg., 22.07.1985, leg. S. Walter (SDEI). Japan: Honshu: 1 ♂ (DEI-GISHym84982), Omeshidake W, Road 112, 1900 m, 36.62400N, 138.45400E, 22.07.2016, leg. A. Taeger (SDEI). Russia: Respublika Bashkortostan (Baskiria): 1 ♀ (DEI-GISHym31837), Burzyanskaya obl. / Baskir Reserve, 53.16666N, 57.50000E, 30.06.1985, leg. V. M. Ermolenko (HNHM). Primorskiy Krai: 1 ♀, Anisimovka: Gribovka 1 km N, 450 m, 43.12600N, 132.79700E, 18.06.2017, leg. A. Taeger (SDEI). Sweden: Skåne : 1 ♀ (NHRS-HEVA000006494), no exact locality, leg. Boheman (NHRS). 1 ♀, Krankesjön, 55.70000N, 13.46666E, 03.08.1974, leg. H. Andersson (MZLU). Småland: 2 ♀ (NHRS-HEVA000006495–6), no further data (NHRS). 1 ♀ (NHRS-HEVA000006500), no further data (NHRS). Östergötland: 1 ♀ (NHRS-HEVA000006498), no exact locality, leg. Wahlgren (NHRS). Bohuslän: 1 ♀ (NHRS-HEVA000006499), no further data, leg. Boheman (NHRS). Uppland: 1 ♀ (NHRS-HEVA000003425), Frescati, leg. Malaise (NHRS). 1 ♀ (NHRS-HEVA000006502), Ulleråkers sjukhus (Asylen) (NHRS). Västmanland: 1 ♀, Sala kommun, Nötmyran (Västerfärnebo), birches at Islingby, Östermyran, 59.94198N, 16.30944E, 25.10.2003–08.06.2004, leg. SMTP (NHRS). Jämtland: 1 ♀ (NHRS-HEVA000006501), no further data (NHRS). Lycksele Lappmark: 2 ♀ (NHRS-HEVA000006503–4), Sorsele, 29.07.1929 and 05.07.1931, leg. Gaunitz (NHRS). Torne Lappmark: 3 ♀ (NHRS-HEVA000006505, 6507, 6508), Torne Träsk, 04/06.07.1918 and one without date, leg. Malaise (NHRS). 2 ♂ (NHRS-HEVA000006510/12), Abisko, 04/08.07.1918, leg. Malaise (NHRS). 1 ♂ (NHRS-HEVA000006511), Torneträsk, 03.07.1918, leg. Malaise (NHRS). 1 ♂ (NHRS-HEVA000006513), Kummavuopio, 23.07.1923, leg. Bruce (NHRS). 1 ♂ (DEI-GISHym20618), Kiruna nr. airport, 450 m, 67.84000N, 20.35000E, 21.06.2012, leg. Liston & Taeger (SDEI). 2 ♀ (DEI-GISHym15387, 15401), Kiruna nr. airport, 450 m, 67.84000N, 20.35000E, 01.07.2012, leg. Liston & Taeger (SDEI). 1 ♂, Abisko National Park, E10, 390 m, 68.35300N, 18.81500E, 30.06.2012, leg. Liston & Taeger (SDEI). 1 ♀, Abisko 9 km E (Stordalen), 400 m, 68.35000N, 19.03500E, 04.07.2016, leg. Liston & Prous (SDEI). 1 ♀, Abisko 6 km W, 650–900 m, 68.34200N, 18.69100E, 02.07.2016, leg. Liston & Prous (SDEI). 1 ♀, Kiruna, near airport, 450 m, 67.84000N, 20.35000E, 22.06.2016, leg. Liston (SDEI). 1 larva (DEI-GISHym83694), on *Betula pubescens* var. *pumila*, Abisko 9 km E (Stordalen) (Sweden: Norrbottens Län), 400 m, 68.35000N, 19.03500E, 05.08.2017, leg. Liston & Prous (SDEI). Switzerland: 3 ♀ (SDEI, ZSM). Ukraine: 12 ♀, 92 ♂ (HNHM), and: 1 ♀ (DEI-GISHym30203: Para-

type of *H. monticola* Ermolenko), Lvivska Oblast, Slavekogo rajona, Tukhovalsky Pass, 16.08.1957, leg. V. M. Ermolenko (ZISP). 1♀ (DEI-GISHym31836), Ivano-Frankivs'ka Oblast', Csernogora, Pozsizsevszkaja, 26.06.1975, leg. V. M. Ermolenko (HNHM).

Hemichroa crocea (Geoffroy, 1785)

Tenthredo crocea Geoffroy in Fourcroy, 1785: 364. Syntype(s) ♀, lost. Type locality: Paris (France).

Tenthredo rufa Panzer, 1799: 72:2. Syntype(s) ♀, lost. Type locality: Germany. Primary homonym of *Tenthredo rufa* Retzius, 1783.

Hemichroa stigma Stephens, 1835: 56. Syntype(s) ♀, most likely lost. Type locality: Ripley (United Kingdom). Listed in synonymy with *Hemichroa rufa* (Panzer) by Dalla Torre (1894: 283).

Leptocercus nigriceps Thomson, 1871: 78. Holotype ♀, not examined, in MZLU. Type locality: Skåne (Sweden). Synonymy with *crocea* by Lindqvist (1954).

Dineura (Leptocera) unicolor Rudow, 1872: 218. Syntype(s) ♀, most likely lost. Type locality: not given [Germany]. Synonymy by Konow (1897: 259).

Dineura americana Provancher, 1882: 292–293. Holotype ♀, not examined, ULQC. Type locality: Chicoutimi (Canada). Synonymy by Ross (1937: 79).

Nematus ardens Zaddach in Brischke, 1883a: 133–134. Holotype ♀, lost. Type locality: Carolath (Siedlisko, Poland). Listed in synonymy by Konow (1905: 49).

Dineura pallida Ashmead, 1890: 15. Holotype ♀, not examined, in USNM. Type locality: West Cliff, Ca. (USA). Synonymy by Ross (1937: 79).

Hemichroa dyari Rohwer, 1918: 170–171. Holotype ♀, not examined, in USNM. Type locality: Woods Hole, Massachusetts (USA). Synonymy by Ross (1937: 79).

Hemichroa (Hemichroa) orientalis Rohwer, 1921: 108–109. Holotype ♀, not examined, in USNM. Type locality: Kumaon, Ramgark (India). Synonymy by Smith (1975: 298).

Hemichroa (Hemichroa) washingtonia Rohwer & Middleton, 1932: 97–98. Holotype ♀, not examined, in USNM. Type locality: Seattle, Washington (USA). Listed in synonymy by Ross (1937: 79).

Description. Body length: female 5.5–8.5 mm, male 5.5 mm (only one examined). Female (Figs 98, 100): Orange-red. Black are (more or less): labrum, propleuron, mesopleuron, metapleuron, metanotum, ventral part of mesepisternum, abdominal tergum 1, valvula 3. Coxae, trochanters and femora brown, with variable black markings. Tibiae basally pale (whitish), apically dark. Tarsi dark. Lancet: Fig. 112. Male (Fig. 102): Head including antennae, and body black, except more or less for tegulae, pronotum, and parts of abdominal terga and sterna. Legs red, except for darkened coxa, more or less trochanters and trochantelli, metatarsus, and apex of metatibia. Penis valve: Fig. 107.

We have only examined one old male specimen (DEI-GISHym31838), without genetic data, which we think belongs to *crocea*, because of the similarity of its penis

valve to that illustrated by Smith (1975; fig. 4) as *crocea*, and differences in the penis valves of *australis* identified by us, using sequence data. This *crocea* male has its abdomen and parts of the mesoscutum extensively yellow, but completely black antennae, as well as darkened metatarsus and metatibia apex. However, the original descriptions of the males of *Hemichroa dyari*, *pallida* and *washingtonia* (Rohwer 1918, Rohwer and Middleton 1932), all of which are currently treated as synonyms of *H. crocea*, indicate that body colouration is variable, and can be as dark as in male *australis*. The metatibia and metatarsus may apparently also be dark or pale, as respectively described by Rohwer (1918) for males of *dyari* and *pallida*. On the other hand, the descriptions of North American *crocea* males suggest that the antennae are completely dark, as described by Benson (1958) for European males.

Similar species. See key and notes on *australis*, above.

Life history. Host plants: *Alnus glutinosa*, *incana*, *viridis*, *Betula pendula*, and sometimes *Corylus avellana* (Pschorn-Walcher and Altenhofer 2000). *Salix* is mentioned repeatedly in various works as a host, but no unambiguous original record of feeding by larvae on *Salix* has been located. Larvae gregarious, and brightly coloured (Fig. 87). Boevé (2015) compared the defensive strategy of *crocea* and *australis* larvae. Usually two overlapping generations in the lowlands (Hopping 1937, Pschorn-Walcher and Altenhofer 2000), but mainly univoltine at subalpine levels (Kriegl 1964). Whereas the subalpine populations are entirely parthenogenetic (Kriegl 1964), approximately 3% males were reared in northern Germany (Pschorn-Walcher and Altenhofer 2000).

Distribution. Found widely in the Holarctic, from the British Isles, through central and northern Europe (Taeger et al. 2006), to the Russian Far East (Sundukov 2017), Japan, northern India (Smith 1975), reaching into the Oriental Region in China (see Specimens examined), and transcontinental in North America (Smith 1975). According to Ross (1932), *Hemichroa crocea* was probably introduced to North America, but Kriegl (1964) concluded that the species occurs there naturally, because a similar assemblage of parasitoid species is found in Europe and North America.

Occurrence in Sweden. Published records: Skåne (Andersson 1962), “sparingly, but distributed from Skåne to Lapland” (Thomson 1871). Material was examined from Skåne, Småland, Öland, Gotska Sandön, Södermanland, Dalarna, Lappmark.

Specimens examined. Canada: Quebec: 1♀ (DEI-GISHym15340), Gatineau Park 1.8km N Eardley, Juniperus virginiana stand, 60–80 m, 45.56667N, 76.09139W, 31.08.–07.09.2012, leg. CNC Hymenoptera Team (SDEI). China: Sichuan: 1♀ (DEI-GISHym17831), Gongga Shan, 2200 m, 29.59700N, 102.05000E, 29.06.2009, leg. Blank, Liston & Taeger (SDEI). Germany: Baden-Württemberg: 1♀ (SDEI). Bayern: 4♀ (BC ZSM HYM 04090, 04091, 16633, 16740) (ZSM). Berlin: 1♀ (SDEI). Brandenburg: 1♀ (DEI-GISHym19401) (SDEI). Hessen: 1♀ (DEI-GISHym17970) (SDEI). Mecklenburg-Vorpommern: 1♀ (DEI-GISHym19402) (SDEI). 1♂ (DEI-GISHym31838), Kalkhorst near Neustrelitz, 53.31666N, 13.06666E, 27.06.1884, leg. F. W. Konow (SDEI). Nordrhein-Westfalen: 1♀ (SDEI). Sachsen: 1♀ (SDEI). Portugal: Viana do Castelo: 1♀ (DEI-GISHym19668), Monção 10 km E, 30 m, 42.08658N, 8.36285W, 09.05.2012, leg. Blank, Jacobs, Liston & Taeger (SDEI). Sweden: Skåne : 1♀ (NHRS-HEVA000006485), leg. Boheman (NHRS). Småland:

1♀ (NHRS-HEVA000006489), Kalmar, 05.1919, leg. Hedgren (NHRS). Öland: 1♀ (NHRS-HEVA000003424), Stora Rör, 08.08.1941, leg. Wieslander (NHRS). Gotska Sandön: 1♀ (NHRS-HEVA000006487), leg. Jansson (NHRS). Södermanland: 1♀ (NHRS-HEVA000006488), Drevviken, leg. Smidt (NHRS). Dalarna: 1♀ (NHRS-HEVA000006486), “Dalecarlia alpina”, leg. Boheman (NHRS). Middle and southern Lapland: 1♀ (NHRS-HEVA000006491), “Lapponia meridionalis”, leg. Boheman (NHRS). 1♀ (NHRS-HEVA000006492), “Lapponia intermedia”, leg. unknown (NHRS).

Hoplocampa Hartig, 1837

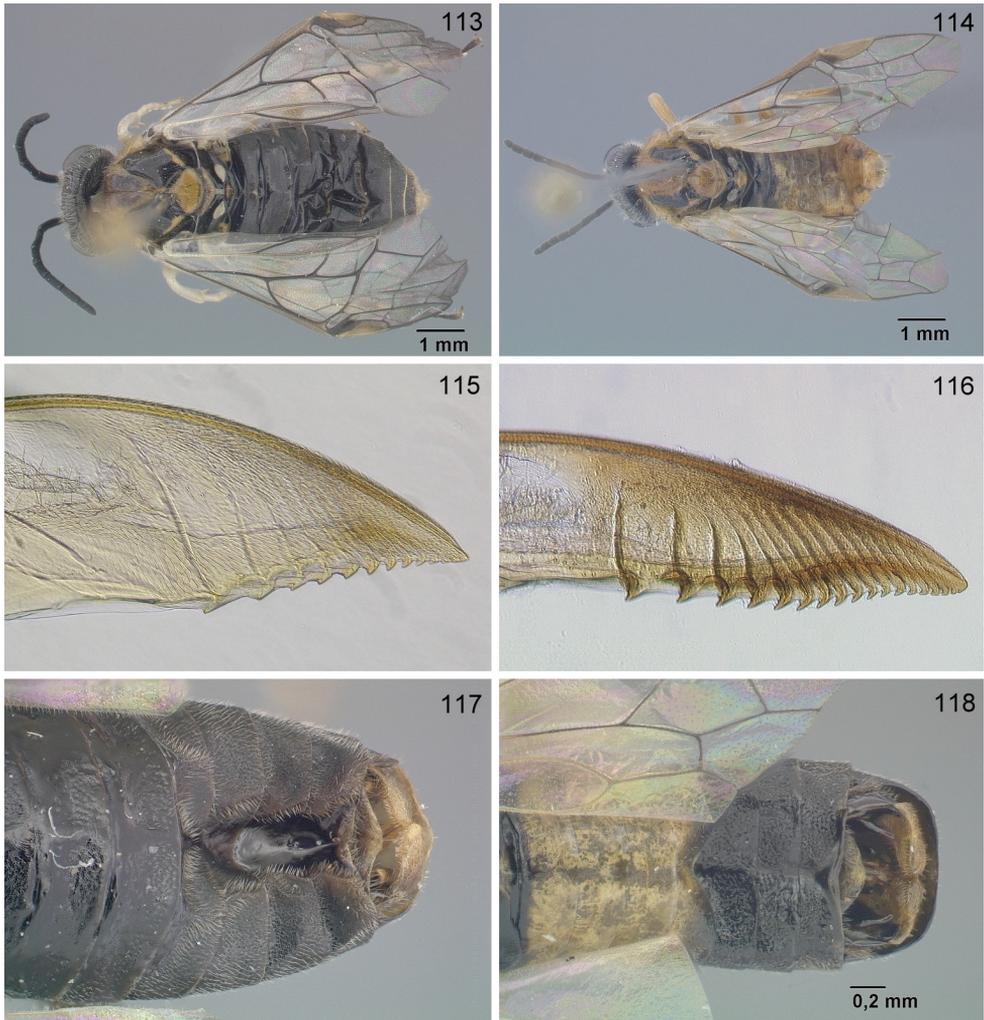
See key and species treatments in Liston et al. (2019c).

Mesoneura Hartig, 1837

Only two species are known from the West Palaearctic (Liston 2012), and only *M. opaca* occurs in north-west Europe. The nominal taxon described as *Tenthredo* (*Selandria*) *umbrosa* Eversmann, 1847 was treated in several works (e.g., Dalla Torre 1894, Konow 1905, Taeger et al. 2010) as a third, valid West Palaearctic *Mesoneura* species, but examination of the type revealed it to be a male specimen close to *Euura clitellata* (Serville, 1823).

Key to West Palaearctic species, based on Liston (2012):

- | | | |
|------|---|------------------------------|
| 1 | a Females | 2 |
| – | aa Males | 3 |
| 2(1) | a Upper side of abdomen mainly black; at least with a continuous black dorsal vitta (Fig. 113); b Lancet with 14–15 annuli; serrulae, particularly basal ones, rather flat (Fig. 115)..... | <i>*Mesoneura opaca</i> ♀ |
| – | aa Upper side of abdomen mainly yellow apart from black 1 st tergum and some black lateral spots (Fig. 114); bb Lancet with ca. 20 annuli; serrulae prominent, hooked (Fig. 116)..... | <i>*Mesoneura lanigera</i> ♀ |
| 3(1) | a Abdominal terga 5–8 with a deep, sharply delimited medial depression edged with a row of long setae (Fig. 117); b All terga mainly black, except for more or less pale extreme apical margins; c Apical margin of sternum 9 medially slightly produced (Fig. 117); d Length 6.5–8.0 mm..... | <i>Mesoneura opaca</i> ♂ |
| – | aa Abdominal terga 5–8 with at most a shallow, ill-defined medial depression, without row of modified setae along edge (Fig. 118); bb Terga 2–4 entirely yellow-brown (Fig. 118); cc Apical margin of sternum 9 truncate or medially even slightly emarginate (Fig. 118); dd Length 5.5–6.5 mm..... | <i>Mesoneura lanigera</i> ♂ |



Figures 113–118. *Mesoneura* **113** *opaca* ♀ DEI-GISHym17936 **114** *lanigera* ♀ DEI-GISHym17933 **115** *opaca* DEI-GISHym17935 lamnium of lancet **116** *lanigera* DEI-GISHym17933 lamnium of lancet **117** *opaca* ♂ DEI-GISHym17937 abdomen apex **118** *lanigera* ♂ DEI-GISHym17934 abdomen apex.

Mesoneura opaca (Fabricius, 1775)

Tenthredo opaca Fabricius, 1775: 323. Syntype(s) ♀, Suecia, lectotype ♀ here designated (ZMUC-GISHym1061), in ZMUC. Type locality: Sweden. Remarks. Lectotype labeled “opaca”, “ZMUC-GISHym1061”. Right antennal flagellomeres 6–7 and fore tarsomere 5 missing. In the lectotype the distal section of the posterior anal vein (2A) is absent on the hind wing and thus the anal cell (A) widely open distally. Otherwise it corresponds with the current concept of *Mesoneura opaca*,

which is quite variable in coloration. This specimen has the median mesoscutal lobes red on both the medial and the lateral edges, and the mesoscutellum black.

Tenthredo (Allantus) verna Klug, 1816: 55–56. Syntypes ♀, Berlin, in ZMHB. Type locality: Berlin (Germany). Synonymy with *Tenthredo opaca* Fabricius, 1775 by Klug (1819: 81). Remarks. In ZMHB are 7 ♀ with the collection catalog number 13747 (GBIF-GISHym2504 to 2510). This number means: [identification:] *Tenthredo opaca* Fabr.; [specimens:] 8.; [locality, collector:] German. Kl.; Dania - Drewsen. Therefore, these specimens were collected in Germany or Denmark, and their unequivocal identification as syntypes (from Germany) is impossible. Images of GBIF-GISHym2504: <https://doi.org/10.6084/m9.figshare.4774588>.

Tenthredo punctigera Serville, 1823: 103. Lectotype ♀, designated by Lacourt (2000: 103) not examined, in MNHN. Type locality: Paris (France). Synonymy (for *Tenthredo punctigera* Lepeletier, 1823) with *Dineura opaca* (Fabricius, 1775) by Hartig (1837: 229).

Tenthredo punctigera Lepeletier, 1823: 110. Lectotype ♀, designated by Lacourt (2000: 103) not examined, in MNHN. Type locality: Paris (France). Synonymy with *Dineura opaca* (Fabricius, 1775) by Hartig (1837: 229). Primary homonym of *Tenthredo punctigera* Serville, 1823.

Selandria biloba Stephens, 1835: 54. Syntype(s) ♀, not examined, in BMNH. Type locality: London (United Kingdom). Synonymy by Kirby (1882: 157).

Dineura (Mesoneura) pallipes Hartig, 1837: 229. Syntype(s) ♀, most likely lost. Type locality: Harz (Germany). Synonymy by Cameron (1875: 252). Remarks. There are three females under *Dineura pallipes* Hartig in the collection of Saxesen, one labelled “Hartig!”. However, these specimens do not fit Hartig’s description.

Dineura dorsalis Förster, 1844: 263. Holotype ♀, most likely lost. Type locality: Aachen (Germany). Synonymy by Cameron (1875: 252).

Mesoneura opaca var. *nigerrima* Enslin, 1914: 271. Syntype(s) ♀, no data, lectotype ♀ here designated (GBIF-GISHym3158, images: <https://doi.org/10.6084/m9.figshare.4775329>), in ZSM. Type locality: Südtirol (Italy).

Mesoneura opaca var. *lucida* Enslin, 1914: 271. Syntype(s) ♀, no data, most likely lost. Type locality: Europe.

Mesoneura opaca var. *obscuriventris* Enslin, 1914: 271. Syntype(s) ♀, no data, lectotype ♀ here designated (GBIF-GISHym3160, images: <https://doi.org/10.6084/m9.figshare.4775341>), in ZSM. Type locality: Erlangen (Germany).

Description. Body length: female 5.5–9.0 mm, male 6.5–8.0 mm. Female (Fig. 113): head including antenna black, except for white clypeus and labrum, and sometimes brown flecks on interantennal area / just dorsal of toruli / lower outer orbits. Thorax black. In darkest specimens only pronotum and tegula pale. Palest specimens with yellow-brown whole median mesoscutal lobe, parts of lateral lobes, mesoscutellum and appendage, upper mesepisternum, and parts of metanotum. Fore wing pterostigma completely pale, to pale in middle with darkened edges. Legs pale, with coxae, femora

and apical tarsomeres more or less darkened. Abdomen from completely black, to completely pale on underside with lateral parts of terga more or less pale, and pale tergum 10 and cerci. Lancet: Fig. 115. Male (only four examined): Black; only ventral parts of clypeus pale, labrum pale to nearly completely dark. Thorax at most with pale edges of pronotum, and more or less tegulae. Leg colour similar to female, but darkest males with apex of metatibia darkened, and palest with tarsi completely pale. Abdomen black except for brownish narrow distal margin of sternum 9 and more or less harpes, and sometimes around the depressed parts of terga 5–8. Penis valve: Liston (2012: fig. 4) [not distinguishable from that of *lanigera*].

Similar species. In the West Palearctic, only *Mesoneura lanigera* Benson, 1954 (south-east Europe, Transcaucasus and Cyprus) could be mistaken for *opaca*: see key.

Life history. Host plants: *Quercus* species, including *robur* (Pschorn-Walcher and Altenhofer 2000), *pubescens*, and *rubra* (Liston 2011). Univoltine species. Oviposition in the leaf midrib or side-veins; maximum two eggs per leaf. Larva (Fig. 69) solitary. Normally entirely parthenogenetic in most of central and northern Europe, where males have so far only been found in the Netherlands (Ad Mol, pers. comm.), but males are apparently more frequent in Greece (Liston 2012, Liston et al. 2015).

Distribution. Widespread in central and southern Europe, from the British Isles, north to Finland (Taeger et al. 2006) and southern Norway (Kiaer 1892); Caucasus (Sundukov 2017); North Africa (Morocco, Middle Atlas: see below).

Occurrence in Sweden. Based on published records: Skåne, Småland (Thomson 1871). Material was examined from Skåne, Halland, Småland, Uppland.

Specimens examined. Bulgaria: 10♀ (SDEI). Germany: 72♀ (SDEI, ZMHB, ZSM). Greece: 4♀ (including DEI-GISHym17935 and 17936), 4♂ (including DEI-GISHym17937) (SDEI). Morocco: Meknes-Tafilelet Region: 1♀, Khénifra 16 km E, 1500 m, 32.93200N, 5.49900W, 18.04.2015, leg. Liston & Prous (SDEI). 3♀, Ifrane 7 km NW, 1590 m, 33.55200N, 5.17500W, 20.04.2015, leg. Liston & Prous (SDEI). Sweden: Skåne: 1♀, Skåralid, 25.05.1965, leg. H. Andersson (MZLU). Halland: 1♀, Kungälv kommun, Särö Västerskog, 57.50521N, 11.92572E, 28.04.–14.05.2004, leg. SMTP (NHRS). Småland: 2♀ (NHRS-HEVA000006560 & 6562), no exact locality or date, leg. Boheman (NHRS). Uppland: 1♀ (NHRS-HEVA000003430), Djurgården, 11.05.1937, leg. R. Malaise (NHRS). 1♀, Uppsala kommun, Ekdalens naturreservat, southern hillside, 59.97153N, 18.35495E, 03.–17.05.2004, SMTP (NHRS). 1♀ (NHRS-HEVA000006561), Eknäs, Värmdö, 15.05.1920, leg. Unknown (NHRS).

Nematinus Rohwer, 1911

No reliable key or species treatments are available to date.

Nematus Panzer, 1801

No reliable key or species treatments are available to date.

Prous et al. (2014) radically altered the circumscription of *Nematus*: see also under *Euura*, above. The following synonyms of *Nematus* have been in recent use as valid: *Craesus* Leach, 1817 [= *Croesus*, misspelling], *Hypolaepus* W.F. Kirby, 1882, and *Paranematus* Zinovjev, 1978. Note that most of the species placed in *Hypolaepus* by Lacourt (1999) are now placed in *Euura*.

Currently, fewer than 20 European taxa are considered to be *Nematus* species: *Nematus lucidus* Panzer 1801 (type species), *N. princeps* Zaddach, 1876, *N. umbratus* Thomson, 1871 (= *N. lucens*), all former *Craesus*, and all former *Paranematus*. *Nesci-neura noblecourti* Lacourt, 2006 also may belong to *Nematus*.

***Neodineura* Taeger, 1989**

Neodineura Taeger, 1989: 150–151. Type species: *Tenthredo* (*Allantus*) *arquata* Klug, 1816 [= *Neodineura arquata*], by original designation and the only known species.

Description. Body stocky, similar to *Mesoneura*. Fore wing radial cell divided. Radial cross vein (2r-rs) arises near the apex of stigma and meets the cell 1Rs2; basalis (M) and 1st medial cross vein (1m-cu) strongly converging; M clearly bent only basally; intercostal crossvein (Sc) lying before the junction of M with the Subcosta (Sc+R+Rs); 1st and 2nd medial cross vein (1m-cu and 2m-cu) join the 2nd cubital cell; submedial crossvein (cu-a) meeting medius (Cul) and brachius (1A) almost perpendicularly; anal cell stalked; humeral vein (3A) straight. Hind wing with 2 middle cells, anal cell with long stalk. Inner eye margins slightly converging downwards; distance between the lower eye corners little longer than the maximum eye diameter; clypeus long, shallowly emarginate, in the middle approx. as long as the diameter of a torulus or ca. 1.5 times as long as the distance between the antennal sockets; labrum weakly emarginate on anterior edge; malar space just under half as long as the anterior ocellus; mandibles almost symmetrical, with subapical tooth, in lateral view tapered approximately evenly to the tip. Antenna approx. twice as long as width of head; scape and pedicel distinctly wider than long. Prepectus separated from mesepisternum by a fine line; inner spur of the fore tibia apically divided. Claws bifid, without basal thickening; inner and outer tooth approx. the same thickness, inner tooth slightly shorter.

***Neodineura arquata* (Klug, 1816)**

Tenthredo (*Allantus*) *arquata* Klug, 1816: 51. Female (existence of syntypes must be assumed). Type locality: Deutschland. Type specimens lost (Enslin 1914, Taeger 1989). See Taeger (1989) for additional nomenclatural history.

Description. This is based on a translation of Taeger (1989), augmented with data gained from examination of specimens which have only recently become available. Body length: female 8.0 mm, male 6.5 mm. Female (Fig. 119) and male (Fig. 120) are

similar in colour, apart from the mesopleura: upper mesepisternum pale in female, entirely dark in male. Head and antenna black, except for pale palps and labrum. Thorax dorsally black, with pale tegula and more or less pronotum. Legs entirely pale except more or less for tarsomeres. Wing venation entirely pale brown. Abdomen yellow except more or less for tergum 1. Antennomere 3 little shorter than 4. Postocellar field ca. twice as wide as long; ocellus diameter : POL : OOL = 1 : 1.7 : 2.0; frontal field enclosed by indistinct bulges; supra-antennal groove indistinct; head weakly punctured and shiny; frontal field partly finely wrinkled; thorax slightly more strongly punctured than head. Mesepisternum shiny, with indistinct punctures, evenly covered with rather dense, pale pubescence. Legs relatively thick: femora 3.5 times as long as wide, 0.66 times as long as the tibia; tibia 6.5 times as long as wide and 1.2 times as long as the metatarsus; inner spur of the metatibia nearly as long as the apical width of tibia.

Female: upper half of mesepisternum pale, lower half black. Pronotum, mesepimeron, and metapleura entirely pale. Propleuron edged with black. Head behind eyes subparallel. Antennomere 8 approx. three times as long as wide. Lancet: Fig. 121.

Male: mesepisternum completely black. Pronotum ventrally black. Mesepimeron and metapleura partly pale. Propleuron completely black. Anterior of abdominal tergum 2 also black. Fore wing length 6.5 mm; antennomere 8 3.5 times as long as wide; head behind the eyes clearly narrowed; tergite 8 without special structures; subgenital plate apically rounded. Penis valve: Fig. 122.

Similar species. In the West Palaearctic, *Mesoneura opaca* and *lanigera* are superficially similar in habitus to *Neodineura arquata*.

Life history. Unknown.

Distribution. Only known from Germany, Switzerland (Taeger et al. 2006), the Czech Republic (Beneš and Holuša 2015), and the Russian Caucasus (see below). We are only aware of the existence of four extant collection specimens: three females and one male. Taeger (1989) interpreted the handwritten label data on the only known male (SDEI) as “Sandbg. [Sandberg] 11.V.91”, and thought it likely that the locality was one of several of that name within the then German-speaking territories. Alternatively, it could refer to “Sonderburg” [German name for the Danish island Sønderborg], although the second letter on the label does look more like an “a” than an “o”. Konow received many sawfly specimens, some still in the Konow Collection at the SDEI, from W. Wüstnei, who resided at Sonderburg, and collected from around the late 1880’s to the early 1900’s.

Occurrence in Sweden. No records.

Material. (to the best of our knowledge, the following are the only known extant collection specimens of this species):

Czech Republic [not examined: data from Beneš and Holuša 2015]: Moravia: 1♀, Stolařka Mt., Lhotka, 700 m, 21.05.1998, leg. J. Holuša (NMPC). Germany, or Denmark?: 1♂ (DEI-GISHym54879 / pr.239.(AZ), examined), “Sandbg.” or “Sondbg.”, 11.05.1891 (SDEI). Russia: 1♀ (DEI-GISHym15240, examined), Teberda Reserve, Alibek, 2000 m, 43.32000N, 41.51000E, 22.06.1972, leg. V. Ermolenko (HNHM). Switzerland: 1♀ (DEI-GISHym19777, examined), Solothurn, Rickenbach, 47.34987N, 7.85025E, 560 m, 24.04.1994, leg. Flücker (SDEI).



Figures 119–122. *Neodineura arquata* **119** DEI-GISHym15240 ♀ dorsal **120** DEI-GISHym54879 ♂ lateral **121** DEI-GISHym15240 lancet **122** DEI-GISHym54879 penis valve. Scale bar: 2 mm.

Nescianeura Lacourt, 2006

Notes. One species, *Nescianeura noblecourti* Lacourt, 2006, only known from three specimens collected in north-east France and south-west Germany. Females and males, which are similarly coloured, are easily recognised by their distinctive colour pattern (Figs 123–126). Penis valve: Fig. 127. Perhaps a *Euura* or *Nematus* species. See further: Lacourt (2006) and Jansen (2017).

Specimens examined. France: Holotype ♀ (DEI-GISHym20818), Lorraine, Saint-Maurice-sur-Moselle, 26.05.1995, leg. Bernard (MNHN). Germany: 1♀ (DEI-GISHym20932), 1♂ (DEI-GISHym20933), Baden-Württemberg, Grenzach-Wyhlen, Ruschbachtal, 355m, 26.04.–10.05.2008, Malaise trap, leg. Doczkal & Ssymank (SDEI).

Platycampus Schiødte, 1839

Notes. Two species have been considered to be represented in the West Palaearctic fauna (Taeger et al. 2010): *luridiventris* (see below), and *obscuripes* (Konow, 1896). The latter was described from two females collected in the St Gotthard area, Switzerland. Konow (1896) stated in the original description that *obscuripes* differed from *luridiventris* in its [translated from German] “much smaller head, the apically more weakly emarginate clypeus, and the somewhat shorter third cubital cell, as well as the



Figures 123–127. *Nescianaura noblecourti* **123, 125** ♀, holotype, France. **124, 126** ♂ DEI-GISHym20933, Germany **127** DEI-GISHym20933 penis valve. Scale bar 1 mm (**123, 125**), 2 mm (**124, 126**).

dark colour of the body and the legs”. Only fragments of one of these specimens now exist. Conde (1937) proposed the synonymy of *obscuripes* with *luridiventris*, basing his concept of *obscuripes* on two female specimens from Piedmont, Italy, leg. Dodero (name of collection not mentioned), and concluded that it is only a dark, alpine form of *luridiventris*. A further female which may belong to *obscuripes*, because it has largely black metafemora, was collected in 1954 in Oberstdorf, Bavaria, by E. Enslin (Manfred Kraus Private Collection). Finally, Weiffenbach (1975) stated that he reared a female *obscuripes* collected on *Alnus viridis*, from Montafon, western Austria, 1800 m. Normally coloured specimens of *luridiventris* are known to occur on *Alnus viridis*, at lower altitudes, in Central Europe (see below). The status of *obscuripes* requires re-assessment, preferably including the use of genetic data.

Platycampus luridiventris (Fallén, 1808)

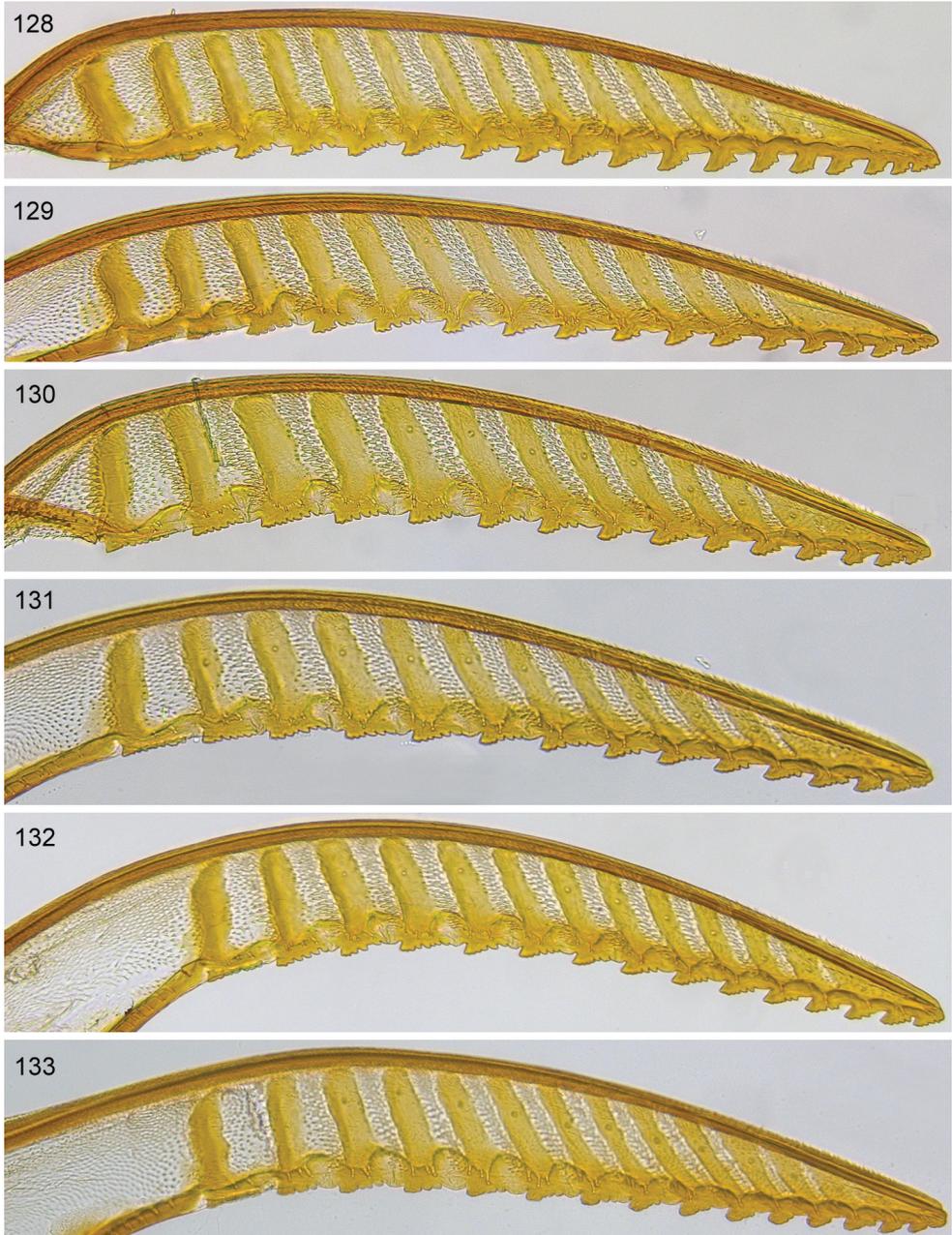
Tenthredo alnicola Bechstein & Scharfenberg, 1805: 867. Syntypes, larvae, lost. Type locality: Germany. Synonymy with *Leptopus luridiventris* by Brischke (1883b: 216). Nomen oblitum after Blank et al. (2009: 47).

- Tenthredo luridiventris* Fallén, 1808: 115–116. Syntype(s) ♀, not examined (revised by Lindqvist 1956: 9), in MZLU. Type locality: Sweden. Nomen protectum after Blank et al. (2009: 47).
- Nematus hypogastricus* Hartig, 1837: 184. Syntypes ♀, Deutschland, lectotype ♀ here designated, (GBIF-GISHym3464, images: <https://doi.org/10.6084/m9.figshare.4788550>), in ZSM. Type locality: Germany. Paralectotype ♀ (GBIF-GISHym3465), in ZSM. Listed in synonymy with *Leptopus luridiventris* by Thomson (1871: 78).
- Nematus alnivorus* Hartig, 1840: 27. Syntypes ♀, Norddeutschland, lectotype ♀ here designated (GBIF-GISHym4675) in NFGV. Type locality: Harz, Roßtrappe (Germany). Paralectotype 1♀, in FMNH. Synonymy by Lindqvist (1965: 31–32).
- Nematus rufipes* Tischbein, 1846: 77. Syntypes ♂♀(?), lost. Type locality: Eutin (Germany). Listed in synonymy with *Leptopus luridiventris* by Konow (1905: 78).
- Leptopus rufipes* Förster, 1854: 276–277. Syntypes ♂, Aachen, lectotype ♂ here designated, (GBIF-GISHym3468, images: <https://doi.org/10.6084/m9.figshare.4788580>), in ZSM. Type locality: Aachen (Germany). Paratype ♂ (GBIF-GISHym3469), in ZSM. Synonymy with *Leptopus luridiventris* by Brischke (1883b: 216).
- Nematus protensus* Förster, 1854: 322–323. Syntype(s) ♀, Aachen, lectotype ♀ here designated, (GBIF-GISHym3467, images: <https://doi.org/10.6084/m9.figshare.4788595>), in ZSM. Type locality: Aachen (Germany).
- Camponiscus Healeai* [sic!] Newman, 1869: 215–217. Syntypes ♂♀, larvae, lost. Type locality: United Kingdom. Synonymy with *Tenthredo luridiventris* by Cameron (1873: 84).
- Nematus Tischbeini* [sic!] André, 1880: 120. Replacement name for *Nematus rufipes* Tischbein, 1846.
- Nematus Fennicus* [sic!] André, 1880: 133. Syntype(s) ♀, deposition unknown. Type locality: Finland. Synonymy by Forsius (1920: 111).
- Nematus alnicola* Zaddach in Brischke, 1883b: 188–189. Holotype ♀, “wohl im westlichen Deutschland”, lost. Type locality: Germany(?). Synonymy with *Leptopus luridiventris* by Brischke (1883b: 216). Secondary homonym of *Tenthredo alnicola* Bechstein & Scharfenberg, 1805.
- Nematus cellularis* Brischke, 1884: 138–139. Syntypes ♂♀, Danzig, lost. Type locality: Gdansk (Poland). Primary homonym of *Nematus cellularis* Dahlbom, 1836. Synonymy with *Leptocercus luridiventris* by Konow (1901: 89).
- Platycampus luridiventris* var. *pleuritica* Enslin, 1915: 322. Syntype(s) ♀, no data, lectotype ♀ here designated (GBIF-GISHym3466, images: <https://doi.org/10.6084/m9.figshare.4788727>) in ZSM. Type locality: Lisieux (France).

Taxonomy. W. Heitland, H. Pschorn-Walcher and J. Herbst studied European populations of *P. luridiventris* feeding on *Alnus glutinosa*, *incana*, and *viridis*. They found the populations on each host to be genetically segregated (Herbst and Heitland 1994), and that the different hosts correlated with differences in behaviour (Heitland and Pschorn-Walcher 2005), and partly in the morphology of larvae (Heitland and Pschorn-Walcher 1992): setae on the head and body of larvae from *glutinosa* tended to be shorter than of

those from *incana*, but setae of larvae from *viridis* usually did not differ from those on *glutinosa*. Our genetic data based on sequences of four genes contradicts, at least partly, the results of Herbst and Heitland (1994). Although six sequenced larvae collected in three different localities (Lower Austria) from three different *Alnus* species do segregate based on mitochondrial COI (1078 bp) into three clusters according to the host plant and locality (maximum distance 2.2%), the nuclear sequences (NaK, POL2, TPI: 5017 bp including introns) are practically identical (only four variable / heterozygous positions, giving a maximal pairwise distance of 0.08%), so that the tree structure for *P. luridiventris* on Fig. 1 is entirely determined by COI. For comparison, nuclear divergence within most other species of Nematinae (based on heterozygous females) is larger, on average 0.2% or up to 1%. In addition, COI sequences of two specimens reared from *A. incana* from Abisko (DEI-GISHym21133, DEI-GISHym21134) are identical to two larvae collected from *A. glutinosa* from Lower Austria (DEI-GISHym21496, DEI-GISHym21497). Since different food plant species can affect gene expression differently in feeding larvae (Yu et al. 2016, Orsucci et al. 2018, Okamura et al. 2019), one can speculate that the allozyme analyses by Herbst and Heitland (1994) were influenced more by differences in the expression of the studied proteins (preferential expression of certain alleles or isoforms) than differences in genetics. Morphologically, we noticed conspicuous differences in the overall shape and spacing of the sawteeth, particularly the apical ones, between the reared Swedish specimens (Figs 128–129) and a German specimen belonging to the other barcoding cluster (Fig. 132). However, examination of further specimens revealed wide variability in the shape and spacing of the sawteeth, with several intermediates (e.g., Figs 130–131), so that finally no clear morphological separation of two groups seemed possible. Perhaps this variability is mainly correlated with geographical occurrence, with a tendency in northern specimens to shorter, more projecting teeth: the lancets of two Abisko specimens (Figs 128–129) have the most clearly projecting and shortest sawteeth (with correspondingly long distances between them), while a specimen from southern Sweden (Småland) has long and flat teeth (more closely spaced) (Fig. 131), and a specimen from Central Sweden is intermediate with regard to the shape of the teeth, although they are widely spaced (Fig. 130). In these examples, the differences are not caused by wear of the saw teeth, because the outlines of the teeth are angular and the denticles are clearly differentiated. A highly worn lancet has rounded edges of the teeth, and the denticles are no longer clearly discernible (Fig. 133). Note that apparent differences in the overall curvature of the illustrated lancets are the result of preparation: each annulus of the lamnium can move slightly, relative to its neighbours, and slight differences in the curvature of the whole lamnium are thus mostly artefacts resulting from preparation. In the light of the foregoing considerations, we conclude that although the three segregates could perhaps be considered to be host plant races [“foodplant races”], as already suggested by Heitland and Pschorn-Walcher (2005), they should certainly not be accorded a formal nomenclatural status.

Description. Body length: female 5.0–7.0 mm, male 4.5–6.0 mm. Female: head black except for palps, and more or less labrum, underside of antennal flagellum, and



Figures 128–133. *Playcampus luridiventris*, lancets, variability and wear of teeth **128** DEI-GISHym21133, Sweden, Torne Lappmark **129** DEI-GISHym21134, Sweden, Torne Lappmark **130** DEI-GISHym31937, Sweden, Ångermanland **131** DEI-GISHym31938, Sweden, Småland **132** DEI-GISHym11313, Germany, Mecklenburg-Vorpommern **133** DEI-GISHym31936, Germany, Mecklenburg-Vorpommern, teeth worn.

sometimes more or less scape and pedicel. Thorax black, except for yellow tegula and more or less posteriodorsal edges of pronotum. Sometimes lateral edges of median mesoscutal lobe, and upper mesepisternum pale. Legs pale (orange), with dark metatarsus and apex of metatibia, and more or less dark bases of coxae. Wing venation mostly brown, with centre of fore wing stigma paler. Cerci pale; rest of abdomen from completely black except for obscurely brown area of hypopygium, to all sterna bright yellow, sometimes also with yellow on downturned lateral edges of terga. One reared female from Abisko has dorsal parts of terga 2–4 pale. Variability in the shape of the teeth of the lancet is considerable (Figs 128–133): see also under Taxonomy above. Male: colour similar to female, but pronotum entirely black. Sternum 9 black to pale. Harpes more or less pale.

Similar species. If the nearly complete loop formed by the curved up base of fore wing vein 2A+3A in *Platycampus* is overlooked, then it might be mistaken for *Stauronematus platycerus*, which is similarly coloured and also has bifid claws (but with an additional basal lobe not found in *Platycampus*), or perhaps a *Pristiphora* species.

Life history. Host plants: *Alnus glutinosa*, *incana*, and *viridis* (Heitland and Pschorn-Walcher 1992). Mentions by Lorenz and Kraus (1957) of *Betula*, *Corylus avellana* and *Rubus* as hosts of *luridiventris* are likely to have been based on misidentifications (Zinovjev 1986, Heitland and Pschorn-Walcher 1992). A strictly univoltine species, although some populations exhibit polymodal emergence patterns. Correlated with its highly distinctive larval morphology (Figs 72–73) compared to other nematine genera (Boevé and Angeli 2010), *Platycampus luridiventris* has many peculiar behavioural traits, such as the extremely long time, of approximately three months, taken by the larva to mature (Heitland and Pschorn-Walcher 2005). Oviposition is into the leaf petiole or midrib, with a maximum of three eggs per leaf. The larva is crepuscular according to Heitland and Pschorn-Walcher (2005), and feeds only for very short periods, making holes in the leaf blade, and during the day is normally found immobile on the leaf underside, often in an angle between the midrib and a lateral vein. Sex ratio appears to be normal for netted specimens, i.e., males about as abundant as females, but is heavily skewed towards males in material collected with Malaise traps.

Distribution. Widespread in Europe, from the British Isles to the Balkans, and north to Norway and Finland (Taeger et al. 2006). Earlier published records of *luridiventris* from the East Palaearctic and Oriental Realms, such as by Benson (1963) from Sichuan, China, probably often refer to other species (Zinovjev 1986). For Russia, Sundukov (2017) lists only European areas and the Ural as definite areas of occurrence.

Occurrence in Sweden. Published records: Thomson (1871) wrote “not rare, throughout Sweden”. Material examined from Skåne, Småland, Östergötland, Västergötland, Bohuslän, Södermanland, Uppland, Norrbotten, Torne Lappmark.

Specimens examined. Estonia: 3♀, 1♂ (SDEI, TUZ). Finland: 1♂ (SDEI). France: 1♀, 1♂ (SDEI). Germany: over 100♀ and 150♂ (SDEI, ZMHB, ZSM), including 1♀ (DEI-GISHym11313), Mecklenburg-Vorpommern, Wrangelsburg 16 km SE Greifswald, 54.01611N, 13.59972E, 07.05.2011, leg. H.-J. Jacobs (SDEI); 1♀ (DEI-GISHym31936), Mecklenburg-Vorpommern, Ventschow, 53.78000N, 11.57000E, 09.06.2012, leg. H.-J. Jacobs (SDEI). Poland: 1♀ (SDEI). Sweden: Skåne: 1♂, Sim-

rishamns kommun, Stenshuvuds nationalpark, Stenshuvud-Krivarboden, 55.66035N, 14.27561E, 06–20.08.2004, leg. SMTP (NHRS). 1 specimen, Bökeberg (NHRS). Småland: 1♀ (DEI-GISHym31938), 1♂ (DEI-GISHym31112), Hultsfred, Kloster Gård, 100 m, 57.49700N, 15.87100E, 31.05.2013, leg. Liston, Prous & Taeger (SDEI). 9♀, 2♂, Nybro kommun, Bäckebo, Grytsjöns naturreservat, 56.93148N, 16.08550E, 18.05.–16.06.2006, leg. SMTP (NHRS). 9 specimens (NHRS). Östergötland: 1♂, Ödeshögs kommun, Omberg, Storpissan, 58.33500N, 14.65521E, 28.05–05.07.2005, leg. SMTP (NHRS). Västergötland: 1 specimen (NHRS). 4 specimens (NHRS). Bohuslän: 1 specimen (NHRS). Södermanland: 1 specimen (NHRS). Uppland: 1 specimen (NHRS). Ångermanland: 1♀ (DEI-GISHym31937), Ramvik, 62.87200N, 17.85800E, 04.06.2013, leg. Liston, Prous & Taeger (SDEI). Norrbotten: 1♂ (DEI-GISHym20975), Pajala 8 km NE, 150 m, 67.25200N, 23.54800E, 10.06.2014, leg. E. Heibo (SDEI). Torne Lappmark: 2♀ (DEI-GISHym21133, 21134), Abisko 9 km E (Stordalen), 400 m, 68.35000N, 19.03500E, larvae 26.08.2013, *Alnus incana kolaensis*, emerged 04.2014, leg. Liston (SDEI). Switzerland: 2♂ (SDEI, ZSM). United Kingdom: 1♀ (SDEI).

***Pristiphora* Latreille, 1810**

Pristiphora Latreille, 1810: 294, 435. Type species: *Pteronus testaceus* Jurine, 1807 [= *Pristiphora testacea* (Jurine, 1807)], by original designation.

Dinematus Lacourt, 2006: 237–238. Type species: *Dinematus krausi* Lacourt, 2006, by original designation. **Syn. nov.**

Notes. As already suggested by Prous et al. (2017), *Dinematus krausi* probably belongs to the *Pristiphora depressa* species group: see also comments under the species name, below. One of the main reasons for the erection of a genus separate from *Pristiphora* for *krausi*, was the presence of vein 2r-rs in the right fore wing of the holotype (this vein absent in the left wing). The presence of this vein in *Pristiphora* is rather rare but has been observed in at least four other West Palaearctic species: *helvetica* (Benson 1960b), *malaisei*, *robusta*, and *staudingeri* (Prous et al. 2014, 2017). Within *Pristiphora*, these species are only distantly related. In our opinion, no characters exist which will reliably distinguish *Dinematus* from *Pristiphora*, and we therefore propose their synonymy. For further synonymy of genus group names with *Pristiphora* see Taeger et al. (2010) but note that *Stauronematus* is now considered to be a separate genus (Prous et al. 2014). The north-west European species groups and the majority of species of *Pristiphora* were recently revised by Prous et al. (2016, 2017, 2018).

***Pristiphora krausi* (Lacourt, 2006) new combination**

Dinematus krausi Lacourt, 2006: 238–239. Holotype ♀ (MNHN, examined; images: <https://doi.org/10.6084/m9.figshare.1157834.v1>). Type locality: Saint Maurice-sur-Moselle (Vosges) [France, Lorraine].

Notes. *Pristiphora krausi* is only known from the holotype. Its character combination of bifid claws, in dorsal view short and emarginate valvula 3, and yellow and black colour pattern of head and body, suggest that it may belong to the *Pristiphora depressa* group (Prous et al. 2017). On the other hand, other currently known female specimens of this group have a mostly dark forewing vein C and pterostigma, whereas these are entirely pale in *krausi*. Furthermore, the distal sawteeth of *krausi* are prominently lobed, and markedly flatter in the other species. *Pristiphora ifranensis* Lacourt, 1973, only known from the male holotype (private collection of Thierry Noblecourt, examined), type locality Ifrane (Morocco, Middle Atlas), resembles *krausi* strongly in coloration, including its pale forewing vein C and pterostigma. Based on its penis valve morphology, *ifranensis* has been placed in the *depressa* group (Prous et al. 2017). If further specimens become available for study, the possibility should be borne in mind that *krausi* and *ifranensis* represent the female and male of the same species.

***Pristiphora malaisei* (Lindqvist, 1952)**

Notes. A single larva was obtained in northern Sweden by combing through the leaves of an isolated clump of *Dryas octopetala*, under which an inverted frisbee was held. The plant was growing on an otherwise bare patch of soil at the edge of a road. Gene sequences of the larva are nearly identical to those of *Pristiphora malaisei* imagines collected in the same area. Although the specimen (Fig. 74) is small (approx. total length 3 mm), and has been conserved in 96% ethanol, it seems to resemble the larva of *P. dasiphorae* as described by Zinovjev (1993) much more closely than the larva of *P. malaisei* (see Fig. 86) described in the same paper [under the name *Pristicampus incisus* (Lindqvist), synonymised with *malaisei* by Prous et al. (2017)], in having only three annulets on abdomen segments [six, as described by Zinovjev for *incisa*, on *Potentilla fruticosa*] and very long body setae [much shorter as described by Zinovjev]. Note that *dasiphorae*, so far only associated with *Potentilla fruticosa* as a host and in Europe known only from the Swedish island of Öland, is genetically clearly separable from *malaisei* (Prous et al. 2017). The larva from *Dryas* cannot, therefore, belong to *dasiphorae*. Zinovjev (1993) based his description of the larva of *malaisei* (as *incisus*) on specimens collected in the East Palaearctic (Siberia). Efforts should be made to obtain mature larvae of *malaisei* from northern or subarctic-alpine areas, in order to check the morphology of the larva, and to test the host association with *Dryas*.

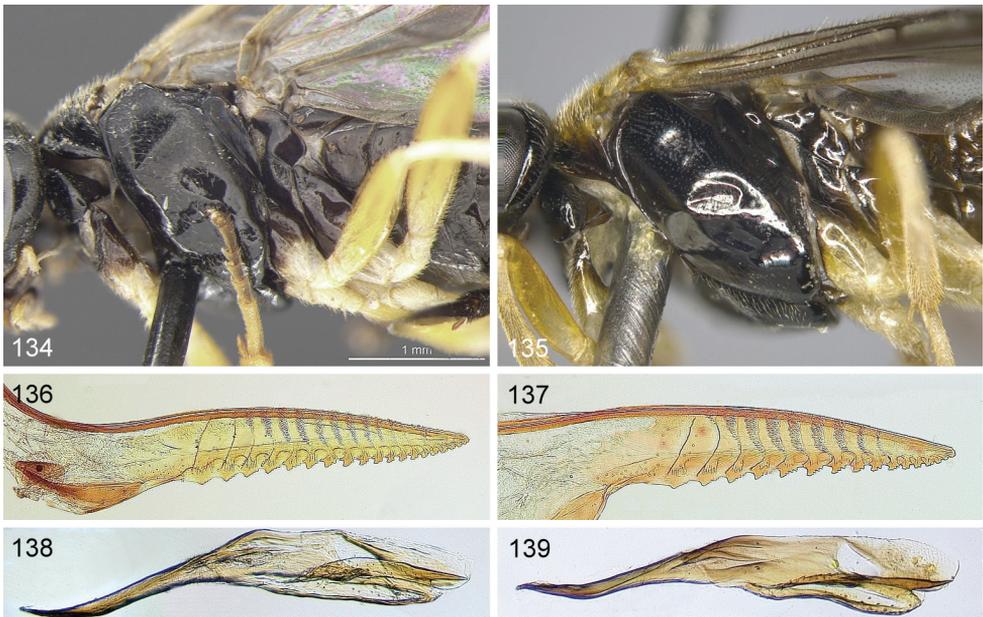
Specimen examined. Sweden: Torne Lappmark: 1 larva (DEI-GISHym83704), from *Dryas octopetala*, Abisko National Park (380 m), 68.35300N, 18.76300E, 06.08.2017, leg. Liston & Prous (SDEI).

***Pseudodineura* Konow, 1885**

Notes. See Liston et al. (2019b).

Stauronematus* Benson, 1953*Key to the European species (after Liston, 2007)**

- 1 **a** Pronotum completely black, or only extreme upper and rear edges brown (Fig. 134); **b** Abdomen entirely black; **c** Mesepisternum more densely pubescent above than below but without extensive entirely glabrous area on lower half (Fig. 134); **d** Hind coxa with at least basal half black (Fig. 134); **e** Wing membrane hyaline; **f** Lancet with ca. 19 teeth (Fig. 136); **g** Penisvalve with ventral margin of paravalva not emarginate (Fig. 138); **h** Body length 5.0–6.5 mm Larval hosts: *Populus* spp., rarely on *Salix* ****Stauronematus platycerus* (Hartig, 1840)**
- **aa** Pronotum almost completely pale white or bright yellow, only ventral margins black (Fig. 135); **bb** Abdomen apically more or less pale: in ♀ at least hypopygial area pale brown, sometimes abdomen medially completely pale (yellow); in ♂ subgenital plate and harpes brown; **cc** Mesepisternum with an extensive glabrous area on lower half (Fig. 135); **dd** Hind coxa with only extreme base black (Fig. 135); **ee** Wing membrane slightly infuscate; **ff** Lancet with ca. 16 teeth (Fig. 137); **gg** Penisvalve with ventral margin of paravalva emarginate (Fig. 139); **hh** Body length 5.0–5.5 mm Larval host: *Salix atrocinerea*. *S. purpurea* requires confirmation. Only known from Corsica and Sardinia ***Stauronematus saliciphilus* Liston, 2007**



Figures 134–139. *Stauronematus* **134** *platycerus* DEI-GISHym19761 ♀ lateral **135** *saliciphilus* holotype ♀ DEI-GISHym11427 lateral **136** *platycerus* DEI-GISHym11317 lancet **137** *saliciphilus* DEI-GISHym11427 lancet **138** *platycerus* DEI-GISHym19762 penis valve **139** *saliciphilus* DEI-GISHym11435 penis valve. Scale bar: 1 mm (**134**).

***Stauronematus platycerus* (Hartig, 1840)**

Nematus platycerus Hartig, 1840: 27. Lectotype ♂, designated by Liston (2007:139), in ZSM (GBIF-GISHym3385, images: <https://doi.org/10.6084/m9.figshare.4791952>). Type locality: Norddeutschland (Germany).

Nematus vallator Snellen van Vollenhoven, 1858: 191–194, pl. 12. Lectotype ♀, examined, designated by Thomas (1987: 72), in RMNH. Type locality: Leiden (Netherlands). Synonymy with *Nematus compressicornis* auct. by Cameron (1878: 267).

Nematus cebrionicornis Costa, 1859: 20. Syntype(s) ♂, not examined, most likely in MZFN. Type locality: Camaldoli Hills, near Naples (Italy). Synonymy with *Nematus compressicornis* auct. by Brischke (1884: 123) (see also Liston 2007: 139).

Nematus callicerus Thomson, 1863: 619–620. Lectotype ♀, designated by Liston (2007:139), in MZLU. Type locality: Ringsjön (Sweden). Synonymy with *Nematus compressicornis* auct. by Cameron (1885: 55).

Description. Body length: female 4.5–7.5 mm, male 4.5–6.0 mm. Head black, except for mandibles and palpi. Pronotum completely black, or only extreme upper and rear edges brown. Mesepisternum more densely pubescent above than below but usually without entirely glabrous area on lower half. Hind coxa with at least basal half black. Trochanters and femora completely pale (yellowish). Tibia more whitish: pro- and mesotibia and pro- and mesobasitarsus entirely pale, with rest of tarsus darkened. Metatibia with approx. apical third black but spurs pale. Metatarsus black. Wing membrane hyaline; venation largely pale except for dark fore wing stigma. Abdomen entirely black. Female: head in dorsal view subparallel behind eyes. Antennae normal; not laterally compressed. Cerci pale to dark. Lancet: Fig. 136. Male: head in dorsal view behind eyes only slightly contracted. Antennae strongly laterally compressed, flagellomeres ventrally somewhat produced; may be reddish. Penis valve: Fig. 138.

Similar species. When the shape of the claw is overlooked, *Stauronematus* adults are frequently misidentified as *Pristiphora*. The long, thin cerci of female *Stauronematus*, and the shape of the valvula 3 in dorsal view, are however quite different to any West Palaearctic *Pristiphora* species.

Life history. Host plants: mainly *Populus* spp., especially *tremula*, but also *nigra*, *balsamifera*, *deltoides*, *alba*, and many cultivated forms (Pschorn-Walcher and Altenhofer 2000, Brischke 1884, Cavalcaselle 1968); less often on *Salix purpurea* (Pschorn-Walcher and Altenhofer 2000, our own observations). Frequently recorded as bivoltine, but possibly has even three generations in warmer areas. Sex ratio appears to be normal for netted specimens, i.e., males about as abundant as females, but is heavily skewed towards males in material collected with Malaise traps. Oviposition in a double row in the leaf petiole. The larvae eat holes in the leaf blade and surround the feeding site with “palisades” (Fig. 85) made of a dried secretion produced in their mandibular glands.

Distribution. Found through much of continental Europe, from the Iberian Peninsula and Balkans, to Finland and Norway, and also the British mainland (Taeger et al. 2006). According to Sundukov (2017) also occurs in Caucasus, Turkey, Iran, Kyrgyzstan, Kazakhstan, China, Korean Peninsula, and Japan.

Occurrence in Sweden. Published records: Skåne (Thomson 1871), Småland, Uppland, Norrbotten Lule Lappmark (Haris 2009). Material examined from Skåne Uppland.

Specimens examined. France: 2♀ (RMNH). Germany: 23♀ (including DEI-GISHym11317 and 19761), 24♂ (including DEI-GISHym19762) (SDEI, ZSM). Netherlands: 4♀, 6♂ (RMNH). Portugal: Aveiro: 1♀, Castelo de Paiva 7 km SSW, 260 m, 41.00033N, 8.27777W, 14.05.2012, leg. Blank, Jacobs, Liston & Taeger (SDEI). Spain: 1♀, 1♂ (SDEI). Sweden: Skåne: 1♂, Malmö, Limhamns Kalkbrott, 55.56760N, 12.93283E, 9.06–25.10.2007, leg. B. W. Svensson & Co. (MZLU). 1♂, Malmö, Limhamns Kalkbrott, 55.56760N, 12.93283E, 27.07.–16.08.2009, leg. B. W. Svensson & Co. (MZLU). Uppland: 1♂, Haninge kommun, Tyresta, Urskogsslingan, hållmark, 59.17685N, 18.24690E, 04–26.08.2004, leg. SMTP (NHRS). 1♂, Huddinge kommun, Sofielunds återvinningsanläggning, avlastningsstation, 59.17656N, 17.99379E, 18.05.–07.06.2004, leg. SMTP (NHRS). 1♂, Älvkarleby kommun, Marma skjutfält, east of Sköldvägen/Kanonvägen, 60.52431N, 17.45151E, 17.06–02.07.2003, leg. SMTP (NHRS). 1♀, 1♂, Älvkarleby kommun, Båtfors, between Milsten and Båtforstorpet, 60.46077N, 17.31782E, 17.06.–03.07.2003, leg. SMTP (NHRS). 1♂, same locality as previous, 14.06.–04.07.2005, leg. SMTP (NHRS). 4♂, Uppsala kommun, Ekdalens naturreservat, southern hillside, 59.97153N, 18.35495E, 07–21.07.2003, leg. SMTP (NHRS). 1♂, same locality as previous, 04–18.08.2003, leg. SMTP (NHRS). 2♂, same locality as previous, 18.08.–01.09.2003, leg. SMTP (NHRS). 1♂, same locality as previous, 02.–16.06.2004, leg. SMTP (NHRS).

Discussion

The conclusions on the phylogeny of Nematinae reached by Niu et al. (2019), based mainly on morphological characters, differ substantially from our results, which are based on molecular data. In our opinion the methodology and data analysis on which their results are based are both seriously flawed. Their results are also affected by misinterpretations of previously published work by other researchers, particularly the papers by Nyman et al. (2006) and Prous et al. (2014). Niu et al. (2019) failed to mention that many of the deepest splits within Nematinae were poorly supported (low statistical support and conflicting relationships in different analyses), although this was acknowledged by both Nyman et al. (2006) and Prous et al. (2014). At the same time, monophyly of Nematinae (including “Hoplocampinae”) was strongly supported in all analyses. In the absence of clear evidence to the contrary, there is no justification for the proposal of alternative classifications: Niu et al. (2019) have not provided such evidence, because they rely solely on the classification proposed by Wei and Nie (1998). Wei and Nie (1998) claimed that their “cladistic analysis” of “Tenthredinoidea” (i.e., Tenthredinidae as currently understood) was based on a “...huge data matrix”, but that “...the complicated analysis process are omitted here for limited space and they will be reported in detail in a separated monograph.” We are unaware of any sources or publications which provide these data. Wei and Nie (1998) basically elevated many existing

taxa to higher rank (tribes to subfamilies, subfamilies to families etc.) with little or no increase in information content. In the absence of publicly available evidence, we are sceptical that Wei and Nie (1998) managed to create a highly informative morphological data matrix that could be used to propose a well-supported and stable phylogeny of Tenthredinidae. The cladistic analyses by Vilhelmsen (2015), based on 146 morphological characters, demonstrate how difficult it is using such methods to achieve a high level of statistical support and stability for phylogenies within Tenthredinidae. At the same time, the statement by Niu et al. (2019: page [2]) that the results of Prous et al. (2014) were based “only on 400-bp sequences of the barcode region”, is simply wrong. As clearly described in Prous et al. (2014: 3) there were two datasets based on four genes (two mitochondrial and two nuclear), one of them (134 specimens) with little missing data (19 specimens missing one gene and seven specimens missing two genes) and the second one (79 specimens) with more missing data (21 specimens missing one gene, eight specimens missing two genes, and 15 specimens missing three genes). This approach was adopted so that type species of some genera for which only one gene was available could be included in the analyses (only one specimen in the second dataset had 422 bp of COI, all others had at least 658 bp of COI). In the end, the new data presented by Niu et al. (2019) are irrelevant to their discussion on the classification of the Nematinae, because of completely inadequate taxon sampling: they analysed only two specimens of Nematinae. Their data are in fact consistent with all previously proposed classifications, not just with Wei and Nie (1998) as they stated.

Although the Nematini and Dineurini both comprise a relatively large number of genera, the large majority of Holarctic nematine species belong to just two genera of Nematini, *Euura* and *Pristiphora*. The proportional representation of genera and species in the Oriental Realm is at present unclear, but compared to the Holarctic Realm, existing data point to a lesser number of *Euura* species, and more *Pristiphora*, while the number of species belonging to diverse genera of non-Nematini may also be greater (Taeger et al. 2010). At the same time, although the number of still undescribed nematine species inhabiting the mountains of the Oriental Region can only be guessed at, it seems unlikely that Nematinae make up such a high proportion of the Oriental sawfly fauna as of the fauna of northern regions of the Holarctic. Outside the Holarctic and Oriental Realms, the Nematinae is represented naturally only in the northern regions of the Neotropical Realm, by a few species of *Pristiphora* (Taeger et al. 2010).

As noted above, the striking abundance and species diversity of nematine sawflies in the northern parts of the Palaearctic, including Fennoscandia, results mainly from the presence of numerous species of *Euura* and *Pristiphora*. Although several factors probably contribute to this pattern (Bogacheva 1994, Kouki et al. 1994), it has long been apparent that at progressively high latitudes in the northern hemisphere *Salix* species are of increasing importance over other plant taxa as hosts of sawflies, particularly Nematinae (Malaise 1931b). On the other hand, it is important to remember that many other plant taxa are hosts of sawfly larvae in the north. An example is our indication that *Dryas octopetala* is a host plant of *Pristiphora malaisei* in the more northern and upland parts of the range of this sawfly species. Currently, this is only the second sawfly species to have been found on this host, the other being the al-

lantine *Empria alpina* Benson (Prous et al. 2011). However, based partly on our own experiences during field-work, we suspect that the relative difficulty of collecting larvae from low-growing potential hosts such as *Dryas*, other herbaceous Rosaceae, Polygonaceae, Fabaceae, grasses and sedges, etc. as opposed to shrubby *Salix*, may have led to at least a slight underestimation of the significance of the former as host plants in the northern nematine fauna. Furthermore, although *Betula* species are clearly the second most frequently used hosts of Nematinae in northern Fennoscandia, most published observations and data are for the tree-birch *Betula pubescens* var. *pumila* (e.g., Tenow 1963), whereas surprisingly little has been published about the sawfly fauna of *Betula nana*.

As can be seen from the key to larvae, the larvae of Nematinae exhibit a high level of morphological variability. This is expressed, for example, in the number of dorsal annulets of abdomen segments varying between three and six. By contrast, all European Tenthredininae larvae have seven annulets, six in Selandriinae [only *Dolerus*] or seven, six in each Athaliinae and Allantinae (Lorenz and Kraus 1957). Only among the Blennocampinae is this character similar in variability to the Nematinae: Blennocampinae have 4–6 annulets, excluding the leaf-mining taxa, in which the number is reduced to two. The variability in Nematinae is all the more remarkable because conspicuous differences such as the number of annulets apparently occur even between species which are certainly quite closely related, such as within the *Pristiphora malaisei* species group. In the Blennocampinae, differences in the number of annulets are usually regarded as generic characters (Lorenz and Kraus 1957).

Although the genera which we have treated in this paper are comparatively species-poor, cases nevertheless occur of the sort of taxonomic problems which are regularly encountered in the much larger genera *Pristiphora* and *Euura*. An interesting example is *Platycampus luridiventris*, where three different (mitochondrial) genetic lineages exist. Earlier studies on this species concluded that genetic segregation was correlated with differences in host plant use, behaviour, and partly even the length of setae of larvae. Our own genetic data partly conflicts with this conclusion. Perhaps the apparent differences are caused by differential gene expression: a sort of host plant conditioning. At present, there are no compelling reasons to treat the lineages as separate taxonomic entities. A similar situation may occur in several groups of closely related nominal species of *Euura*, such as the gall-makers of the *dolichura* group and *oblita* group (*ischnocera* complex), which are thought to be highly host specific, but often exhibit neither clear morphological nor genetic differences (Liston et al. 2017).

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Checklist and key for the identification of fish fauna of the Uberaba River, Upper Paraná River system, Brazil

Douglas de Castro Ribeiro¹, Jumma Miranda Araújo Chagas²,
Mariana Ribeiro Thereza¹, Francisco Langeani¹

1 UNESP, Universidade Estadual Paulista, Instituto de Biociências, Letras e Ciências Exatas, Departamento de Zoologia e Botânica, Laboratório de Ictiologia, Rua Cristóvão Colombo, 2265, 15054-000 São José do Rio Preto, SP, Brazil **2** UNESP, Universidade Estadual Paulista, Instituto de Biociências, Departamento de Biologia e Zootecnia, Laboratório de Ecologia do Parasitismo, Ilha Solteira, SP, Brazil

Corresponding author: *Douglas de Castro Ribeiro* (dcribeiro.bio@gmail.com)

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Abstract

The Uberaba River is an important right-bank tributary to the Grande River, in the Upper Paraná River system, Brazil, and the main water source for the public supply of the Uberaba city, Minas Gerais state. An inventory, an identification key, and photographs of the fish species of the Uberaba River are provided, based on samples made between 2012 and 2014 at 14 sampling sites in the river system. A total of 73 species was recorded from six orders, 20 families, and 49 genera. Characiformes and Siluriformes are the most speciose orders and Characidae and Loricariidae are the most commonly recorded families. Most species are autochthonous, nine are considered allochthonous, and two species are exotic. The Uberaba River has a diverse and heterogeneous ichthyofauna, typical of rheophilic environments, with endemic species and few non-native species.

Keywords

Brazilian Cerrado, freshwater fish, Neotropical Region, rheophilic environment, threatened species

Introduction

Approximately 34,797 species of fish have been formally described worldwide (Fricke et al. 2018), and recent estimates suggest that ca. 13,000 species are partially or exclusively freshwater (Nelson 2016). The Neotropical region has a unique and diverse freshwater fish fauna (Albert and Reis 2011), with 9,100 species exclusively distributed in South America (Reis et al. 2016), an impressive number when compared to the global estimates. Approximately 43% of the Neotropical fish diversity occurs in Brazil (Buckup et al. 2007), and the Amazon and La Plata river drainages bear the largest fish diversity in South America (Langeani et al. 2007).

With geological origin dating from the Mesozoic (Neocretaceous), the La Plata River has an estimated drainage area of ca. 3 million km² across five countries, Bolivia, Brazil, Paraguay, Argentina, and Uruguay, and is the second largest drainage in South America, with the main drainages the Paraná-Paraguay drainage and Uruguay River (Albert and Reis 2011). The Upper Paraná River system is a catchment above the Sete Quedas Falls, currently flooded by the Itaipu hydroelectric dam, located at the border between Brazil, Paraguay, and Argentina. In the Brazilian portion, the Upper Paraná River system drains the states of Goiás, Minas Gerais, São Paulo, Mato Grosso do Sul, and Paraná, comprising the subsystems of the Grande, Paranaíba, Tietê, and Paranapanema rivers (Souza-Filho and Stevaux 1997; Langeani et al. 2007).

The Upper Paraná River, according to Langeani et al. (2007), harbors approximately 360 of fish species. Subsequently, Fagundes et al. (2015) provide 46 new records for this system. Additionally, at least 28 new species have been described since the last twenty years (e.g., Silveira et al. 2008; Martins and Langeani 2011a, 2011b; Carvalho and Langeani 2013; Serra and Langeani 2015). The increased number of species recorded in the Upper Paraná River in the last decade reflects intense sampling carried out in the region. Some authors (e.g., Langeani et al. 2007; Oyakawa and Menezes 2011) report that the Upper Paraná River is among the most well-sampled Brazilian regions, especially the São Paulo state (Oyakawa and Menezes 2011), and is one of the most impacted by dams, which considerably altered the hydrological regime and natural environments, affecting the dynamics and recruitment in fish populations (Agostinho et al. 2004). Fagundes et al. (2015) carried out intense samplings in tributaries of the Paranaíba, Araguari, and Grande rivers in the state of Minas Gerais, northwest, east, and southeast of the Triângulo Mineiro region, contributing significantly to the knowledge on local fish faunas. However, despite the recent contributions to the Upper Paraná River system, some areas were poorly sampled (e.g., south and southwest of the Triângulo Mineiro region, northeast and south parts of the Minas Gerais state, most of the Mato Grosso do Sul and Goiás states) and information on fish fauna composition and distribution is still missing.

The Uberaba River is a right-bank tributary of the Grande River, in the Upper Paraná River system, Brazil, and it is the main water source for Uberaba city in Minas Gerais state. In the driest period, the water level of the Uberaba River is very low and it is not able to be the only source of public water supply to the Uberaba city. This problem becomes worse with the intensive anthropogenic impact on the environment which results in modifications of hydrological dynamics and associated biotic struc-

tures (Candido et al. 2010; Cruz 2003; Valera et al. 2016). A dam located in the middle section of the Uberaba River, designed to capture and treat water for human consumption, significantly altered the natural characteristics and self-depuration capacity of the river (Sousa et al. 2016), even more aggravated by the high loads of raw sewage released into some river sections (Cruz 2003).

The fish fauna of the Uberaba River is only partially known, with only few sections sampled and no seasonal investigations (see SEMEA 2004; Souza et al. 2016). In this paper, we present an inventory of the fish fauna of the Uberaba River based on samples from several sections of the river system. In addition, an identification key and photographs of some species are presented.

Materials and methods

Study area

The Uberaba River catchment area is located in the southeastern region of Minas Gerais state, Brazil, center-south of the Triângulo Mineiro region, 19°30'37"S – 20°07'40"S; 47°39'2"W – 48°34'34"W (Figure 1). The Uberaba River system covers an area of approximately 2, 428.73 km² and is subordinated to the “Comitê da Bacia Hidrográfica dos Afluentes Mineiros do Baixo Rio Grande (CBH-GD)”. The Uberaba River extends for 184.90 km, with a gap of approximately 554 m, and is supplied by 86 tributaries of diverse orders along its course. Its headwaters are located east of the municipality of Uberaba-MG, a hydromorphic field along the BR-262 road, at 1,014 m of altitude. The Uberaba River discharges in the right side of the Grande River in the municipality of Planura, Minas Gerais state, at 460 m of altitude (CODAU 2005). Along its route, the Uberaba River crosses five municipalities, Uberaba (1,198.75 km²), followed by Conceição das Alagoas (643.19 km²), Veríssimo (568.65 km²), Planura (33.39 km²), and Campo Florido (4.59 km²) (IGAM 2010).

The average annual precipitation in the region ranges between 1,300 mm and 1,700 mm, characterized by a rainy period of six to seven months (October to March) and the driest period (April to September) with less than 60 mm. The thermal regime is defined by an average annual temperature ranging from 20 to 24° Celsius, with a minimum of 18° C in colder months (June/July). These climatic factors characterize two major seasons in the region, one, cold and dry, between autumn and winter, and the other, hot and rainy, between spring and summer (Gomes et al. 1982).

Data

The collections were carried out between 2012 and 2014 in 14 sampling sites (Figures 1, 2; Table 1) along the entire system. Permission for collecting was provided by IEF / DPBIO / GPFF No.44551-1156-2011. The samplings were performed both during the daytime and nighttime, using gill nets (2.5 to 120 mm mesh), dip nets (0.5 mm

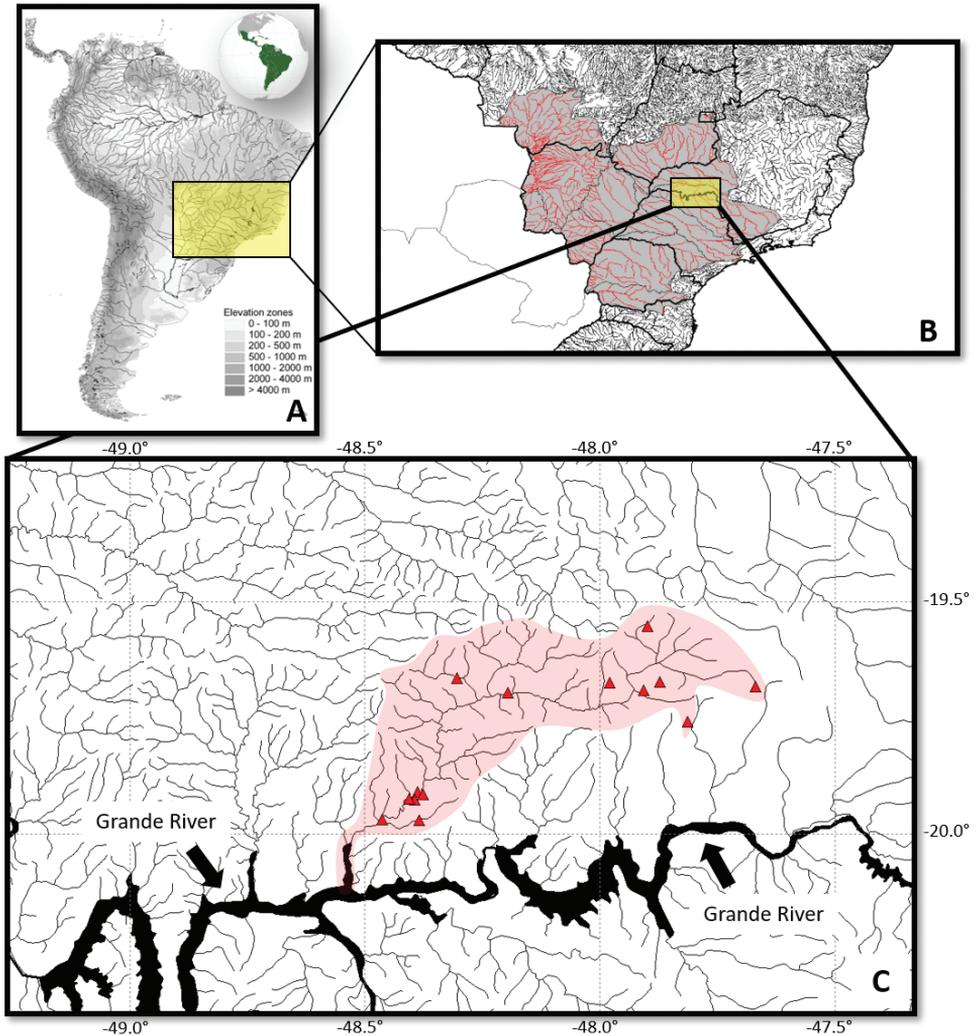


Figure 1. Map of the Uberaba River drainage. **A** Upper Paraná River system highlighted in the Neotropical region **B** location of the Uberaba River drainage in the Upper Paraná River system **C** red triangles showing the sampling sites in the Uberaba River.

mesh), seines (1.5 mm mesh), and cast nets (2.5 to 100 mm mesh sizes). After sampling, the specimens were anesthetized in a solution containing 100 mg of eugenol by L⁻¹ previously dissolved in 100% ethanol in proportion of 1:1 v/v, fixed in 10% formalin buffered with sodium phosphate (pH 7.0 and 0.2 Mol) for 24 to 72 hours, and then transferred to 70° G.L. ethanol.

Specimens were identified using appropriate literature sources (e.g., Langeani et al. 2007; Langeani and Rêgo 2014; Castro et al. 2004; Ota et al. 2018) or by direct comparisons with specimens in museum collections. Vouchers are in the DZSJRP fish collection of the Departamento de Zoologia e Botânica do Instituto de Biociências, Letras

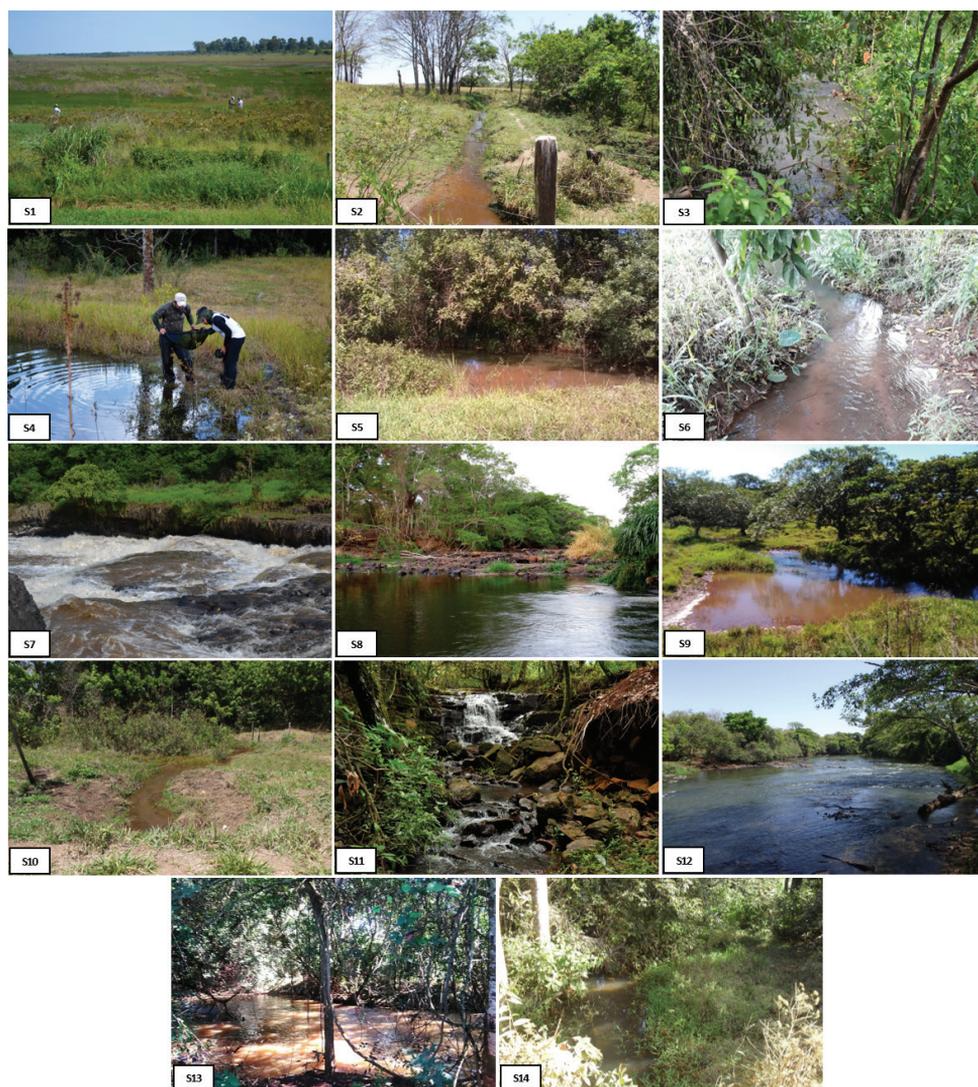


Figure 2. Sampling sites in the Uberaba River, Upper Paraná River system, Brazil. Detailed description of sites in Table 1.

e Ciências Exatas, Universidade Estadual Paulista 'Júlio de Mesquita Filho', São José do Rio Preto, SP, Brazil. Some groups are in need of a taxonomic revision, consequently the particle aff. (meaning “not the referred species, but very similar”) is used. The morphometric measurements were taken on the left side of the body, using a digital caliper with an accuracy of 0.01 mm. Lower-level taxonomy and species names follow Fricke et al. (2018) and suprageneric taxonomic groups are those listed in Betancur et al. (2017), except for Cynolebiidae and Bryconidae that follow van der Laan (2016). Allochthonous species are those with their origins from any other hydrographic system in South America outside the Upper Paraná River as defined above. Exotic species are those with origins from any other continent.

Table 1. Description of sampling sites (S1 to S14) of the Uberaba River, Upper Paraná River system, Brazil.

Site	Locality	Coordinates	Elevation	Characteristics
S1	Serra do Grotão, headspring of the Uberaba River, on the margins of BR 262, Ponte Alta, MG	19.40575S, 47.405430W	1015	Lentic environment; organic sediment and sand as substrate; clear and warm water, 1 m deep; abundant aquatic plants
S2	Small stream (no name), unpaved road at BR262, tributary of Veríssimo River, Veríssimo, MG	19.39538S; 48.181390W	622	Lotic environment, medium flow; clay as substrate; shallow water, less than 80 cm deep; few marginal plants
S3	Small stream (no name), unpaved road at Mula Preta farm, tributary of the Lageado River, Uberaba, MG	19.45312S; 47.484494W	715	Medium flow stream; sand and clay as substrate; turbid water; less than 1.5 m deep; riparian vegetation and open areas
S4	Small stream (no name), into APP Vale encantado, tributary of the Saudade stream, Uberaba, MG	19.33573S; 47.534852W	901	Lentic environment; organic sediment and sand as substrate; clear and warm water; 0.5 m depth; few aquatic plants
S5	Alegria stream, unpaved road at Alegria farm, tributary of the Uberaba River, Uberaba, MG	19.40224S; 47.522022W	803	Lotic environment, medium flow; clay soil as a substrate; shallow and turbid water, 1 m depth; dense riparian forest and pasture area
S6	Small stream (no name), Rocinha farm, unpaved road at Pará Pereira Gomes road, tributary of the Lageado stream, Uberaba, MG	19.41135S; 47.542032W	778	Lotic environment, medium flow; sand and leaves as substrate; shallow and crystalline waters, 30 cm deep; riparian forest sparse
S7	Uberaba River, below of the PCH Monjolo, Veríssimo, MG	19.41466S; 48.113035W	632	Lotic environment, fast flowing, several rapids and small backwaters, basaltic rocks and sand as substrate, riparian vegetation well preserved.
S8	Uberaba River, Conceição das Alagoas, MG	19.54288S; 48.23155W	495	Lotic environment, fast flowing, several rapids and small backwaters, basaltic rocks and sand as substrate, riparian vegetation well preserved, urban effluent present.
S9	Ribeirão das Alagoas stream (or Eliezer stream), Eliezer farm, unpaved road at MG427, Conceição das Alagoas, MG	19.58451S; 48.274545W	495	Medium-flow lotic environment; sand and clay as substrate; turbid waters, 1.5 m deep; degraded area
S10	Small stream (no name), unpaved road at a sanitary landfill, tributary of the Uberaba River, Conceição das Alagoas, MG	19.55268S; 48.233689W	507	Lotic environment, low flow, clay soil as a substrate, very shallow water, less than 30 cm deep; few marginal plants, very degraded area
S11	Small stream (no name), 0.7 km at IFTM campus, affluent of the Uberaba River, Uberaba, MG	19.67431S; 47.978456W	779	Medium flow stream, gravel and basaltic rocks as substrate; crystalline waters, 1 m deep, dense riparian vegetation
S12	Uberaba River, Carijó farm, 4.5 km upstream from Gorfo waterfall, Conceição das Alagoas, MG	19.92382S; 48.404833W	490	Lotic environment, fast flow, several rapids, basaltic rocks and gravel as a substrate, well preserved riparian vegetation, urban effluent present.
S13	Ribeirão das Alagoas stream (or Eliezer stream), near the confluence with the Uberaba River, Conceição das Alagoas, MG	19.97009S; 48.384722W	506	Lotic environment, medium flow, sand and clay as substrate, large basaltic rocks, turbid water, 1 m depth, degraded riparian vegetation
S14	Small stream (no name), unpaved road at Conceição das Alagoas city, tributary of the Uberaba River, Conceição das Alagoas, MG	19.91363S; 48.375123W	516	Lotic environment, low flow, loam and sand as substrate; shallow water, 70 cm deep; many marginal grasses, degraded area

Results

In total, 2,722 specimens were collected and assigned to 49 genera and 73 species. The identified taxa are listed in Table 2. Most of the species in the Uberaba River are autochthonous (80.0%). Nine species (12.3%) have been recognized as allochthonous (*Galeocharax gulo* (Cope), *Metynnis lippincottianus* (Cope), *Knodus* aff. *moenkhausii* (Eigenmann & Kennedy), *Hoplerythrinus unitaeniatus* (Spix & Agassiz), *Gymnotus inaequilabiatus* (Valenciennes), *Trichomycterus brasiliensis* Lütken, *Megalechis thoracata* (Valenciennes), *Poecilia reticulata* Peters, and *Cichla piquiti* Kullander & Ferreira), and only two (2.7%) species are exotic (*Coptodon rendalli* (Boulenger) and *Oreochromis niloticus* (Linnaeus)). Six orders were recognized, of which Characiformes and Siluriformes were the most representative (90.3%), with eight families and 33 species for the former and five families and 27 species for the latter. Gymnotiformes (two families and three spp.), Cichliformes (one family and seven spp.), Cyprinodontiformes (two families and three spp.), and Synbranchiformes (one sp.) together represent 9.7% of the groups collected (Figure 3). Characidae (48.8%) and Loricariidae (16.8%) correspond to the most abundant families (Figure 4) and occur

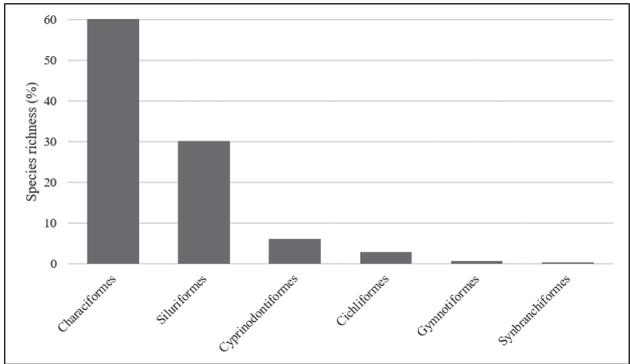


Figure 3. Species richness for each fish order collected in Uberaba River, Upper Paraná River system, Brazil.

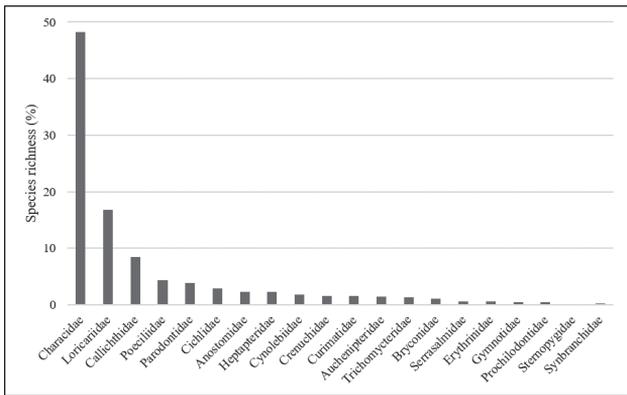


Figure 4. Species richness of each fish family collected in Uberaba River, Upper Paraná River system, Brazil.

Table 2. List of fish species from the Uberaba River, Upper Paraná River system, Brazil. Vouchers and origin/status are provided.

	Taxa	Voucher	Origin
CHARACIFORMES			
Anostomidae			
1	<i>Leporinus amblyrhynchus</i> Garavello & Britski, 1987	DZSJRP15809	Autochthonous
2	<i>Leporinus frederici</i> (Bloch, 1794)	uncataloged	Autochthonous
3	<i>Leporinus octofasciatus</i> Steindachner, 1915	DZSJRP16097	Autochthonous
4	<i>Leporinus striatus</i> Kner, 1858	DZSJRP21396	Autochthonous
5	<i>Schizodon nasutus</i> Kner, 1858	DZSJRP21388	Autochthonous
Bryconidae			
6	<i>Brycon nattereri</i> Günther, 1864	DZSJRP17489	Autochthonous/VU
Characidae			
7	<i>Astyanax bockmanni</i> Vari & Castro, 2007	DZSJRP15819	Autochthonous
8	<i>Astyanax</i> aff. <i>fasciatus</i> (Cuvier, 1819)	DZSJRP15818	Autochthonous
9	<i>Astyanax lacustris</i> (Lütken, 1875)	DZSJRP21399	Autochthonous
10	<i>Astyanax</i> aff. <i>paranae</i> Eigenmann, 1914	DZSJRP17486	Autochthonous
11	<i>Astyanax paranae</i> Eigenmann, 1914	DZSJRP15823	Autochthonous
12	<i>Bryconamericus turiuba</i> Langeani et al., 2005	DZSJRP05533	Autochthonous
13	<i>Galeocharax gulo</i> (Cope, 1870)	DZSJRP16096	Allochthonous
14	<i>Hasemanina uberaba</i> Serra & Langeani, 2015	DZSJRP18781	Autochthonous
15	<i>Hyphessobrycon uaiso</i> Carvalho & Langeani, 2013	DZSJRP18783	Autochthonous
16	<i>Knodus</i> aff. <i>moenkhausii</i> (Eigenmann & Kennedy, 1903)	DZSJRP15825	Allochthonous
17	<i>Oligosarcus pintoii</i> Campos, 1945	DZSJRP05553	Autochthonous
18	<i>Piabarchus stramineus</i> (Eigenmann, 1908)	DZSJRP21383	Autochthonous
19	<i>Piabina argentea</i> Reinhardt, 1867	DZSJRP17487	Autochthonous
Serrasalminidae			
20	<i>Metynnis lippincottianus</i> (Cope, 1870)	DZSJRP21397	Allochthonous
21	<i>Myloplus tiete</i> (Eigenmann & Norris, 1900)	DZSJRP21398	Autochthonous/EN
22	<i>Serrasalmus maculatus</i> Kner, 1858	DZSJRP21386	Autochthonous
Curimatidae			
23	<i>Steindachnerina insculpta</i> (Fernández-Yépez, 1948)	DZSJRP15812	Autochthonous
Erythrinidae			
24	<i>Hoplerethrinus unitaeniatus</i> (Spix & Agassiz, 1829)	DZSJRP21402	Allochthonous
25	<i>Hoplias intermedius</i> (Günther, 1864)	DZSJRP21389	Autochthonous
26	<i>Hoplias</i> aff. <i>malabaricus</i> (Bloch, 1794)	DZSJRP10546	Autochthonous
Parodontidae			
27	<i>Apareiodon affinis</i> (Steindachner, 1879)	DZSJRP21391	Autochthonous
28	<i>Apareiodon ibitiensis</i> Campos, 1944	DZSJRP15813	Autochthonous
29	<i>Apareiodon piracicabae</i> (Eigenmann, 1907)	DZSJRP16100	Autochthonous
30	<i>Parodon nasus</i> Kner, 1859	DZSJRP21400	Autochthonous
Crenuchidae			
31	<i>Characidium</i> aff. <i>zebra</i> Eigenmann, 1909	DZSJRP17484	Autochthonous
32	Crenuchidae (undescribed genus and species)	DZSJRP15806	Autochthonous
Prochilodontidae			
33	<i>Prochilodus lineatus</i> (Valenciennes, 1837)	DZSJRP21385	Autochthonous
GYMNOTIFORMES			
Sternopygidae			
34	<i>Eigenmannia trilineata</i> López & Castello, 1966	DZSJRP21392	Autochthonous
Gymnotidae			
35	<i>Gymnotus inaequilabiatus</i> (Valenciennes, 1839)	uncataloged	Allochthonous
36	<i>Gymnotus sylvius</i> Albert & Fernandes-Matioli, 1999	DZSJRP16101	Autochthonous

Taxa	Voucher	Origin
SILURIFORMES		
Callichthyidae		
37 <i>Aspidoras fuscoguttatus</i> Nijssen & Isbrücker, 1976	DZSJRP18785	Autochthonous
38 <i>Corydoras diffluviatilis</i> Britto & Castro, 2002	DZSJRP15824	Autochthonous
39 <i>Megalechis thoracata</i> (Valenciennes, 1840)	DZSJRP21106	Allochthonous
Heptapteridae		
40 <i>Imparfinis borodini</i> Mees & Cala, 1989	DZSJRP17488	Autochthonous
41 <i>Pimelodella avanhandavae</i> Eigenmann, 1917	DZSJRP21105	Autochthonous
42 <i>Rhamdia quelen</i> (Quoy & Gaimard, 1824)	DZSJRP16799	Autochthonous
43 <i>Rhamdiopsis</i> sp.	DZSJRP15817	Autochthonous
Loricariidae		
44 <i>Curculionichthys insperatus</i> (Britski & Garavello, 2003)	DZSJRP21120	Autochthonous
45 <i>Hypostomus albopunctatus</i> (Regan, 1908)	DZSJRP21390	Autochthonous
46 <i>Hypostomus ancistroides</i> (Ihering, 1911)	DZSJRP15810	Autochthonous
47 <i>Hypostomus butantanis</i> (Ihering, 1911)	DZSJRP16098	Autochthonous
48 <i>Hypostomus fluviatilis</i> (Schubart, 1964)	DZSJRP21114	Autochthonous
49 <i>Hypostomus</i> aff. <i>hermanni</i> (Ihering, 1905)	DZSJRP21107	Autochthonous
50 <i>Hypostomus margaritifer</i> (Regan, 1908)	DZSJRP02107	Autochthonous
51 <i>Hypostomus nigromaculatus</i> (Schubart, 1964)	DZSJRP16103	Autochthonous
52 <i>Hypostomus</i> aff. <i>paulinus</i> (Ihering, 1905)	DZSJRP21108	Autochthonous
53 <i>Hypostomus regani</i> (Ihering, 1905)	DZSJRP21124	Autochthonous
54 <i>Hypostomus strigaticeps</i> (Regan, 1908)	DZSJRP21125	Autochthonous
55 <i>Hypostomus topavae</i> (Godoy, 1969)	DZSJRP21098	Autochthonous
56 <i>Loricaria lentiginosa</i> Isbrücker, 1979	uncataloged	Autochthonous
57 <i>Microlepdogaster dimorpha</i> Martins & Langeani, 2012	DZSJRP18784	Autochthonous
58 <i>Proloricaria prolixa</i> (Isbrücker & Nijssen, 1978)	DZSJRP16102	Autochthonous
59 <i>Rineloricaria latirostris</i> (Boulenger, 1900)	DZSJRP15811	Autochthonous
Trichomycteridae		
60 <i>Trichomycterus brasiliensis</i> Lütken, 1874	DZSJRP21116	Allochthonous
61 <i>Trichomycterus candidus</i> (Miranda-Ribeiro, 1949)	DZSJRP15820	Autochthonous
Auchenipteridae		
62 <i>Tatia neivai</i> (Ihering, 1930)	DZSJRP21111	Autochthonous
CYPRINODONTIFORMES		
Cynolebiidae		
63 <i>Melanorivulus giarettai</i> Costa, 2008	DZSJRP18782	Autochthonous
Poeciliidae		
64 <i>Phalloceros harpagos</i> Lucinda, 2008	DZSJRP17485	Autochthonous
65 <i>Poecillia reticulata</i> Peters, 1859	DZSJRP17483	Allochthonous
CICHLIFORMES		
Cichlidae		
66 <i>Cichla piquiti</i> Kullander & Ferreira, 2006	DZSJRP21401	Allochthonous
67 <i>Cichlasoma paranaense</i> Kullander, 1983	DZSJRP21394	Autochthonous
68 <i>Coptodon rendalli</i> (Boulenger, 1897)	DZSJRP05549	Exotic
69 <i>Crenicichla britskii</i> Kullander, 1982	DZSJRP21393	Autochthonous
70 <i>Crenicichla jaguarensis</i> Haseman, 1911	DZSJRP21387	Autochthonous
71 <i>Geophagus brasiliensis</i> (Quoy & Gaimard, 1824)	DZSJRP21395	Autochthonous
73 <i>Oreochromis niloticus</i> (Linnaeus, 1758)	uncataloged	Exotic
SYNBRANCHIFORMES		
Synbranchidae		
73 <i>Synbranchus marmoratus</i> Bloch, 1795	DZSJRP21384	Autochthonous

Species	Sites													
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14
<i>Microlepidogaster dimorpha</i>					X									
<i>Myloplus tiete</i>								X					X	
<i>Oligosarcus pintoii</i>														X
<i>Oreochromis niloticus</i>							X	X						X
<i>Parodon nasus</i>							X	X	X			X	X	
<i>Phalloceros barpagos</i>					X									
<i>Piabarchus stramineus</i>							X	X						
<i>Piabina argentea</i>		X						X						
<i>Poecilia reticulata</i>								X		X		X		
<i>Prochilodus lineatus</i>							X							
<i>Proloricaria proluxa</i>								X				X		
<i>Rhamdia quelen</i>							X	X				X	X	
<i>Rhamdiopsis</i> sp.						X								
<i>Rineloricaria latirostris</i>								X				X		
<i>Schizodon nasutus</i>								X						
<i>Serrasalmus maculatus</i>								X						
<i>Steindachnerina insculpta</i>							X	X	X			X	X	
<i>Synbranchus marmoratus</i>								X		X		X		
<i>Tatia neivai</i>								X				X		
<i>Trichomycterus brasiliensis</i>											X			
<i>Trichomycterus candidus</i>						X								
Species richness	4	2	2	3	4	4	24	53	15	5	2	31	24	2

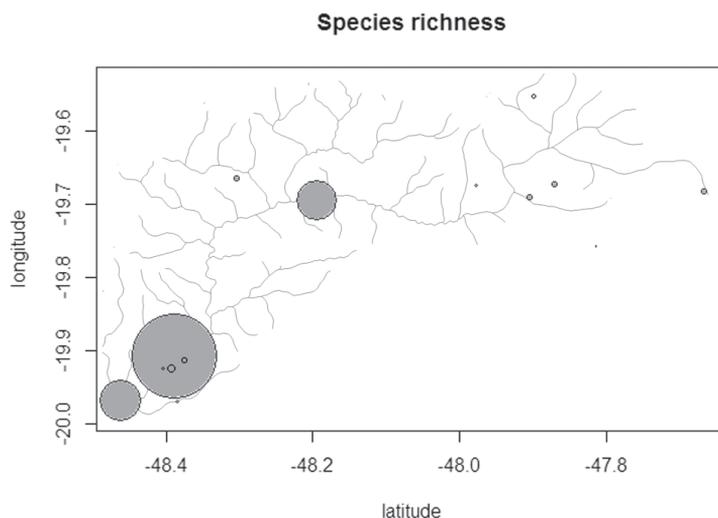


Figure 5. Species richness along longitudinal gradient in Uberaba River, Upper Paraná River system, Brazil. Circle diameter corresponds to species richness.

in the entire river system. The species richness suggested a longitudinal gradient, with more species in the lower reaches whereas in the upper reaches the richness does not exceed ten species (Figure 5 and Table 3). The loricariids are mainly represented by *Hypostomus* species, up to 92% of the total loricariid number. The most abundant species is *Knodus* aff. *moenkhausii* with 507 collected specimens comprising 38% of all characiform species. All other species have already been recorded in the Upper Paraná River.

Key to fish species of the Uberaba River drainage

- 1 Single mid-ventral gill opening; eel-shaped body *Synbranchus marmoratus*
 – Two laterally located gill openings; not eel-shaped body 2
 2 Dorsal and pelvic fins absent; anal-fin rays more than 100 3
 – Dorsal fin present; pelvic fin commonly present; anal-fin rays up to 50 5
 3 Body uniformly clear with relatively inconspicuous longitudinal stripes; anal fin not reaching the tail end; terminal mouth, both jaws approximately equal *Eigenmannia trilineata*
 – Body dark with clear transverse bands; anal fin extending to the tail end; prognathous, lower jaw longer than upper jaw 4
 4 Obliquely-oriented dark transversal bars fragmented, forming a pattern of irregular spots; anal-fin posterior membrane striped
 *Gymnotus inaequilabiatus*
 – Obliquely-oriented dark transversal bars not fragmented; anal-fin posterior region darkly pigmented or translucent *Gymnotus sylvius*
 5 Body naked or covered by bony plates 6
 – Body covered by scales 30
 6 Body covered by bony plates, at least partially 7
 – Body covered by thick skin; bony plates absent 24
 7 Mouth forming a ventral oral disk; bony plates rows on flanks 3–5 8
 – Mouth not forming ventral oral disk, with terminal or subterminal opening; bony plates rows on flank 2 22
 8 Adipose fin absent 9
 – Adipose fin present 12
 9 Caudal peduncle very elongate and depressed 10
 – Caudal peduncle rounded or elliptical in cross-section 13
 10 Lips with small papillae, occasionally with short, thick, non-filamentous projections *Rineloricaria latirostris*
 – Lips fringed, with filamentous projections 11
 11 Head with dark brown spots, much smaller than the eye diameter
 *Loricaria lentiginosa*
 – Head light brown without spots *Proloricaria proluxa*
 12 Scapular bridge fully exposed; well-developed and pointed odontodes on the anterior portion of the snout *Curculionichthys insperatus*
 – Scapular bridge exposed only laterally; small and spatulate odontodes on the anterior portion of the snout *Microlepidogaster dimorpha*
 13 Body light with dark spots 14
 – Body dark with light spots or vermiculations 17
 14 Lateral keels on body present (three rows), with hypertrophied odontodes ...
 *Hypostomus ancistroides*
 – Lateral keels on body absent 15

- 15 Pectoral-fin spine claviform, with well-developed odontodes on distal portion; eyes small, 6–6.5 × in head length ***Hypostomus nigromaculatus***
- Pectoral-fin spine not claviform, with subequal odontodes along entire spine; eyes large, 3.5–5 × in head length ***Hypostomus fluviatilis***
- 16 Abdomen completely covered by plates; dentary angle more than 60°; bony plates between dorsal and adipose fins 5 pairs ***Hypostomus topavae***
- Abdomen without plates on pelvic-fin region; dentary angle approximately 45°; bony plates between dorsal and adipose fins 4 pairs
..... ***Hypostomus aff. hermani***
- 17 Pectoral-fin spine equal to or shorter than pelvic-fin spine
..... ***Hypostomus albopunctatus***
- Pectoral-fin spine longer than pelvic-fin spine **18**
- 18 Premaxillary and dentary with short and sturdy teeth (18–32), arranged in obtuse angle **19**
- Premaxillary and dentary with long and thin teeth (more than 35), arranged in acute angle **20**
- 19 Body and fins with light spots, aligned longitudinally, but not forming continuous line ***Hypostomus margaritifer***
- Head and fins with light vermiculations, with four longitudinal yellow lines on flank, from dorsal fin to caudal-fin base ***Hypostomus butantanis***
- 20 Pectoral girdle covered with large plates; bony plates between anal and caudal fins 10 or 11; dentary teeth more than 140 ***Hypostomus aff. paulinus***
- Pectoral girdle covered with very small plates or skin; bony plates between anal and caudal fins 12 or 13; dentary teeth up to 130 **21**
- 21 Mid-lateral plates series 28 or 29; snout-operculum distance greater than the width of the lips; dorsal fin large, reaching adipose fin; premaxillary and dentary teeth more than 65 ***Hypostomus regani***
- Mid-lateral plates series 25 or 26; snout-operculum distance equal to width of the lips; dorsal fin of moderate size, distant from adipose fin; premaxillary and dentary teeth up to 60 ***Hypostomus strigaticeps***
- 22 Mental barbels absent; jaws teeth present; nuchal plate covered by skin; caudal fin truncated ***Megalechis thoracata***
- Mental barbels present; jaws teeth absent; nuchal plate exposed; caudal fin forked **23**
- 23 Supraoccipital long and reaching the nuchal plate; pectoral-fin rays anterior portion without posterior bone lamellae ***Corydoras difluviatilis***
- Supraoccipital short, not reaching the nuchal plate; pectoral-fin rays anterior portion with posterior bone lamellae (more evident in the first rays)
..... ***Aspidoras fuscoguttatus***
- 24 Operculum and preoperculum with odontodes; dorsal-fin origin situated posterior the middle of the body **25**
- Operculum and preoperculum without odontodes; dorsal-fin origin situated approximately at the middle of the body **26**

- 25 Pelvic fin present..... *Trichomycterus brasiliensis*
 – Pelvic fin absent *Trichomycterus candidus*
- 26 Adipose fin short, shorter than anal fin length; nuchal plate reaching the posterior portion of head..... *Tatia neivai*
 – Adipose fin long, approximately 2 × anal fin length; nuchal plate not reaching the posterior portion of head 27
- 27 Body very elongate, depth contained 8.0 × in standard length; 4 dark brown dorsal transverse bands (first at vertical passing at pectoral fin, second at vertical passing anterior portion of dorsal-fin base, third at vertical passing at last third of dorsal-fin base, and the last one at vertical passing at adipose-fin origin); eyes dorsally placed *Imparfinis borodini*
 – Body short, depth contained up to 6.0 × in standard length; dark brown dorsal transverse bands absent; eyes laterally placed 28
- 28 Body uniformly clear; longitudinal black stripe on flank present; maxillary barbels long, and reaching or surpassing the anal-fin origin.....
 *Pimelodella avanhadavae*
 – Body with small dark spots or irregular vermiculations; longitudinal black stripe on flank absent; maxillary barbels short, never reaching the anal-fin origin..... 29
- 29 Anal-fin rays up to 12; eyes large, approximately 5 × head length.....
 *Rhamdia quellen*
 – Anal-fin rays more than 15; eyes small, more than 7.5 × head length.....
 *Rhamdiopsis* sp.
- 30 Dorsal and anal fins anterior rays modified into spines; pelvic fin in thoracic position, below of pectoral fin; lateral line divided into 2 branches, 1 anterior, near the base of the dorsal fin and another posterior, along the middle portion of the body and caudal peduncle; ctenoid scales..... 31
 – Dorsal and anal fins anterior rays not modified into spines; pelvic fin posteriorly located, close to anal fin; lateral line not divided into 2 branches; cycloid or spinoid scales..... 37
- 31 Dorsal-fin spines separate from soft rays by notch..... *Cichla piquiti*
 – Dorsal-fin spines not separate from soft rays by notch..... 32
- 32 Body elongate (fusiform), 3.6–5.2 × in standard length; preoperculum posterior margin serrated 33
 – Body deep, more than 3.5 × in standard length; preoperculum posterior margin smooth 34
- 33 Scales in longitudinal series 33–40; flank with black transverse bands; dorsal fin with XVI + 14 or 15 rays; anal fin with III + 9 or 10 rays; black humeral blotch present *Crenicichla britskii*
 – Scales in longitudinal series 41–50; flank without black transverse bands (crossing the longitudinal stripe); dorsal fin with XIX–XXI + 10–12 rays; anal fin with III + 7 or 8 rays; black humeral blotch absent.....
 *Crenicichla jaguarensis*

- 34 Anterior lateral line with 19 or fewer scales; scales in longitudinal series 22–27; black lateral spot present.....**35**
- Anterior lateral line with 20 or more scales; scales in longitudinal series 28–35; black lateral spot absent**36**
- 35 Posterior lateral line with 10–14 scales; scales in longitudinal series 24–27; dorsal fin with XV or XVI + 10–13 rays; black lateral spot on flank larger than the eye diameter..... ***Geophagus brasiliensis***
- Posterior lateral line with 5–8 scales; scales in longitudinal series 22 or 23; dorsal fin with XIII or XV + 10–15 rays; black lateral spot approximately equal than the eye diameter***Cichlasoma paranaense***
- 36 Scales in transverse series above the lateral line 3 or 3½; gill rakers in inferior branch of the first branchial arch 18 or more ***Oreochromis niloticus***
- Scales in transverse series above the lateral line 2 or 2½; gill rakers in inferior branch of the first branchial arch 15 or fewer..... ***Coptodon rendalli***
- 37 Top of head covered by scales; upper jaw protractile**38**
- Top of head not covered by scales; upper jaw non-protractile.....**40**
- 38 Dorsal fin closer to caudal fin than to middle of body; gonopodium absent.....
.....***Melanorivulus giarettai***
- Dorsal fin at middle of body; gonopodium present.....**39**
- 39 Males with intense colored spots in life, black when preserved; females without spots; gonopodium with moderate size (3.2–3.6 × in standard length), with terminal portion almost straight..... ***Poecilia reticulata***
- Males and females with vertically elongate black spot on medium portion of flank; gonopodium long (2.6–3.1 × in standard length), with terminal portion trifid and ventrally oriented***Phalloceros harpagos***
- 40 Teeth absent in adults ***Steindachnerina insculpta***
- Teeth present in all life stages**41**
- 41 Teeth small, numerous and depressibly implanted in the lips
.....***Prochilodus lineatus***
- Teeth well-developed, non-depressibly implanted in the jaw bones**42**
- 42 Body fusiform or moderately compressed laterally; abdominal serrae absent.....
.....**43**
- Body very compressed laterally; abdominal serrae present**70**
- 43 Teeth incisiform (rabbit-like), truncated or cuspidate, premaxillary and dentary with 3 teeth each, premaxillary with 3 and dentary with 3 or 4 teeth, or premaxillary and dentary with 4 teeth each.....**44**
- Teeth conical or multicuspid, no incisiform; teeth number variable, but not as above**48**
- 44 Teeth cuspidate; flank silver in life, spots or bands absent; a conspicuous, horizontally elongate black spot at end of caudal peduncle extending to the median caudal-fin rays***Schizodon nasutus***
- Teeth truncated; body with large black spots or longitudinal stripes; horizontally elongate black spot on end of caudal peduncle absent**45**

- 45 Premaxillary and dentary with 4 teeth each; 3 large black spots on flank (first bellow dorsal fin, second above the anal-fin base and third at the end of caudal peduncle ***Leporinus friderici***
- Premaxillary with 3 teeth; dentary with 3 or 4 teeth, body with longitudinal black stripes or transverse bars, large black spots on flank absent..... **46**
- 46 Premaxillary and dentary with 3 teeth each; black longitudinal stripe on flank present; dorsal dark transverse bars (but not reaching the longitudinal stripe) 10 or more; subterminal mouth; prominent snout.....
- ***Leporinus amblyrhynchus***
- Premaxillary with 3 teeth; dentary with 4 teeth; black dorsal transverse bars absent; terminal or subterminal mouth; non-prominent snout **47**
- 47 Body elongate, depth 4.1 × in standard length; four longitudinal black stripes on flank; fins usually hyaline or slightly red..... ***Leporinus striatus***
- Body deep, depth 3.2 × in standard length; eight black transverse bars on flank; fins yellow, orange or red in life..... ***Leporinus octofasciatus***
- 48 Premaxillary teeth in 1 row **49**
- Premaxillary teeth in 2 or more rows..... **57**
- 49 Adipose fin absent; posterodorsal portion of head with straight margin; caudal fin rounded or truncate **50**
- Adipose fin usually present; posterodorsal portion of head convex or with a posterior projection; caudal fin forked or emarginate **52**
- 50 Dorsal-fin rays up to 11; pectoral, pelvic and anal fins without dark brown stripes; teeth canine on maxillary absent ***Hoplerythrinus unitaeniatus***
- Dorsal-fin rays more than 12; pectoral, pelvic and anal fins with dark brown stripes; teeth canine on maxillary present **51**
- 51 Medial margin of dentary bones parallel in ventral view; denticles on tongue absent ***Hoplias intermedius***
- Medial margin of dentary bones converging towards the symphysis in ventral view; denticles on tongue present..... ***Hoplias aff. malabaricus***
- 52 Teeth on anterior portion of dentary absent; lower jaw anterior portion straight **53**
- Teeth on anterior portion of dentary present; lower jaw anterior portion rounded..... **56**
- 53 Dentary teeth present ***Parodon nasus***
- Dentary teeth absent..... **54**
- 54 Black lateral stripe with broad projections above and below, giving a zig-zag appearance; body greenish in life..... ***Apareiodon ibitiensis***
- Black lateral stripe without broad projections above and below; 6–8 transverse, rectangular or triangular black thin bars above; body silver in life.....
- **55**
- 55 Scales in pre-anal series 29 or fewer; premaxillary teeth cusps up to 12 ***Apareiodon piracicabae***
- Scales in pre-anal series 29½ or more; premaxillary teeth cusps 12–15.....
- ***Apareiodon affinis***

- 56 Adipose fin absent; pectoral-fin unbranched rays 10–13; principal caudal-fin rays 16..... *Crenuchidae* (undescribed genus and species)
- Adipose fin present; pectoral-fin unbranched rays 3; principal caudal-fin rays 18 or 19..... *Characidium aff. zebra*
- 57 Premaxillary teeth in three rows; teeth conical in the symphysis region present..... *Brycon nattereri*
- Premaxillary teeth in two rows; teeth conical in the symphysis region absent..... 58
- 58 Teeth on the palate present..... *Oligosarcus pintoi*
- Teeth on the palate absent..... 59
- 59 Anal-fin branched rays more than 30; spinoid scales..... *Galeocharax gulo*
- Anal-fin branched rays up to 29; cycloid scales..... 60
- 60 Lateral line incomplete..... 61
- Lateral line complete..... 62
- 61 Adipose fin present..... *Hyphessobrycon uaiso*
- Adipose fin absent..... *Hasemanian uberaba*
- 62 Internal series of premaxillary with 4 teeth; body relatively elongate, depth 3.0–4.2 × in standard length..... 63
- Internal series of premaxillary with 5 teeth; body relatively deep, depth 1.8–3.6 × in standard length..... 66
- 63 Upper jaw projecting anteriorly; premaxillary teeth misaligned..... *Piabina argentea*
- Upper and lower jaws of equal size; premaxillary teeth aligned..... 64
- 64 Supraorbital groove present; caudal-fin lobes covered by small scales..... *Knodus aff. moenkhausii*
- Supraorbital groove absent; scales only at the caudal-fin base..... 65
- 65 Dorsal stripe broad, extending from the supraoccipital crest to the caudal-fin base, with a gap at the region of the adipose fin; humeral spot conspicuous.... *Bryconamericus turiuba*
- Dorsal stripe narrow, continuous, extending from the supraoccipital crest to the caudal-fin base; humeral spot inconspicuous or absent.... *Piabarchus stramineus*
- 66 Maxillary teeth absent; humeral spot clearly defined, horizontally elongate associated with two diffuse vertical black stripes; fins yellow in life..... *Astyanax lacustris*
- Maxillary teeth present; humeral spot absent or inconspicuous; fins orange or red in life..... 67
- 67 Flank with a silvery longitudinal stripe; scales on abdomen without chromatophores on distal portion..... *Astyanax aff. fasciatus*
- Flank without silvery longitudinal stripe; scales on abdomen with black chromatophores on distal portion..... 68
- 68 Body relatively deep, up to 3.0 × in standard length; anal-fin rays 22 or more..... *Astyanax bockmanni*
- Body relatively elongate, more than 3.1 × in standard length; anal-fin rays 20 or fewer..... 69

- 69 Eye with light iris, silver in life; pelvic-fin tip reaching anal fin.....
*Astyanax aff. paranae*
- Eye with dark iris, gold or brown in life; pelvic-fin tip not reaching anal fin.....
*Astyanax paranae*
- 70 Teeth tricuspid present; premaxilla and dentary teeth in 1 row
*Serrasalmus maculatus*
- Teeth tricuspid absent; premaxilla and dentary teeth in 2 rows (the inner
 dentary row represented by 2 small conical teeth71
- 71 Adipose-fin base longer than taller; dorsal-fin rays 20 or fewer; pre-dorsal
 spine present..... *Metynnis lippincottianus*
- Adipose-fin base taller than longer; dorsal-fin rays 20 or more; pre-dorsal
 spine absent *Myloplus tiete*

Discussion

The diversity recorded in the Uberaba River (73) is slightly greater than in similar tributaries of the Grande River in São Paulo state, in which 64 species have been recorded in the tributaries of the Pardo, Turvo, and Sapucaí rivers (Castro et al. 2004). Our data increase the number of species previously recorded for the Uberaba River by 44, which corresponds to an increase of 150% of the species referred so far in the region (see more details in SEMEA 2004; Souza et al. 2016). However, these figures may reflect the differences in sampling methods used by us and the previous authors as well as a larger area investigated in this study. Estimates of species richness and diversity considerably depend on methods used as discussed by Oliveira et al. (2014).

The number of species (73) recorded in the Uberaba River comprises ca. 19% of the total species number known in the Upper Paraná River system when compared to the data in Langeani et al. (2007). The ichthyofauna of the Uberaba River is composed mainly of autochthonous species, few allochthonous species and only two exotic species. The autochthonous origin of some of these species in the Upper Parana River still needs further research. For example, the scarcity of data on the origin or taxonomic status of some putative species such as *Knodus aff. moenkhausii*, *Trichomycterus brasiliensis* or *Megalechis thoracata*, does not allow to reasonably hypothesize on their origin.

Some species recorded in the Uberaba River potentially correspond to new species and some considerations are provided. *Astyanax fasciatus* (Cuvier) is described for the São Francisco River basin and it is widely distributed in the Paraná-Paraguay drainage and coastal drainages of eastern of Brazil. However, based on the definitions by Eigenmann (1921) it is possible to infer the existence of a "*A. fasciatus* species complex" in the Paraná-Paraguay and other coastal drainages. Thus, the name *A. fasciatus* should be used strictly for the São Francisco River lineage (Melo and Buckup 2006). In the La Plata drainage, the *Hoplias malabaricus* species group is constantly corroborated by morphological, cytogenetic and molecular evidence, and a recognition and taxonomic delineating of new entities is currently in progress (Rosso et al. 2018). Additionally, the nominal

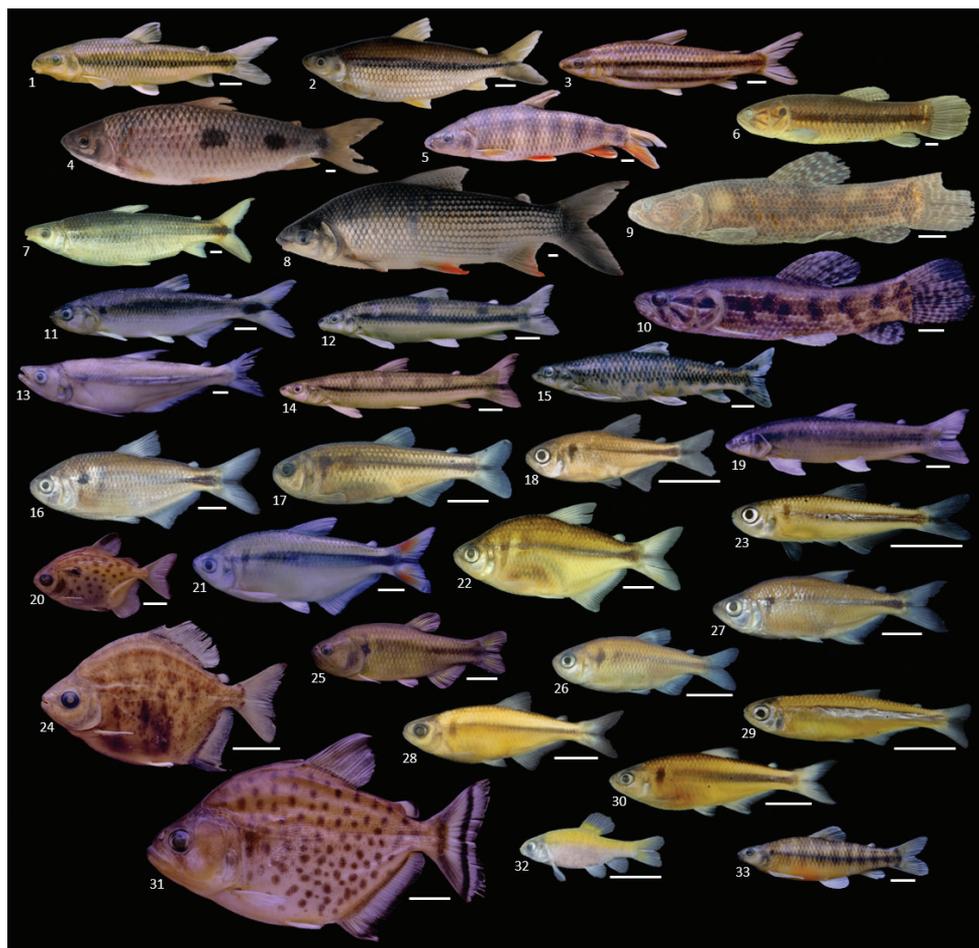


Figure 6. Characiformes collected in the Uberaba River. **1** *Leporinus amblyrhynchus* **2** *Steindachnerina insculpta* **3** *Leporinus striatus* **4** *Leporinus friderici* (uncataloged) **5** *Leporinus octofasciatus* **6** *Hoplerythrinus unitaeniatus* **7** *Schizodon nasutus* **8** *Prochilodus lineatus* **9** *Hoplias intermedius* **10** *Hoplias* aff. *malabaricus* **11** *Brycon nattereri* **12** *Apareiodon piracicabae* **13** *Galeocharax gulo* **14** *Apareiodon affinis* **15** *Apareiodon ibitiensis* **16** *Astyanax lacustris* **17** *Astyanax paranae* **18** *Astyanax* aff. *paranae* **19** *Parodon nasus* **20** *Metynnis lippincottianus* **21** *Astyanax* aff. *fasciatus* **22** *Astyanax bockmanni* **23** *Bryconamericus turiuba* **24** *Myloplus tiete* **25** *Hasemania uberaba* **26** *Hyphessobrycon uaiso* **27** *Oligosarcus pintoi* **28** *Knodus* aff. *moenkhausii* **29** *Piabarchus stramineus* **30** *Piabina argentea* **31** *Serrasalmus maculatus* **32** Crenuchidae (undescribed genus and species) and **33** *Characidium* aff. *zebra*. Photographs are of specimens presented in Table 2. Scale bar: 10 mm.

species name *Hoplias malabaricus* (Bloch) should be applied exclusively to the Guiana shield lineage (Rosso et al. 2018). Similarly, some authors (see Buckup 1992) suggest that populations of *Characidium zebra* Eigenmann throughout South America represent more than one species. *Characidium zebra* was described in tributaries of the Branco River (Negro River system) in the Amazon. Recent evidence suggests that *C. zebra* popu-

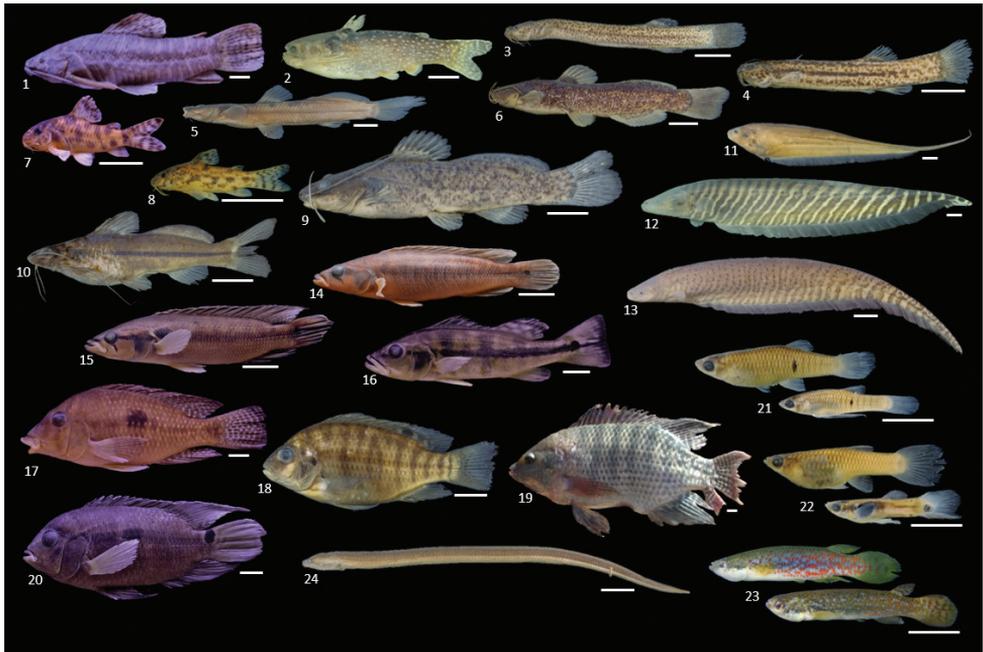


Figure 7. Siluriformes (Loricariidae absent), Gymnotiformes, Cichliformes, Cyprinodontiformes, and Synbranchiformes collected in the Uberaba River. **1** *Megalechis thoracata* **2** *Tatia neivai* **3** *Trichomycterus candidus* **4** *Trichomycterus brasiliensis* **5** *Imparfinis borodini* **6** *Rhamdiopsis* sp. **7** *Corydoras difluviatilis* **8** *Aspidoras fuscoguttatus* **9** *Rhamdia quelen* **10** *Pimelodella avanhadavae* **11** *Eigenmannia trilineata* **12** *Gymnotus sylvius* **13** *Gymnotus inaequilabiatus* (uncataloged) **14** *Crenicichla jaguarensis* **15** *Crenicichla britskii* **16** *Cichla piquiti* **17** *Geophagus brasiliensis* **18** *Coptodon rendalli* **19** *Oreochromis niloticus* (uncataloged) **20** *Cichlasoma paranaense* **21** *Phalloceros harpagos* (female above and male below) **22** *Poecilia reticulata* (female above and male below) **23** *Melanorivulus giarettai* (male above and female below) and **24** *Synbranchus marmoratus*. Photographs are of specimens presented in Table 2. Scale bar: 10 mm.

lations in the San Francisco and Paraná rivers correspond to the same species (Serrano et al. 2018) distinct from the *C. zebra* populations of the Amazon drainage.

Astyanax aff. *paranae* Eigenmann collected from the Uberaba River may represent a distinct species in the complex “*Astyanax scabripinnis* species complex” sensu Moreira-Filho and Bertollo (1991), a group with an underestimated diversity (Bertaco and Malabarba 2001) as it differs by a number of features (e.g., eye coloration and some measurements). *Knodus moenkhausii* (Eigenmann & Kennedy) was described from the Arroyo Trementina in the Paraguay River system. The specimens from the Upper Paraná River and identified so far as *K. moenkhausii* apparently represents an undescribed species (F. R. Carvalho pers. comm.).

The taxonomic boundaries of the *Hypostomus* species are unclear. Some species of the genus *Hypostomus* are highly variable morphologically and widely distributed. In addition, some important diagnostic characters, such as color pattern, cannot be seen at present in type specimens collected more than 100 years ago, making identification of the species difficult (Zawadzki et al. 2004). For example, *Hypostomus hermanni* Ihering is widely dis-



Figure 8. Loricariidae, genus *Hypostomus* collected in the Uberaba River (dorsal, lateral, and ventral photographs). **1** *Hypostomus ancistroides* **2** *Hypostomus albopunctatus* **3** *Hypostomus strigaticeps* **4** *Hypostomus margaritifera* **5** *Hypostomus butantanis* **6** *Hypostomus regani* **7** *Hypostomus* aff. *paulinus* **8** *Hypostomus topavae* and **9** *Hypostomus nigromaculatus*, Photographs are of specimens presented in Table 2. Scale bar: 10 mm.

tributed within the Upper Paraná River system. A comparison of the specimens collected in the Uberaba River with specimens from other locations revealed a discrepancy in some meristic and color traits. The Uberaba specimens are especially different from specimens from the Piracicaba River, the type locality of *H. hermanni*. It has been also shown that



Figure 9. Another loricariids collected in the Uberaba River (dorsal, lateral, and ventral photographs). **1** *Hypostomus* aff. *hermanni* **2** *Hypostomus fluviatilis* **3** *Rineloricaria latirostris* **4** *Proloricaria prolixa* **5** *Curculionichthys insperatus* **6** *Microlepodogaster dimorpha* and **7** *Loricaria lentiginosa* (uncataloged). Photographs are of specimens presented in Table 2. Scale bar: 10 mm.

different populations of *Hypostomus paulinus* (Ihering) are effectively reproductively isolated and characterized by a high degree of inbreeding (Zawadzki et al. 2004).

The occurrence of *Metynnys lippincottianus* may be a result of accidental introduction (Ota 2015). Among the allochthonous species, *Poecilia reticulata* was introduced to control mosquito larvae (Ota et al. 2018). *Cichla piquiti* was probably introduced for sport fishing (Langeani et al. 2007; Ota et al. 2018), and *Gymnotus inaequilabiatus* originally from the Lower Paraná River, Paraguay and Uruguay rivers (Maxime and Albert 2014), colonized the upper reaches of the Paraná River after the construction of the Itaipu hydroelectric dam in the 1980s. Ota et al. (2018) suggested that the occurrence of *Hoplerhythrinus unitaeniatus* in the Upper Paraná River can be associated with its introduction as a live bait or after inundation of the Sete Quedas Falls after the construction of the Itaipu dam. *Galeocharax gulo* is widely distributed in almost all Upper Amazon River systems, also in the Orinoco, Oyapok, Araguaia-Tocantins, and Paraná rivers (Giovannetti et al. 2017). The occurrence of this species in the Upper Paraná system may be a result of natural dispersion. *Coptodon rendalli* and *O. niloticus* probably represent results of escapes from fish farms (Langeani et al. 2007; Ota et al. 2018) and the populations of both species are probably established in the region as they have been regularly registered since long ago. Finally, Souza et al. (2016) report the occurrence of *Cyphocharax nagelii* (Steindachner) and *Steindachnerina brevipinna* (Eigenmann & Eigenmann) in the system, but we could not confirm these data and refrained from including them in the species list.

New taxa have been described from the Uberaba River system over the past decade, e.g., *Hasemaniania uberaba* (Serra and Langeani 2015), *Hyphessobrycon uaiso* (Carvalho and Langeani 2013), and *Microlepidogaster dimorpha* (Martins and Langeani 2011). These newly described species are only known from their type localities or from a few localities corroborating several examples of endemism in the Upper Paraná River, previously indicated by some authors (e.g., Langeani et al. 2007). This clearly demonstrates the importance of inventories and consequent conservation measures. Two species registered in the Uberaba River are definitely threatened: *Brycon nattereri* Günther and *Myloplus tiete* (Eigenmann & Norris) are assigned to “Vulnerable” (VU) and “Endangered” (EN) respectively, on the IBAMA Red List of Endangered Species (ICMBio 2015). The main threats to the local fauna are related to changes in hydrological cycles and the loss of riparian vegetation, as well as overexploitation of natural stocks (Lima et al. 2008; Lima et al. 2015). In addition, the presence of migratory rheophilic species such as *Prochilodus lineatus* (Valenciennes), *Leporinus friderici* (Bloch), *B. nattereri*, and *M. tiete*, is because these species use local resources, at least partially, to complete their life cycle, as suggested by Carolsfeld et al. (2003). Considering all the factors discussed above, the Uberaba River contains a diverse and heterogeneous fish fauna, with two endemic species, *H. uberaba* and an undescribed crenuchid (a description is in the process by Ribeiro et al.) and a low number of allochthonous and exotic species. The Uberaba River has undergone several anthropogenic actions over the last decades, such as the increase of the area destined to grazing, resulting in only 17.7% of native vegetation remains (Valle-Junior et al. 2010) and the reduction of the lotic environments due to damming. The impact of human-induced environmental change is dramatic on the structure and composition of the local fauna. Development of management plans on conservation areas such as the implementation of “Área de Proteção Ambiental Rio Uberaba – APA-Rio Uberaba” project (SEMEA 2004) is necessary to mitigate the effects and help the sustainable use of local natural resources.

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