ZooKeys 1067: 1–17 (2021)
doi: 10.3897/zookeys.1067.68105
https://zookeys.pensoft.net

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An overview of Estonian woodlice (Isopoda, Oniscidea)

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Academic editor: Ivan H. Tuf | Received 6 June 2021 | Accepted 25 September 2021 | Published 29 October 2021

http://zoobank.org/0B7D181D-5647-42A7-B1CB-A01BD31FC52D

Citation: Sammet K, Orgusaar G, Ivask M, Kurina O (2021) An overview of Estonian woodlice (Isopoda, Oniscidea). ZooKeys 1067: 1–17. https://doi.org/10.3897/zookeys.1067.68105

Abstract

An overview of the Estonian terrestrial isopod fauna is given, based on literature data and material collected from 1984 to 2021. The identified material consisted of 10915 specimens belonging to 14 species and collected from 172 localities throughout Estonia. In combination with previous data from the literature data, there are now reliable records of 16 species of woodlice from Estonia. Two species, viz. *Platyarthrus hoffmannseggii* Brandt, 1833 and *Hyloniscus riparius* (C. Koch, 1838), are new for the fauna. The latter has probably colonised Estonia recently and range expansions have been reported elsewhere. The data on *Philoscia muscorum* (Scopoli, 1763) are dubious, and this species is currently excluded from the Estonian list.

Keywords

Estonia, Oniscidea, range shifts, soil arthropods

Introduction

The knowledge on Estonian terrestrial isopods is scattered in various publications, without a modern overview of the fauna. Some publications are in Estonian and may be thus inaccessible to the wider audience.

Data on this group were first given by J. B. Fischer, who mentioned the presence of *Oniscus asellus* Linnaeus in Livonia (Fischer 1778: 167), an earlier administrative

division, which covered the southern part of present-day Estonia and northern Latvia. The identity of the abovementioned species is unclear, as most of European species were yet to be described. At the beginning of 20th century, W. Herold collected material in many places in Estonia and Latvia, published the results in several works (Herold 1927, 1928, 1930), and provided the first reliable overview of the fauna, which included 13 Estonian species. Later, Estonian entomologist J. Vilbaste published new records in three local faunistic studies (Vilbaste 1970; Vilbaste et al. 1985; Vilbaste and Vilbaste 1993) and K. Remm added one record (Remm 1988).

A lot of unidentified material from various research projects and fieldwork made over many years (1984–2020) has been stored in the entomological collection of Estonian University of Life Sciences (including the zoological collections of the former Institute of Zoology and Botany of the Estonian Academy of Sciences) and Tallinn University of Technology (TalTech) soil biology laboratory. Based on these materials and literature records, an account of the current knowledge is given below.

Material and methods

As complete as possible, a bibliography of historical records of terrestrial isopods in Estonia was compiled. New material was collected using: (1) pitfall traps, (2) Tullgren funnels, (3) sifting moss, leaf litter, and detritus with standard entomological sieves, (4) manual searching in suitable habitats, and (5) as bycatch of non-target species with window traps (attached to tree trunks; Sammet et al. 2016) and Malaise traps (for details of the Estonian Malaise trap project, see Tomasson et al. 2014). The material was collected from 172 localities throughout Estonia (Table 1; Figure 1). All studied material is preserved in 80% ethanol and deposited in the entomological collection of Estonian University of Life Sciences (**IZBE**) and soil biology laboratory of TalTech Tartu College (**TTUSB**), both in Tartu, Estonia. Various keys for European woodlice were used for identification (Palmen 1946; Frankenberger 1959; Vandel 1960, 1962; Gruner 1966; Oliver and Meecham 1993). The distributions of Estonian species (Fig. 5) are presented in a 50 × 50 km UTM grid (compiled using Adobe Photoshop CS5 Extended). The images of the general habitus were combined using the LAS V.4.1.0 software from multiple gradually focused images of the specimens in alcohol taken by a Leica DFC 450 camera attached to Leica 205C stereomicroscope.

Results

Altogether 14142 specimens were collected. Of these, 10915 were identified to the species level. The following list contains all the known published records of Estonian woodlice, followed by numbers of studied specimens and collecting localities. Full details for each record from each locality are given in Suppl. material 1. An asterisk (*)

Table 1. Collecting localities of Estonian Oniscidea. The localities' numbers correspond to those on Figure 1. Localities within a range of less than 10 km are presented by one number, the different place names (sub-localities) under one number are designated consecutive letters (the coordinates apply only to the first of them).

No.	Latitude, Longitude	Name	Methods used
1	58.3132°N, 21.9089°E	a Eeriksaare 1, b Eeriksaare 2, c Kõruse 1, d Kõruse 2, e Tammese, f Neeme	manual collecting; pitfall trapping; Tullgren funnel
2	58.3009°N, 21.9351°E	a Atla 1, b Atla 2, c Atla 3	manual collecting; pitfall trapping
3	57.9767°N, 21.9954°E	a Türju, b Sõrve south	manual collecting; pitfall trapping
4	58.2731°N, 22.0114°E	a Leedri, b Kipi, c Viidu-Mäebe, d Audaku, e Sutru, f Nakimetsa, g Pitkasoo	sifting soil and litter; manual collecting; pitfall trapping, Tullgren funnel
5	58.1213°N, 22.1966°E	Kaugatoma	manual collecting; pitfall trapping
6	58.0000°N, 22.1667°E	Viieristi	manual collecting
7	58.5167°N, 22.2167°E	a Mustjala, b Kugalepa, c Panga	manual collecting; Tullgren funnel
8	58.3186°N, 22.3057°E	a Mõnnuste, b Paadla	manual collecting; pitfall trapping
9	58.2425°N, 22.4249°E	Nasva	manual collecting; pitfall trapping
10	58.2496°N, 22.4800°E	Kuressaare	manual collecting; pitfall trapping
11	58.9445°N, 22.4361°E	a Paope b Reigi	manual collecting; pitfall trapping
12	58.1225°N, 22.5013°E	Abruka	manual collecting; Tullgren funnel
13	58.3005°N, 22.6337°E	Ilpla	manual collecting; pitfall trapping
14	58.2433°N, 22.6741°E	a Vanamõisa 1, b Vanamõisa 2, c Vanamõisa 3	manual collecting; pitfall trapping
15	58.4563°N, 22.7076°E	a Tika, b Võrsna	manual collecting; pitfall trapping; Tullgren funnel
16	58.7683°N, 22.8143°E	Kassari	manual collecting; pitfall trapping
17	58.8639°N, 22.9836°E	a Aruküla 1, b Aruküla 2, c Saarnaki, d Heltermaa, e Sarve	manual collecting; pitfall trapping; Tullgren funnel
18	58.7769°N, 23.0472°E	a Hanikatsi, b Langekare	manual collecting; pitfall trapping
19	58.5842°N, 23.0236°E	Orinõmme	manual collecting; pitfall trapping
20	58.4389°N, 23.0681°E	Asva 1	manual collecting; pitfall trapping
21	58.5557°N, 23.0879°E	Orissaare	manual collecting; pitfall trapping
22	58.6132°N, 23.0850°E	Koguva	manual collecting; pitfall trapping
23	58.7421°N, 23.1349°E	Ahelaid	Tullgren funnel
24	58.6412°N, 23.1536°E	a Paenase, b Pallasmaa, c Nõmmküla, d Üügu	manual collecting; pitfall trapping; Tullgren funnel
25	58.9917°N, 23.1928°E	Vormsi	manual collecting; pitfall trapping; Tullgren funnel
26	58.4617°N, 23.2111°E	a Kahtla, b Kübassaare	manual collecting; pitfall trapping Tullgren funnel
27	57.8006°N, 23.2283°E	a Ruhnu 1, b Ruhnu 2	manual collecting; window pane trap
28	58.5786°N, 23.2653°E	a Mäla 1, b Mäla 2, c Võiküla 3, d Võiküla 1	manual collecting; pitfall trapping
29	58.6501°N, 23.3133°E	a Lõetsa 1, b Lõetsa 2	manual collecting; pitfall trapping
30	58.6413°N, 23.5133°E	Hanila	manual collecting; pitfall trapping
31	58.5880°N, 23.5286°E	a Virtsu, b Puhtu, c Laelatu, d Pivarootsi	manual collecting; pitfall trapping; Tullgren funnel
32	59.0084°N, 23.6934°E	Linnamäe	manual collecting; pitfall trapping
33	58.5337°N, 23.8299°E	Paadermaa	manual collecting; pitfall trapping
34	58.8312°N, 23.8785°E	a Keskvere, b Patsu	manual collecting; pitfall trapping; Tullgren funnel
35	58.3818°N, 23.9810°E	a Ermistu, b Tõhela	manual collecting; pitfall trapping; Tullgren funnel
36	58.9020°N, 24.0287°E	a Marimetsa, b Kullamaa 1, c Kullamaa 2	manual collecting; Tullgren funnel
37	58.9947°N, 24.0559°E	Risti	manual collecting; Tullgren funnel
38	58.6455°N, 24.1253°E	Kurese	manual collecting; Tullgren funnel
39	58.7760°N, 24.2496°E	Vigala	manual collecting; Tullgren funnel
40	58.8960°N, 24.3758°E	Sõtke	manual collecting; pitfall trapping; Tullgren funnel
41	58.3864°N, 24.3695°E	a Valgeranna, b Pärnu	manual collecting; Tullgren funnel
42	58.0195°N, 24.4532°E	Kabli	manual collecting; Tullgren funnel
43	58.0807°N, 24.4889°E	a Häädemeeste, b Palitsa	manual collecting; Tullgren funnel
44	58.2429°N, 24.4965°E	Tahkuranna	manual collecting; Tullgren funnel
45	59.3339°N, 23.9703°E	Väike-Pakri	manual collecting; Tullgren funnel
46	59.5933°N, 24.5025°E	Naissaar	manual collecting; Tullgren funnel
47	59.4425°N, 24.5228°E	a Rannamõisa MKA b Muraste c Tõmmiku	manual collecting; pitfall trapping; Tullgren funnel
48	59.3411°N, 24.6386°E	a Tänassilma cave, b Vana-Mustamäe	manual collecting; pitfall trapping; Tullgren funnel
49	59.2661°N, 24.6483°E	Kasemetsa	manual collecting; Tullgren funnel
50	59.4293°N, 24.7777°E	central Tallinn	manual collecting; Tullgren funnel
51	59.5297°N, 24.8578°E	Lubja	manual collecting; Tullgren funnel
52	59.2378°N, 24.9311°E	Sõmeru	manual collecting; Tullgren funnel
53	59.4631°N, 24.9378°E	a Maardu, b Muuga, c Ülgase cave	manual collecting; pitfall trapping; Tullgren funnel
54	58.9703°N, 24.7294°E	a Kuusiku, b Raela, c Raikküla	manual collecting; pitfall trapping; Tullgren funnel
55	58.3333°N, 25.3000°E	Kõpu	manual collecting; Tullgren funnel
56	58.1562°N, 25.3390°E	Koodioru	manual collecting

No.	Latitude, Longitude	Name	Methods used
57	58.1557°N, 25.4360°E	a Halliste, b Viivre	manual collecting; pitfall trapping; Tullgren funnel
58	59.0835°N, 25.4053°E	Mustla	manual collecting; Tullgren funnel
59	58.8893°N, 25.5725°E	Paide	manual collecting; Tullgren funnel
60	58.6304°N, 25.6196°E	a Koksvere, b Kirivere, c Kõo	manual collecting; Tullgren funnel
61	58.3738°N, 25.6127°E	Viljandi	manual collecting; Tullgren funnel
62	59.2553°N, 25.6669°E	Aegviidu	manual collecting; Tullgren funnel
63	59.6049°N, 25.9230°E	a Käsmu, b Natturi	manual collecting; pitfall trapping; Tullgren funnel
64	58.6548°N, 25.9685°E	Põltsamaa	manual collecting; Tullgren funnel
65	58.5332°N, 25.9468°E	a Kolga-Jaani, b Lalsi	manual collecting; Tullgren funnel
66	58.9996°N, 26.1168°E	Liigvalla	manual collecting; Tullgren funnel
67	59.0970°N, 26.1826°E	Vao	manual collecting; Tullgren funnel
68	59.2742°N, 26.1955°E	a Lasila, b Karunga, c Levala	manual collecting; pitfall trapping; Tullgren funnel
69	59.0233°N, 26.2444°E	Kamariku	manual collecting; pitfall trapping; Tullgren funnel
70	58.8669°N, 26.2625°E	a Tooma, b Kärde	manual collecting; pitfall trapping; Tullgren funnel
71	58.5948°N, 26.3631°E	a Kursi, b Tõrve, c Altnurga	manual collecting; Tullgren funnel
72	58.1072°N, 26.2767°E	Atra	manual collecting; pitfall trapping; Tullgren funnel
73	58.2066°N, 26.3825°E	a Käärdi, b Peedu	manual collecting; pitfall trapping; Tullgren funnel
74	57.5962°N, 26.2855°E	Olina	manual collecting; Tullgren funnel
75	57.7193°N, 26.5000°E	Mähkli	manual collecting; Tullgren funnel
76	57.8611°N, 26.5241°E	Vana-Antsla	manual collecting; Tullgren funnel
77	57.9510°N, 26.4368°E	Ilmjärve	manual collecting; Tullgren funnel
78	58.0062°N, 26.6073°E	Kaagvere	manual collecting; Tullgren funnel
79	57.5727°N, 26.6413°E	Mõisamõtsa	manual collecting; Tullgren funnel; window pane trap
80	58.5604°N, 26.6285°E	Valgma	manual collecting; Tullgren funnel
81	58.4103°N, 26.6394°E	a Tiksoja, b Tähtvere bog, c Õssu, d Maramaa, e TartuTähtvere, f Tartu central, g Tartu Aardla, h Raadi, I Aruküla cave	manual collecting; pitfall trapping; Tullgren funnel
82	58.2302°N, 26.7011°E	Kambja	manual collecting; Tullgren funnel
83	58.5950°N, 26.7719°E	a Tüükri, b Kalvi, c Oru, d Aseri	manual collecting; pitfall trapping; Tullgren funnel
84	59.3019°N, 26.8818°E	a Ilmaste, b Nüri, c Aidu	manual collecting; pitfall trapping; Tullgren funnel
85	59.2289°N, 27.3247°E	Mäetaguse NR	window pane trap
86	59.4448°N, 27.3348°E	Valaste	manual collecting; Tullgren funnel
87	58.7841°N, 26.9330°E	a Nõmme b Ruskavere	manual collecting; pitfall trapping; Tullgren funnel
88	58.7279°N, 26.8260°E	Odivere	manual collecting; pitfall trapping; Tullgren funnel
89	58.5170°N, 26.9224°E	a Välgi b Pataste	manual collecting; pitfall trapping; Tullgren funnel
90	58.6033°N, 27.1304°E	Alatskivi	manual collecting; Tullgren funnel
91	58.4968°N, 27.2376°E	Varnja	manual collecting; Tullgren funnel
92	58.2750°N, 27.3250°E	Järvselja	manual collecting; sifting soil and litter; Tullgren funnel
93	58.1148°N, 27.0474°E	Saessaare	manual collecting; Tullgren funnel
94	58.0965°N, 27.4744°E	Ristipalo	manual collecting; Tullgren funnel
95	57.7447°N, 27.3335°E	a Mõldri b Parmu	manual collecting; Tullgren funnel
96	57.8433°N, 27.4655°E	Piusa	manual collecting; Tullgren funnel
97	59.3573°N, 28.1970°E	Narva	manual collecting; Tullgren funnel

indicates a species new to Estonia. The full list of records with all details will be available through the Estonian eBiodiversity portal (http://elurikkus.ut.ee; Abarenkov et al. 2010) and Global Biodiverdsity Information Facility (https://www.gbif.org). Nomenclature and synonymics follow Schmalfuss (2003).

Ligiidae

Ligidium hypnorum Cuvier, 1792

Figs 4B, 5A

Published sources. Herold 1930: 478–479; Vilbaste and Vilbaste 1993: 317.

Studied material. 117 specimens from 13 localities (loc. 30a, 47b, 47c, 54c, 57b, 83c, 87a, 87b, 88a, 89a, 92a, 95a, 95b).

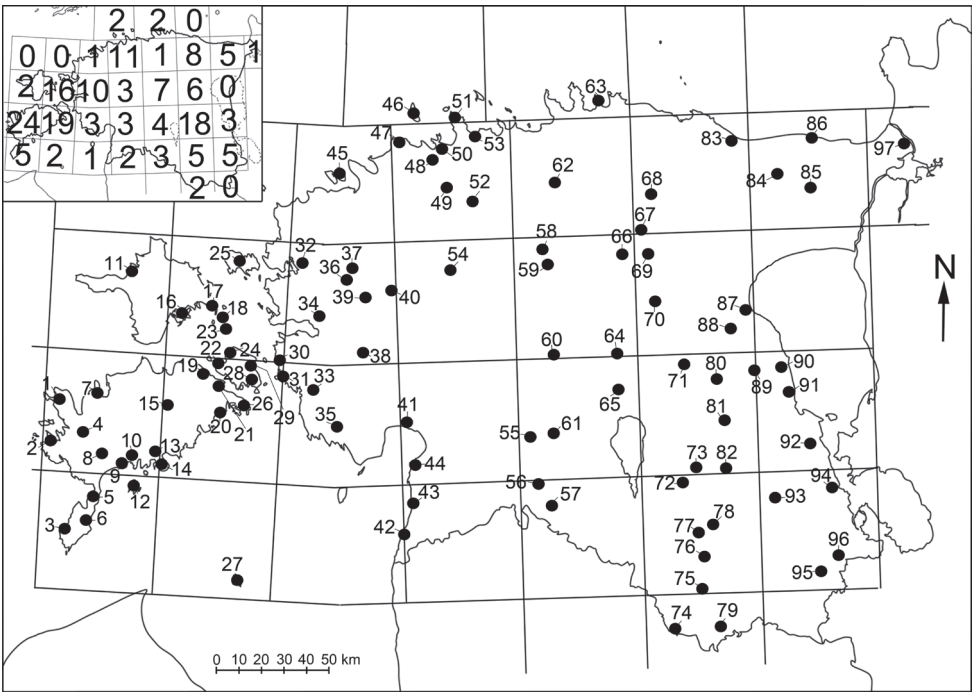

Figure 1. Collecting localities of Estonian Oniscidea and numbers of sampled localities per 50 × 50 km UTM squares. For further details, see Table 1.

Comments. A locally abundant species, with no records from Estonian islands. It has been described as widespread in Estonia also in the past (Herold 1930). The findings are from different habitats: fresh to mesic forests, meadows, arable fields and gardens. Present also in Lithuania (Vilisics et al. 2012) and Latvia (Spuņģis 2008) but not Finland (Boxhall 2013).

Trichoniscidae

Trichoniscus pusillus Brandt, 1833

Figs 3A, 5B

Published sources. Herold 1927: 6; Herold 1928: 215; Herold 1930: 479 (as *T. elisabethae* Herold, 1923; *T. elisabethae var. estoniensis* Herold, 1927; *T. caelebs* Verhoeff, 1917); Vilbste 1970: 170 (as *T. pusillus caelebs* Vh.); Vilbaste et al. 1985: 151 (as *T. pusillus caelebs* Vh.); Remm 1988: 127 (as *T. pusillus caelebs* Vh.); Vilbaste and Vilbaste 1993: 317.

Studied material. 117 specimens from 24 localities (loc. 1e, 4d, 17a, 23b, 25a, 34a, 35a, 39a, 40c, 47a, 50a, 51a, 57a, 58c, 68a, 74a, 78a, 78b, 78e, 80a, 80d, 83a, 89b, 92a).

Comments. Once reported as the most common species of Trichoniscidae (e.g. Herold 1927, 1930), the species appears to have become less abundant. It is

widespread in various habitats (bogs, different types of forests, meadows, and urban areas), but is more common in moist habitats and is often associated with decaying wood. The species is known to be mainly parthenogenetic (Gruner 1966; De Smedt et al 2016), and the collected material consisted only of female specimens. Thus, no male characters were available for study and it cannot be ruled out that some specimens were misidentified and other *Trichoniscus* species may also be present in Estonia as very rare (e.g. *T. provisorius* or *T. pygmaeus*). The taxonomic status of the described varieties *T. elisabethae* Herold, 1923 and *T. elisabethae* var. *estoniensis* Herold, 1927 is unclear, but we follow the Schmalfuss (2003) catalogue and treat them as *T. pusillus*. Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946; Vilisics and Terhivuo 2009).

****Hyloniscus riparius* (C. Koch, 1838)**
Figs 3B, 5C

Studied material. 202 specimens from 22 localities (loc. 12a, 23b, 35b, 39a, 39a, 49a, 50a, 52b, 53a, 55b, 57a, 58b, 59a, 60b, 61a, 69c, 70b, 78a, 78e, 78g, 83a, 85a).

Comments. The species is widespread and common, but has only recent records and is probably extending its range in the Europe. It has been often found in human settlements, but also seashore habitats and different types of forests, except the very dry ones. Present also in Latvia (Spuņģis 2008) and Finland (Vilisics and Terhivuo 2009).

***Haplophthalmus mengii* (Zaddach, 1844)**
Fig. 5D

Published source. Herold 1930: 479–480.

Comments. Reported as rare, with only one finding locality in northern Estonia (Herold 1930). No recent records. Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

Platyarthridae

****Platyarthrus hoffmannseggii* Brandt, 1833**
Figs 4A, 5E

Studied material. 3 specimens from 1 locality (loc. 80g).

Comments. A myrmecophilous species, found from a nest of *Lasius niger* (Linnaeus, 1758). There are no records from the northern Baltic region so far, but it has recently been found in Lithuania (Šatkauskienė 2017), and a population has also been found in Finland (Lehtinen 1961). However, due to the destruction of the only known locality, the species could be extinct there now (Vilisics and Terhivuo 2009).

Trachelipodidae

***Trachelipus rathkii* (Brandt, 1833)**
Figs 2A, 5F

Published sources. Herold 1927: 52 (as *Porcellio rathkei*); Herold 1930: 476 (as *Tracheoniscus rathkei* (Brandt, 1833)); Vilbaste 1970: 170 (as *Tracheoniscus rathkei* (Brandt, 1833)); Vilbaste et al. 1985: 151 (as *Tracheoniscus rathkei* (Br.)).

Studied material. 3180 specimens from 114 localities (loc. 1a, 1c, 1e, 1f, 3a, 3b, 4c, 6a, 7a, 9a, 9b, 10a, 10b, 11a, 12a, 13a, 14b, 15a, 15b, 16a, 17a, 17b, 17c, 17d, 18a, 18b, 18c, 19a, 20a, 21a, 22a, 23a, 23b, 23c, 25a, 27a, 28a, 28b, 29a, 30a, 30c, 30d, 33a, 33b, 34a, 34b, 35b, 35b, 35c, 35c, 37a, 38a, 39a, 40a, 40b, 41a, 41b, 42a, 46b, 51a, 51b, 52a, 52b, 53a, 55a, 56a, 57a, 58a, 58b, 59a, 60b, 61a, 62a, 63b, 64a, 65a, 66a, 66b, 66c, 66c, 67a, 68b, 69a, 69b, 70a, 71a, 72a, 73a, 76a, 77a, 78a, 78d, 78e, 78f, 78f, 79a, 80a, 80b, 80c, 80d, 81a, 81b, 81c, 82a, 83a, 84a, 85a, 86a, 87a, 90a, 91a, 91b).

Comments. One of the most common species in Estonia, in all kinds of habitats (both anthropogenic and natural, except bogs). It has also been described as widespread and common in Estonia in the past (Herold 1927, 1930). Present also in Leningrad region (European Russia, Kuznetsova and Gongalsky 2012), Latvia (Spuņģis 2008), and Finland (Palmén 1946).

Porcellionidae

***Porcellio scaber* Latreille, 1804**
Figs 2B, 5G

Published sources. Herold 1927: 52; Herold 1930: 481; Vilbaste et al. 1985: 151.

Studied material. 217 specimens from 13 localities (loc. 3b, 24a, 26a, 26b, 30b, 35c, 46b, 48a, 63a, 78c, 78e, 78f, 84a).

Comments. The species was described as purely synanthropic in continental Estonia and free-living in western Estonian islands (Herold 1927, 1930). The studied material contains findings from and outside of human settlements (including different forests, grasslands, and seashore) both from western islands and continent. Present also in Novgorod region (European Russia, Kuznetsova and Gongalsky 2012), Latvia (Spuņģis 2008), and Finland (Palmén 1946).

***Porcellio spinicornis* Say, 1818**
Figs 2C, 5H

Published sources. Herold 1927: 52; Herold 1930: 481 (as *P. pictus* Brandt, 1833); Vilbaste et al. 1985: 151 (as *P. pictus* Br.).)

Studied material. 68 specimens from 19 localities (loc. 4b, 6b, 20b, 32a, 35b, 39a, 40b, 46a, 51c, 52b, 60a, 61a, 78f, 78h, 78i, 84a, 89a, 93a, 97).

Comments. A common and widespread species, often found on stone walls in human settlements, but also in mesic deciduous forests. Present also in Leningrad region (European Russia, Kuznetsova and Gongalsky 2012), Latvia (Spuņģis 2008), and Finland (Palmén 1946).

***Porcellionides pruinosus* (Brandt, 1833)**

Published source. Herold 1930: 476.

Comments. No recent records. This species has been described as purely synanthropic in Estonia (Herold 1930). Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

Cylisticidae

***Cylisticus convexus* (De Geer, 1778)**
Figs 2D, 5I

Published sources. Herold 1927: 51; 480 Herold 1930: 480.

Studied material. 825 specimens from 5 localities (loc. 46b, 66a, 78e, 78f, 78g).

Comments. This species is widespread and locally quite abundant, both in human settlements and in forests, under stones or in rotten logs. It has been described as widespread and mainly synanthropic in Estonia by W. Herold, with free-living populations in northern and western Estonian islands (Herold 1930). Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

Oniscidae

***Oniscus asellus* Linnaeus, 1758**
Figs 2E, 5J

Published sources. Fischer 1778: 167 (questionable; see comment in Introduction); Herold 1930: 480.

Studied material. 433 specimens from 5 localities (loc. 4b, 6, 36b, 47b, 48b).

Comments. The species seems to be free-living on the island of Saaremaa, but synanthropic and sometimes quite abundant elsewhere. Herold (1930) described it as being widespread but purely synanthropic in Estonia. Present also in Latvia (Spuņģis 2008), Pskov region (European Russia, Kuznetsova and Gongalsky 2012), and Finland (Palmén 1946).

Armadillidiidae

***Armadillidium opacum* (Koch, 1841)**
Figs 3D, 5K

Published sources. Herold 1927: 53; Herold 1930: 483–485; Vilbaste et al. 1985: 151.

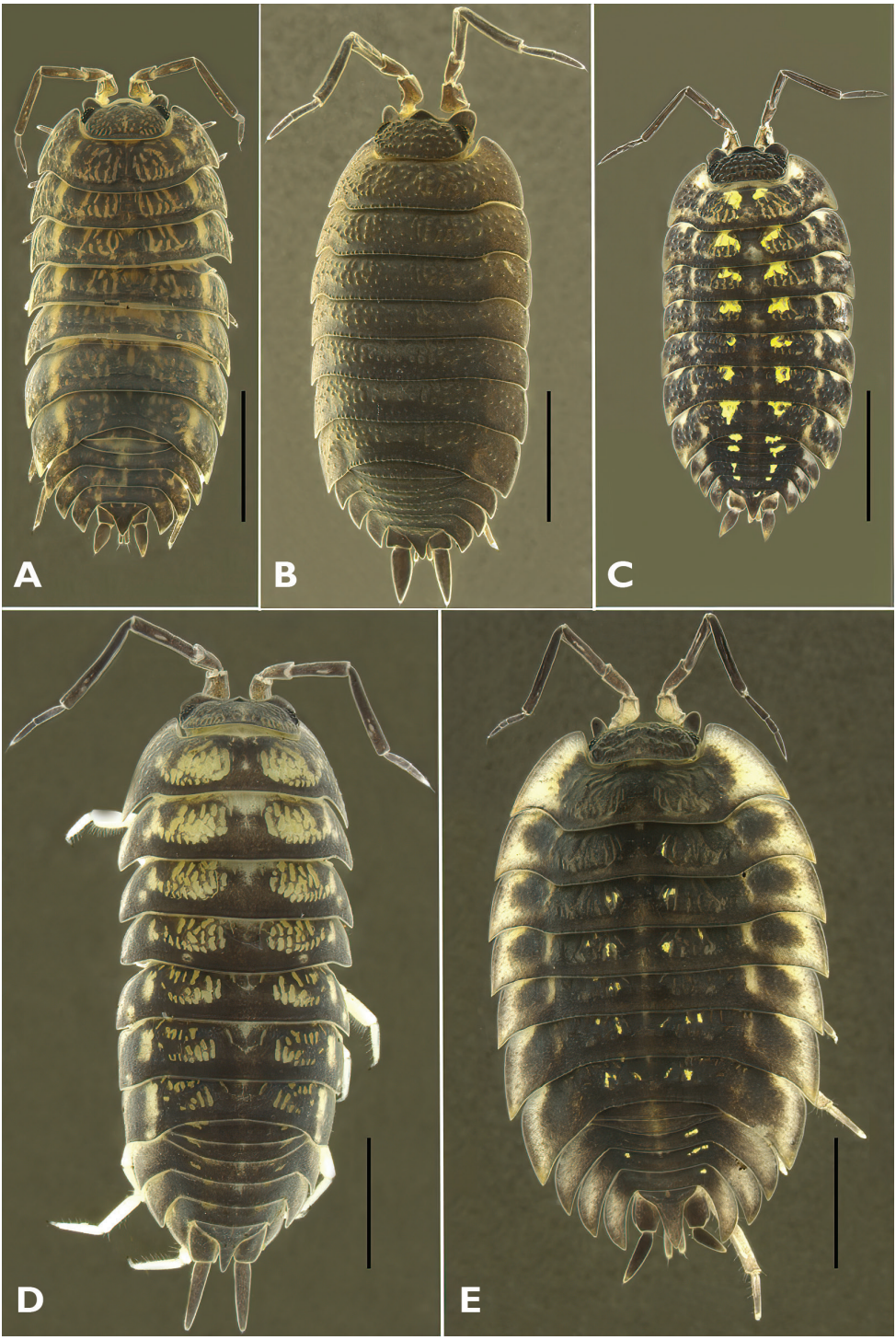

Figure 2. Habitus of Estonian Oniscidea species **A** *Trachelipus rathkii* **B** *Porcellio scaber* **C** *Porcellio spinicornis* **D** *Cylisticus convexus* **E** *Oniscus asellus*. Scale bars: 2 mm.

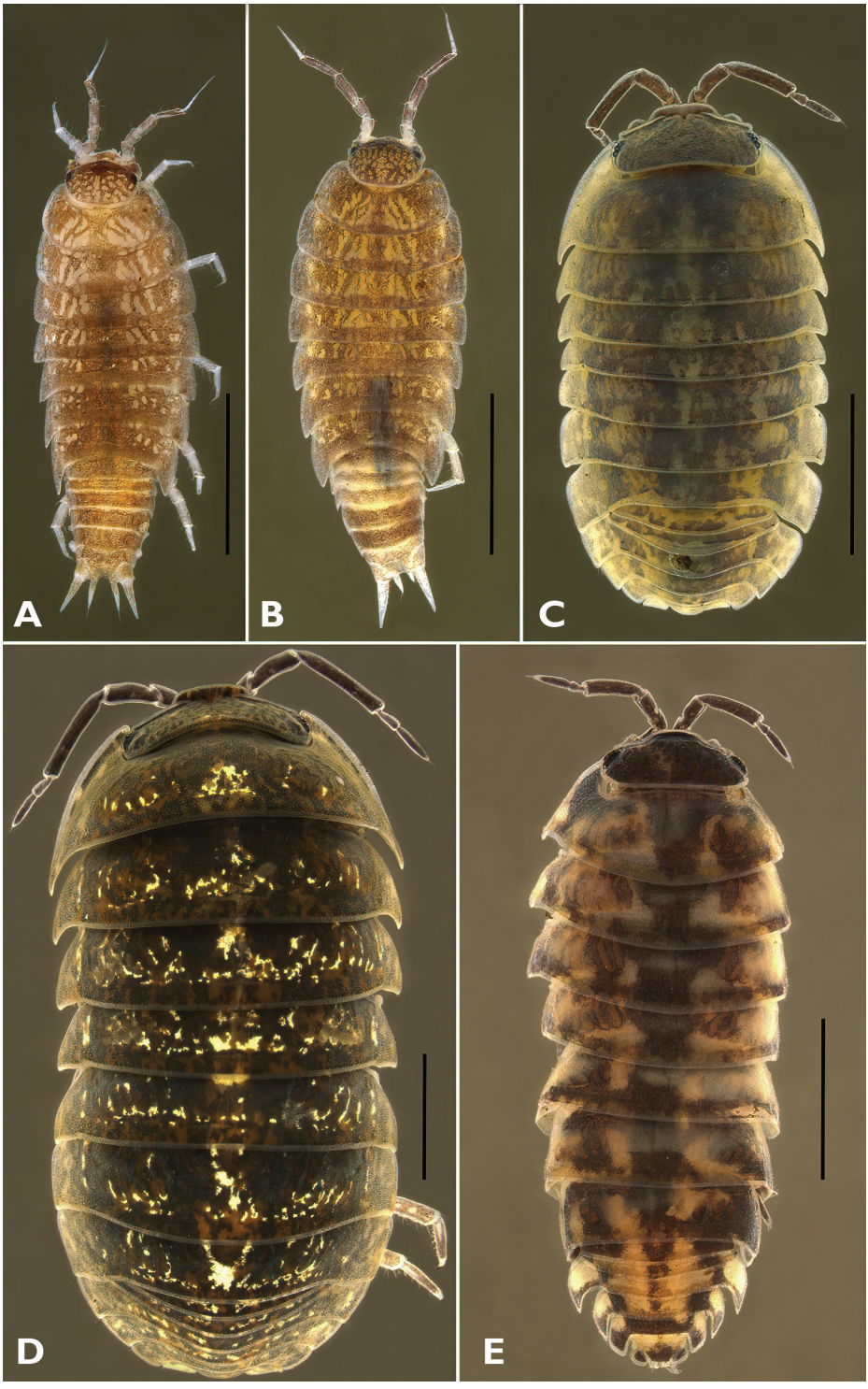

Figure 3. Habitus of Estonian Oniscidea species **A** *Trichoniscus pusillus* **B** *Hyloniscus riparius* **C** *Armadillidium zenckeri* **D** *Armadillidium opacum* **E** *Armadillidium pulchellum*. Scale bars: 1 mm.

Figure 4. Habitus of Estonian Oniscidea species **A** *Platyarthrus hoffmannseggii* **B** *Ligidium hypnorum*. Scale bars: 0.5 mm (**A**); 1 mm (**B**).

Studied material. 5294 specimens from 44 localities (loc. 1a, 1b, 1c, 1d, 1e, 1f, 2a, 2b, 2c, 4b, 5a, 6a, 8a, 8c, 9a, 9b, 11a, 13a, 14a, 14b, 14c, 14c, 15b, 16a, 17a, 17b, 17c, 17d, 18b, 19a, 20a, 21a, 23a, 23c, 25a, 25b, 27a, 28a, 28b, 29a, 30a, 30d, 31a, 35a, 37a).

Comments. Very common in western Estonia and islands (in forests, grasslands, and coastal habitats) but rare elsewhere. Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

Armadillidium pictum Brandt, 1833

Fig. 5L

Published sources. Herold 1927: 53; Herold 1930: 482–483.

Studied material. 5 specimens from 3 localities (loc. 28a, 44a, 45a).

Comments. A rare species found only in northern Estonia and Muhu island in coastal habitats (broad-leaved forest under limestone escarpment, pine forest near seashore, alvar grassland). Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

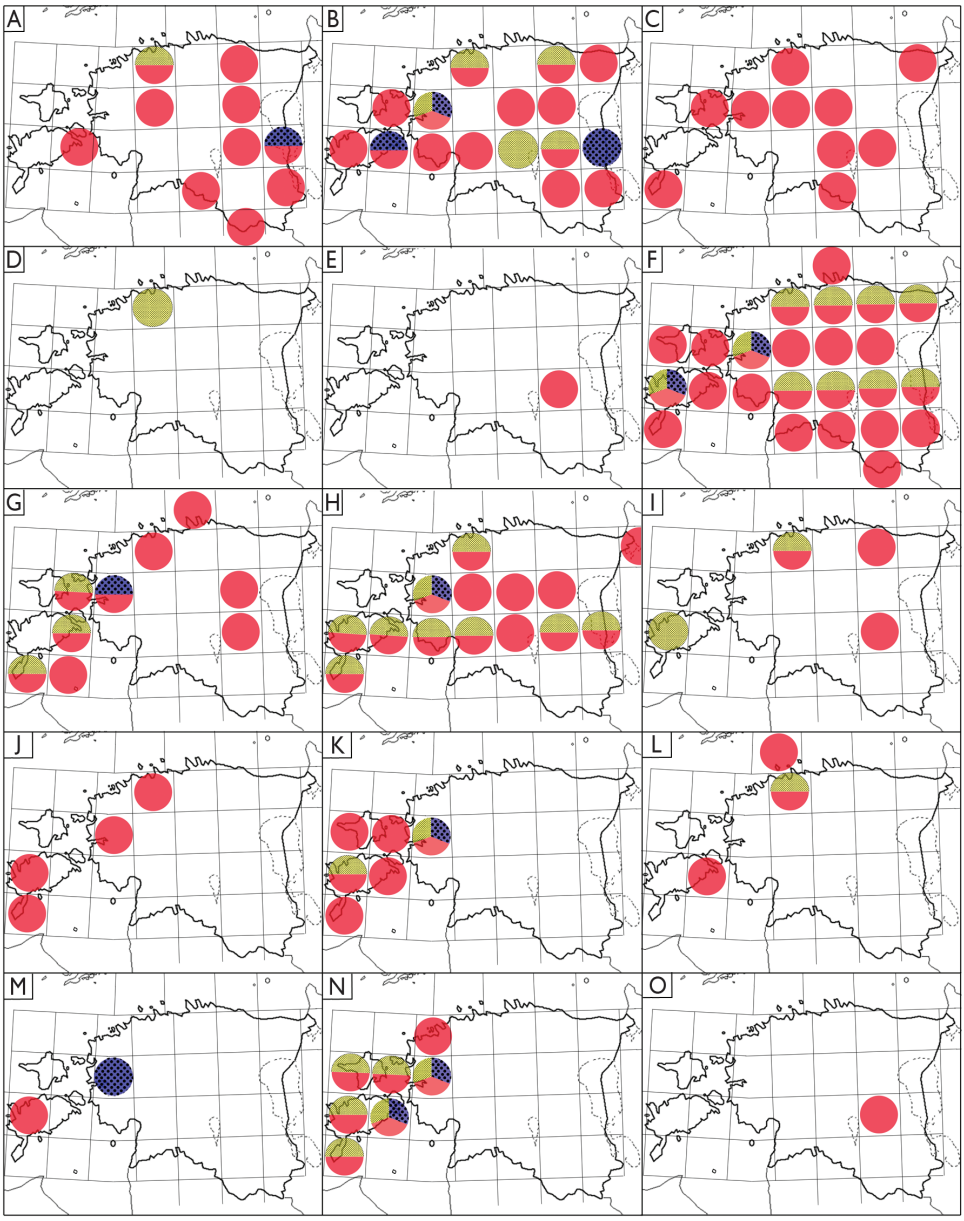

Figure 5. Distribution of Estonian Oniscidea. Red denotes studied specimens (1984–2020), blue = literature data 1970–1993, yellow = literature data 1927–1930 **A** *Ligidium hypnorum* **B** *Trichoniscus pusillus* **C** *Hyloniscus riparius* **D** *Haplophthalmus mengii* **E** *Platyarthrus hoffmannseggii* **F** *Trachelipus rathkii* **G** *Porcellio scaber* **H** *Porcellio spinicornis* **I** *Cylisticus convexus* **J** *Oniscus asellus* **K** *Armadillidium opacum* **L** *Armadillidium pictum* **M** *Armadillidium pulchellum* **N** *Armadillidium zenckeri* **O** *Armadillidium vulgare*. *Porcellionides pruinosus* has been omitted since the published source mentions no specific localities.

***Armadillidium pulchellum* (Zenker, 1798)**
Figs 3E, 5M

Published sources. Herold 1930: 481–482; Vilbaste et al. 1985: 151.

Studied material. 1 specimen from 1 locality (loc. 4d).

Comments. A rare species found only on Saaremaa island in western Estonia (in a spring fen). Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

***Armadillidium vulgare* (Linnaeus, 1758)**
Fig 5O

Published source. Chinery 2005: 300.

Studied material. 1 specimen from 1 locality (loc. 81a).

Comments. A rare synanthropic species with only one finding from Estonia (from suburban area in Tartu). Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

***Armadillidium zenckeri* Brandt, 1833**
Figs 3C, 5N

Published sources. Herold 1927: 53; Herold 1930: 485–490; Vilbaste 1970: 170; Vilbaste et al. 1985: 151.

Studied material. 452 specimens from 44 localities (loc. 1a, 1b, 1d, 1e, 1f, 2a, 2b, 2c, 3a, 4a, 4c, 4e, 5a, 7a, 8b, 9a, 9b, 11a, 13a, 14a, 14b, 15b, 16a, 17a, 17b, 17c, 17d, 19a, 20a, 21a, 23a, 23b, 23c, 25a, 28a, 28b, 29a, 30a, 30d, 36a, 37a, 37a, 37a, 43a).

Comments. Common in western Estonia and islands, but rare elsewhere. Present in dry to mesic forests and different grasslands. Present also in Latvia (Spuņģis 2008) and Finland (Palmén 1946).

Discussion

There are reliable records of 16 species of terrestrial isopods from Estonia. One species has been dubiously claimed to occur in Estonia, and it is presently not included in the checklist. We failed to find any records or specimens to support the occurrence of *Philoscia muscorum* (Scopoli, 1763) in Estonia, although marked as "present" in Fauna Europaea database (Boxhall 2013). The species is, however, present in the neighbouring Latvia (Spuņģis 2008), and its occurrence in Estonia is not impossible. Two species, viz. *Haplophthalmus mengii* (Zaddach, 1844) and *Porcellionides pruinosus* (Brandt, 1833), have not been recently collected and are included here based on literature records only. The fauna is very similar to neighbouring Latvia and southern Finland, with which all species shared, except for *Ligidium hypnorum* and *P. hoffmannseggii*,

but the apparent absence of the latter in Latvia can be possibly explained by its rarity and lack of studies in its specific habitat (ant nests). Comparing the recent records with older ones, it seems that the distribution and abundance of some species have remained approximately the same over the past century, whereas some other species appear to have become rarer or have expanded their ranges. *Porcellio scaber* was reported as a synanthropic species in continental Estonia (Herold 1930), but we found it also in the field there. The same applies to *Oniscus asellus*. The existing Baltic records of *Hyloniscus riparius* are from Lithuania and southern Latvia (Spuņģis 2008; Tuf et al. 2014). The first Estonian records are from 2015, and given that the species was found during the 2003–2007 studies only in south-western Latvia (Spuņģis 2008), its range may have shifted remarkably quickly (by more than 300 km northwards in only a decade). An expansion of the species range northwards and eastwards has also been detected in European Russia in recent decades (Gongalsky et al. 2013) and has recently reached also the Russian Far East (Gongalsky and Kuznetsova 2021). The first Finnish record of the species was from a greenhouse in 1946, but the first finding outside dates from 2007 (Vilisics and Terhivuo 2009). Several species are only found or are more common in western and northern Estonia, characterized by milder maritime climate and calcareous soil (*Armadillidium opacum*, *A. pictum*, *A. pulchellum*, *A. zenckeri*, *Haplophthalmus mengii*). Seven species are known from areas neighbouring Estonia and may have been not collected due to rarity or very local distribution: *Porcellium conspersum* (C.Koch, 1841), *Philoscia muscorum* (Scopoli, 1763), *Haplophthalmus danicus* Budde-Lund, 1879, *Porcellio dilatatus* Brandt, *Porcellio laevis* Latreille, 1804, and *Armadillidium nasatum* Budde-Lund 1885. The range of *Trichoniscus provisorius* Racovitza, 1908 reaches Poland (Jędryczkowski 1979), and there are other widespread *Trichoniscus* species, e.g. *T. alemannicus* or *T. pygmaeus* Sars 1898, in central Europe (the latter reaching southern Russia in the east; Kuznetsova and Gongalsky 2012), but due to lack of male specimens these species may remain as yet undetected in the Baltic countries. Introduced species can sometimes be found in greenhouses and may be expected to be found in the future too; several of the 25 species found in Finland (Vilisics and Terhivuo 2009) are found only indoors. It seems probable that the number of naturally occurring species might be closer to 19 as in neighbouring Latvia (Spuņģis 2008).

Acknowledgements

We would like to thank Mart Meriste, Ilmar Süda, Tõnu Talvi, Allan Selin, Urmas Jürivete, Tõnu Kesküla, Märt Kruus, Heli Kirik, Erki Õunap, Miina Oras, Elisabeth Prangel, Ene Kook and Hannes Järve who collected material for the present study. We are also grateful to Konstantin Gongalsky and Ferenc Vilisics for the helpful comments to the initial draft of the manuscript. This work was partially financed by Estonian Environmental Board grant "Large-scale restoration of calcareous grasslands, implications for biodiversity" (3-2_7/8555-5/2018) and funding programme RITA "Enhancing farmland biodiversity" (2014-2020.4.02.16-0025).

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Supplementary material 1

Supplementary data

Authors: Kaarel Sammet

Data type: occurences

Explanation note: Finding details of studied Estonian Oniscidea specimens from each locality (repeated findings from exactly the same locality are omitted).

Link: https://doi.org/10.3897/zookeys.1067.68105.suppl1

ZooKeys 1067: 19–56 (2021)
doi: 10.3897/zookeys.1067.72369
https://zookeys.pensoft.net

RESEARCH ARTICLE

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The giant pill-millipede genus *Zephronia* Gray, 1832 from Thailand, with a redescription of *Z. siamensis* Hirst, 1907 and descriptions of three new species (Diplopoda, Sphaerotheriida, Zephroniidae)

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Academic editor: Pavel Stoev | Received 30 July 2021 | Accepted 8 September 2021 | Published 29 October 2021

http://zoobank.org/AEAF44EE-2CCD-4E31-9CBC-A4C5ACB0E2EB

Citation: Srisonchai R, Sutcharit C, Likhitrakarn N (2021) The giant pill-millipede genus *Zephronia* Gray, 1832 from Thailand, with a redescription of *Z. siamensis* Hirst, 1907 and descriptions of three new species (Diplopoda, Sphaerotheriida, Zephroniidae). ZooKeys 1067: 19–56. https://doi.org/10.3897/zookeys.1067.72369

Abstract

Material of the giant pill-millipede genus *Zephronia* Gray, 1832 recently collected from Thailand contains three new species: *Zephronia enghoffi* **sp. nov.**, *Zephronia golovatchi* **sp. nov.**, and *Zephronia panhai* **sp. nov.** The first *Zephronia* species recorded for Thailand, *Z. siamensis* Hirst, 1907, is also redescribed based on new specimens collected both from the type locality in Chonburi Province and from neighboring areas. Morphological characters of all new species, *Z. phrain* Likhitrakarn & Golovatch, 2021, and *Z. siamensis* are illustrated, and a distribution map of the confirmed *Zephronia* species occurring in Thailand is also provided.

Keywords

Diplopods, key, map, Southeast Asia, taxonomy

Introduction

One of the remarkable diplopod groups, the giant pill-millipede genus *Zephronia* Gray, 1832 is one of the most speciose not only in the family Zephroniidae, but also in the entire order Sphaerotheriida. It currently contains 44 described species ranging from the Himalayas of India in the west, to mainland Southeast Asia in the east (Wesener 2016, 2019). Although several species have been revised and new species described from a number of areas in Asia, e.g., Myanmar, Northeast India, and Vietnam, *Zephronia* diversity still remains understudied in many other countries, e.g., Cambodia, Laos, and Thailand. Thailand is located within one of the global hotspots of biodiversity (Indo-Burma) (Clements et al. 2006), and even though recent progress in revealing its diplopod fauna is considerable, especially as regards the orders Spirobolida, Spirostreptida, and Polydesmida. (Pimvichai et al. 2009, 2010; Likhitrakarn et al. 2011, 2014; Srisonchai et al. 2018a, b), only four species of *Zephronia* have hitherto been reported from Thailand. These are as follows: *Z. siamensis* Hirst, 1907, *Z. lannaensis* Likhitrakarn & Golovatch, 2021, *Z. phrain* Likhitrakarn & Golovatch, 2021, and *Z. viridisoma* Rosenmejer & Wesener, 2021. Recent intense collecting efforts made by Thai specialists in collaboration with the Department of National Parks, Wildlife and Plant Conservation across the country have revealed numerous interesting millipedes, especially in limestone areas. From these efforts, several new genera and numerous new species have been recorded and described (Pimvichai et al. 2018, 2020; Srisonchai et al. 2018a, b, c, d; Likhitrakarn et al. 2020, 2021). The present contribution provides descriptions of three new species of the genus *Zephronia*, as well as a redescription of *Z. siamensis* Hirst, 1907 as based both on topotypes and near-topotypes.

Materials and methods

Specimen collection and preservation

The millipedes were collected by active search in daytime during the field trips in Thailand. All material was collected by **ASRU** (Animal Systematics Research Unit) members. Live specimens of both sexes were photographed with a Nikon D700 camera equipped with a AF-S VR Micro-Nikkor 105 mm lens. Specimens were then euthanized based on the methods of AVMA guidelines for the euthanasia of animals (American Veterinary Medical Association 2020) with a permission of the Animal Care and Use. Most of the specimens were stored in 70% ethanol for morphological examination. Latitude, longitude, and elevation were recorded using a Garmin GPSMAP 60 CSx at the field sites, and all coordinates of the precise locations were mapped with Google Earth.

Morphological study, description, and illustrations

All morphological characters were analyzed under a NIKON SMZ-445 stereo microscope. For Scanning Electron Microscopy (SEM), the specimens were mounted on aluminum stubs, coated with pure gold and studied using a JOEL JSM-6610LV

scanning electron microscope. The descriptions are applied to both males and females. Species delimitation and morphological descriptions were based on Wesener and Sierwald (2005), Wesener (2016, 2019), Semenyuk et al. (2018, 2020) and Likhitrakarn et al. (2021). Illustrations of external morphological characters were sketched from one view, whereas the telopods were depicted from three sides (anterior, posterior, and lateral views) under the stereo microscope and all were modified using Adobe Photoshop CS6 software in order to generate plates of figures.

Depositions of holotypes, paratypes, and other new specimens

All material of each species is referred to each species description. The holotypes are deposited in the Chulalongkorn University Museum of Zoology (**CUMZ**, CUMZ-Zeph0005-0010) and some paratypes are shared with three other museums including the Natural History Museum of Denmark, University of Copenhagen, Denmark (**NHMD**), the Zoological Museum, State University of Moscow, Russia (**ZMUM**), and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, Singapore (**ZRC**).

Acronyms used in the descriptions

cp cuticular impression
cr-T crenulated teeth
cx coxa
is inner section
ML membranous lobe
ms middle section
o operculum of vulva
ot outer section
pm posterior margin
pre prefemur
sp sclerotized process
st-pl stigmatic plate
syn-cx syncoxite

Other acronyms and words used in the text

ASRU Animal Systematics Research Unit, Chulalongkorn University, Thailand
a.s.l. above sea-level
ca. about, around, circa
CUMZ Chulalongkorn University Museum of Zoology, Thailand
Koh the Thai word for "island"
NHMD Natural History Museum of Denmark, University of Copenhagen, Denmark
Wat the Thai word for "temple"
ZMUM Zoological Museum, State University of Moscow, Russia.

Positional and directional terms used in the descriptions

See the details in species descriptions by Wesener (2019), Likhitrakarn et al. (2021), and also some definitions in Srisonchai et al. (2018a, b).

Results

Family Zephroniidae Gray, 1843
Subfamily Zephroniinae Gray, 1843
Tribe Zephroniini Jeekel, 2001

Genus *Zephronia* Gray, 1832

Diagnosis. See complete and recently updated diagnoses in Golovatch et al. (2012: 283), Wesener (2016: 30), and Likhitrakarn et al. (2021: 13).

Confirmed species recorded from Thailand. 1. *Zephronia siamensis* Hirst, 1907 2. *Zephronia lannaensis* Likhitrakarn & Golovatch, 2021 3. *Zephronia phrain* Likhitrakarn & Golovatch, 2021 4. *Zephronia viridisoma* Rosenmejer & Wesener, 2021 5. *Zephronia enghoffi* sp. nov. 6. *Zephronia golovatchi* sp. nov. 7. *Zephronia panhai* sp. nov.

Unconfirmed species recorded for Thailand. *Zephronia* cf. *viridescens* Attems, 1936.

***Zephronia siamensis* Hirst, 1907**
Figures 1A–D; 3; 4; 13A, B; 14A

Zephronia siamensis Hirst, 1907: 218; Attems 1914: 147; Attems 1936: 182; Jeekel 2001: 21; Enghoff 2005: 89; Golovatch et al. 2012: 276; Wongthamwanich et al. 2012a: 30; Wesener 2016: 35.
Zephronia cf. *siamensis* – Decker 2010: 25.

Material examined. Thailand – Chonburi Province • 2 ♂♂ 17 ♀♀; Sichang District, Koh Sichang; 13°9'3.8"N, 100°48'56"E; 7 m a.s.l.; 14 November 2020; R. Srisonchai, N. Likhitrakarn, P. Jirapatrasilp leg.; • 2 ♀♀; same collection data; NHMD • 2 ♀♀; same collection data; ZMUM • 3 ♀♀; same Province, Mueang District, Grand Cayon Chonburi; 12°31'23"N, 100°57'18"E; 7 m a.s.l.; 2 August 2019; ASRU members leg.; • 1 ♀; same Province, Sattahip District, Koh Chuang; 12°31'23"N, 100°57'18"E; 7 m a.s.l.; 8 August 2013; R. Srisonchai, P. Jirapatrasilp leg.; • 2 ♀♀; same Province, Bo Thong District, Wat Tham Khao Cha-ang-on; 13°12'31.7"N, 101°39'5.7"E; 128 m a.s.l.; 4 July 2016; R. Srisonchai, P. Tongkerd leg.; • 1 ♀; Rayong Province, Mueang District, Koh Samet; 12°34'22.6"N, 101°27'52.6"E; 128 m a.s.l.; 12 January 2010; ASRU members leg.

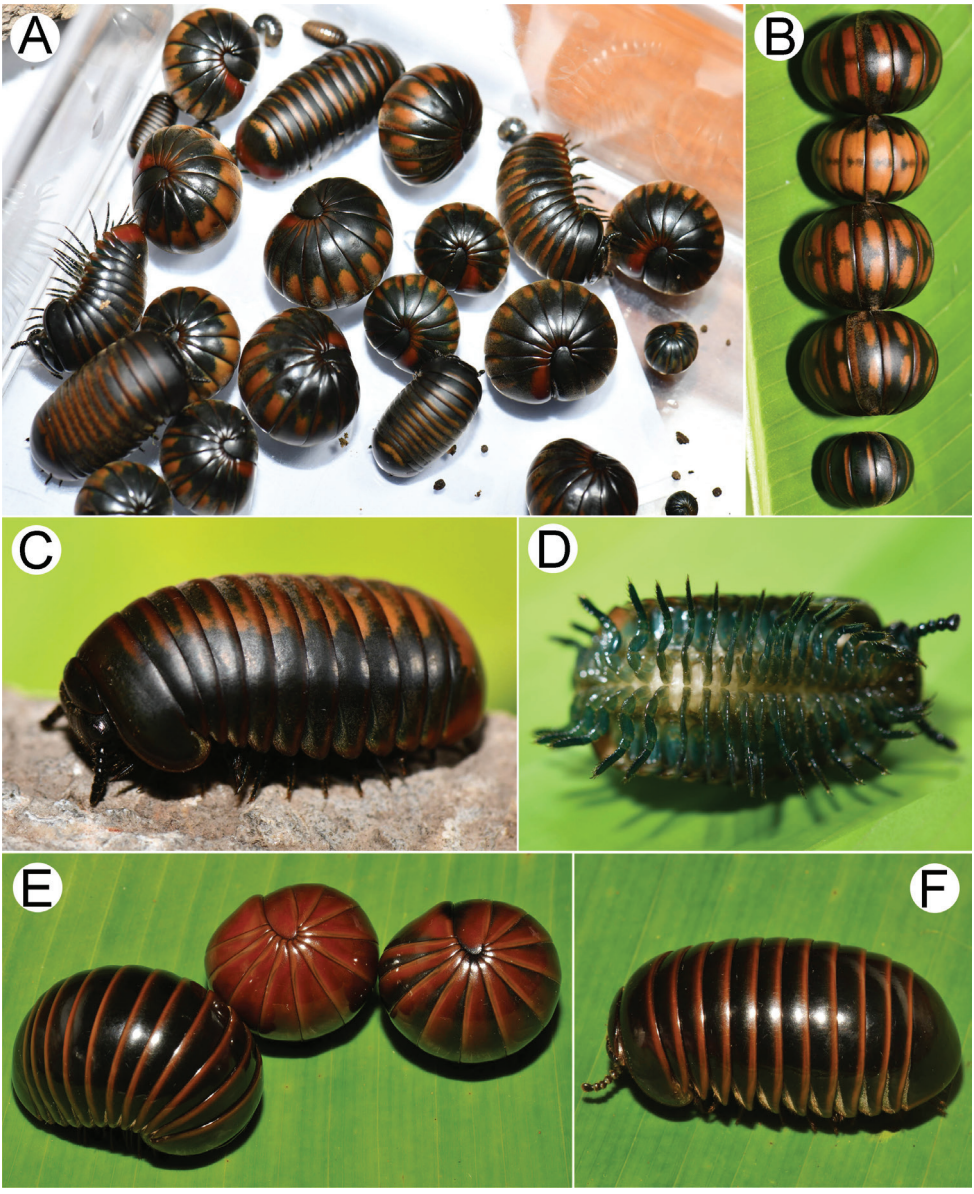

Figure 1. Photographs of living *Zephronia* spp. **A–D** *Zephronia siamensis* **E, F** *Zephronia phrain*. Photographs not to scale.

Type locality. Kosichang and Chantaboon, Siam (Hirst 1907), [Koh Sichang (Island) is in Chonburi Province, Chantaboon is in Chantaburi Province].

Diagnosis. A member of *Zephronia* s. s. in which the position of Tömösváry's organ located next to the aberrant ommatidia, not inside the antennal groove. Adult body length relatively small, usually ca. 20 mm, < 26.5 mm, tip of subanal plate con-

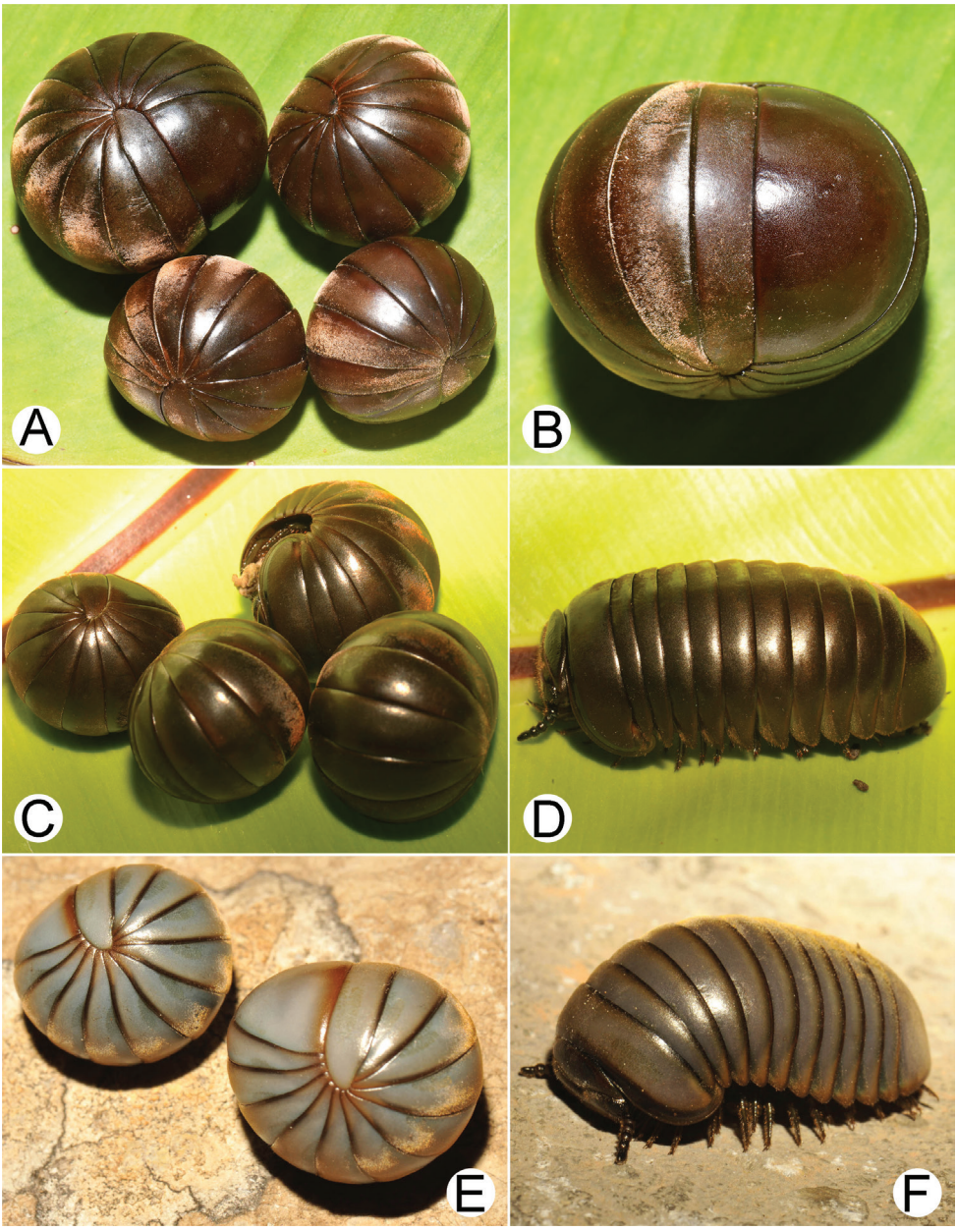

Figure 2. Photographs of living *Zephronia* spp. **A, B** *Zephronia enghoffi* sp. nov., paratypes (CUMZ-Zeph0006) **C, D** *Zephronia golovatchi* sp. nov., paratypes (CUMZ-Zeph0008) **E, F** *Zephronia panhai* sp. nov., paratypes (CUMZ-Zeph0010). Photographs not to scale.

cave, process of telopoditomere 2 of anterior telopod rather short and strongly curved distally, and process of telopoditomere 2 of anterior telopod shorter than the combination of telopoditomeres 3 and 4. Similar in these respects to *Z. laotica* Wesener, 2019

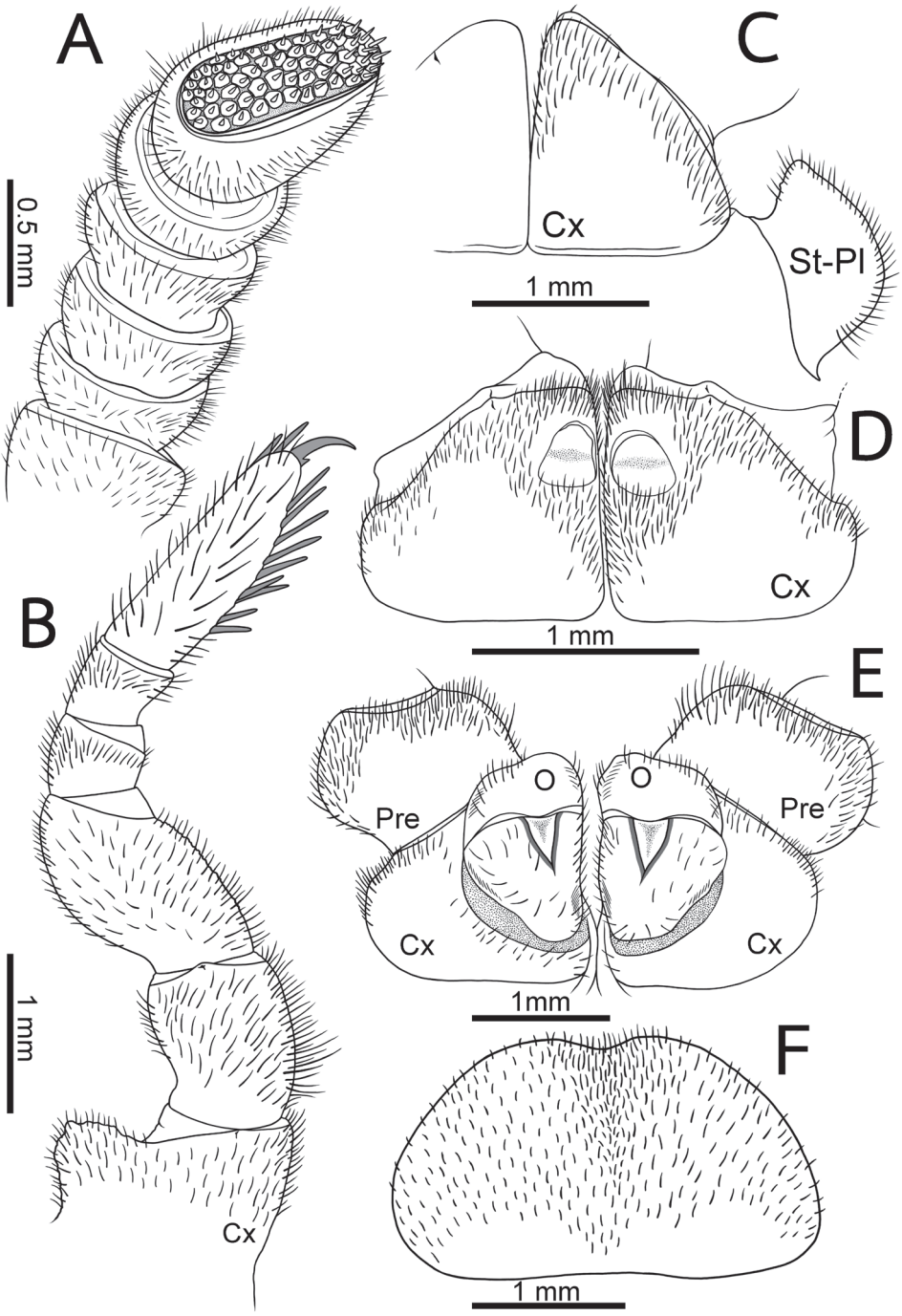

Figure 3. *Zephronia siamensis* **A–C** male **D, E** female (CUMZ-Zeph0013) **A** right antenna, ventral view **B** the ninth left leg, posterior view **C** first coxae with stigmatic plates, posterior view **D** coxae of second legs with gonopores, posterior view **E** coxae and prefemur of second legs with vulvae, posterior view **F** subanal plate, ventral view. Abbreviations: cx = coxa, o = operculum, pre = prefemur, syn-cx = syncoxite, St-Pl = stigmatic plate.

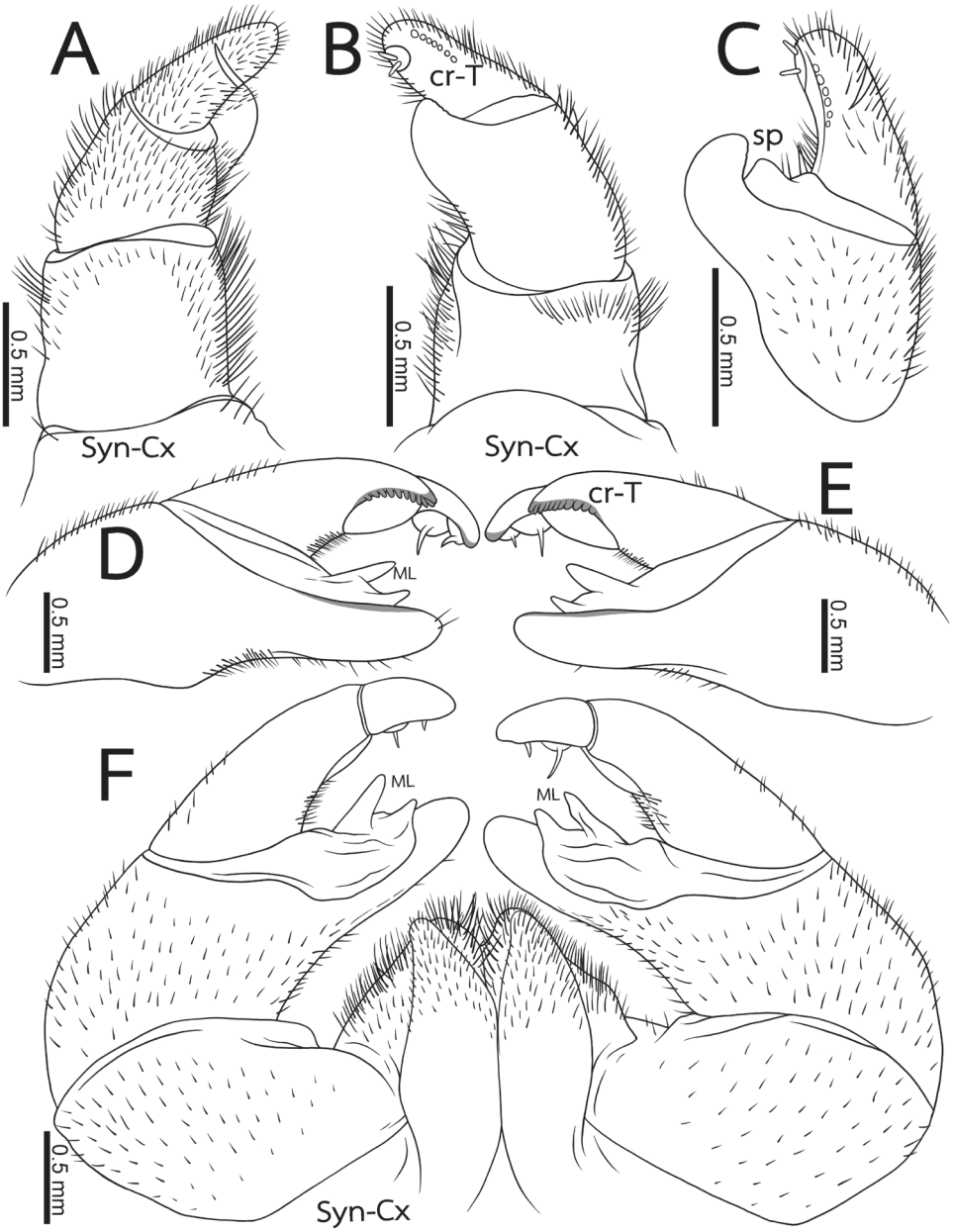

Figure 4. *Zephronia siamensis* **A–C** left anterior telopod, anterior, posterior and sublateral views, respectively **D, E** Left and right posterior telopods, posterior view **F** Posterior telopod, anterior view. Abbreviations: cr-T = crenulated teeth, cx = coxa, ML = membranous lobe, sp = sclerotized process, syn-cx = syncoxite.

and *Z. dawydoffi* Attems, 1953. Differs from these two species by showing a body length > 16.7 mm, live specimens with unique dark green, tergites with two yellow-brown patches located in anterior half of tergites, surface of tergites with conspicuous

setae, femur of leg extended with conspicuous teeth, and telopoditomere 4 of anterior telopods posteriorly with a row of conspicuous crenulated teeth (cr-T).

Redescription. ***Body size*****:** Male: body length 15.0–26.5 mm. Width of thoracic shield 9.0–12.5 mm, of tergite 8 9.5–11.4 mm. Height of thoracic shield 5.2–6.4 mm, of tergite 7, 6.1–7.4 mm. Female: body length 15–23.0 mm. Width of thoracic shield ca. 12.1 mm, of tergite 8 ca. 12.8 mm. Height of thoracic shield ca. 7.3 mm, of tergite 7 ca. 8.2 mm.

Color (Fig. 1A–D): Live specimens dark green; antennae dark brown; head, collum, thoracic shield, paratergites brown; legs bluish green. Tergites with two big patches, brown or yellowish brown, arranged in almost central part of anterior half; lateral part of tergites greenish dark, middle part of tergites brown. Anal shield with two colors contrasting each other, posterior half reddish brown, anterior half greenish dark brown. Color in alcohol after three months of preservation changed to greenish brown, head and collum dark greenish, tergites with a dark posterior margin, legs pale yellowish, distal podomeres rusty brown, antennae dark green.

Head**:** Trapezoid, anterior part of head clothed with numerous long setae, posterior part sparsely punctate; anterior margin of labrum with a single tooth. Each eye with 75–92 ommatidia. Aberrant ocellus located inside antennal groove.

Antennae (Fig. 3A): Short, with rounded joints, extending posteriorly to leg-pair 2. Lengths of antennomeres: 6 > 3 > 5 = 4 > 2 = 1. Antennomere 6 densely pubescent, sensilla basiconica surrounding apical disc. Last antennomere thickened, widened apically and axe-shaped. Shape of antennae sexually dimorphic, cylindrical in female; thickened, widened apically and slightly flattened in male. Apical disc with 51–61 (males) or 49–54 apical cones (females). No sclerotized crest/ridge between antennal socket and ommatidia.

Tömösváry's organ**:** Located separately at a small, projected brim between ommatidia and antennal socket.

Gnathochilarium**:** Ventral surface with setae, other structures typical of the order. Palpi with sensory cones arranged in clusters. Mandibles not dissected.

Stigmatic plates (Fig. 3C): First stigmatic plate subtriangular, apex broadly rounded, slightly curved towards coxa 1.

Laterotergites**:** 1 and 2 with a broad and well-rounded projection.

Collum**:** With glabrous surface, sparsely setose with very long setae, except for anterior and posterior margins which are densely setose.

Thoracic shield**:** Surface with tiny setae as on tergites. Shallow grooves filled with numerous long setae, no keels.

Tergites (Fig. 1A–C): Surface shining, entirely clothed with dense and tiny setae, each seta located in a tiny pit. Tip of paratergites weakly projecting posteriorly.

Endotergum (Figs 13A, B, 14A): Posterior margin with lobes, 'rectangle-wavy' margin. Inner section (inner area) smooth, with a few setae. Middle section (middle area) with a single row of conspicuous, elliptical cuticular impressions; distance between impressions as wide as individual diameter. Bristles arranged in one row, tip of the longest bristles not extended beyond posterior margin or not reaching to posterior margin.

***Anal shield*:** Sexually dimorphic, in female large and well-rounded, in male slightly more rectangular, in both sexes glabrous. Surface similar to that of tergites. Inner surface (underside) with a single, long, black locking carina half as long as width of last laterotergite.

Legs (Fig. 3B): Leg-pair 1 with one ventral spine, leg-pair 2 with two or three, leg-pair 3 with 4–6 ventral spines. Leg-pairs 4–18 with eight or nine ventral spines and two or three apical ones; thereafter slightly reduced into 5–8 ventral spines. In leg 9, femur ca. 1.7×, tarsus ca. 3.2× longer than wide. Length of tarsus > femur > prefemur > coxa > tibia ≥ postfemur. All podomeres densely setose. Coxa large, with dentate ridge marginally (coxal process). Coxal process absent in leg-pairs 1 and 2. Prefemur without teeth. Femur large and stout, extended mesally, with 7–11 conspicuous teeth.

Subanal plate (Fig. 3F): Large and wide, semicircular, divided by a conspicuous mesal constriction; central margin (tip) concave, wide; lateral margin slightly convex. Densely setose.

Male sexual characters (Fig. 3D): Male gonopore large, covered with a single, undivided, triangular, sclerotized plate.

Anterior telopods (Fig. 4A–C): First telopoditomere rectangular, slightly longer than wide. Telopoditomere 2 large, as long as telopoditomeres 3 and 4 combined. Process of telopoditomere 2 located posteriorly, but partly visible laterally in anterior view. Process of telopoditomere 2 wide, broader than telopoditomeres 3 and 4. Process of telopoditomere 2 conspicuously unciform, protruding as high as basal part of telopoditomere 4, apically with a well-rounded tip. Margin towards telopoditomere 3 with a membranous area carrying a rather small and sclerotized process (sp), apically with a rounded tip. Telopoditomere 3 slender, 1.4X longer than wide, 1.5X longer than telopoditomere 4. Telopoditomere 4 posteriorly with a row of 7 small and crenulated teeth (cr-T) with two prominent spines. All podomeres covered with long sparse setae, except for central part of telopoditomere 1 and posterior surfaces of 2–4.

Posterior telopods (Fig. 4D–F): Inner horns with sharply edged tips, slightly curved caudad. Telopodite consisting of four podomeres. First podomere stout and narrow, nearly twice as wide as long. Immovable finger (process of telopoditomere 2) shorter than movable finger (consisting of telopoditomeres 3 and 4). Immovable finger stout and narrow, 1.6X longer than wide, not curved, glabrous distally. Margin towards movable finger with two massive, triangular, membranous lobes (ML). Telopoditomere 3 elongated, slightly curved, twice as long as telopoditomere 4; with a large, swollen, membranous ledge; postero-apically slightly enlarged, with a row of 11 or 12 crenulated teeth (cr-T). Telopoditomere 4 slender, twice as long as wide, slightly tapering apically; with a large, swollen, membranous ledge; with two long and sclerotized spines. Telopoditomeres 1 and 2 on both sides covered with few setae. Telopoditomere 3 at base of inner margin with a few setae, remaining parts of telopoditomeres 3 and 4 almost glabrous.

Female sexual characters (Fig. 3E): Vulva large, covering ca. 2/3 coxa, located at mesal side, extending mesally to basal third of prefemur. Operculum regularly rounded, margin straight, mesal margin not protruding.

Distribution and habitats (Figs 15A, 16). The newly collected specimens from the type locality were found under groups of *Pandanus* trees in a limestone area near a beach,

while the other material from the Chonburi and Rayong provinces were likewise taken from limestone habitats. Currently, this species is known to occur only in eastern Thailand.

Remarks. The live coloration of adults is generally dark green with two yellowish brown patches in the anterior half of tergites, this being quite unique for this species.

Almost 114 years since the original description, a redescription of *Z. siamensis* Hirst, 1907 has been made in this study based on the newly collected specimens from Koh Srichang (Srichang Island), here regarded as strict topotypes.

Considerable variation has been found in body size of the specimen described by Hirst (1907) compared to the topotypes: the type specimen was ca. 26.5 mm in length, whereas the new material we examined were within the size range of 16.7–23.5 mm.

Zephronia lannaensis Likhitrakarn & Golovatch, 2021

Zephronia lannaensis Likhitrakarn & Golovatch, 2021 in Likhitrakarn et al. 2021: 13.

Distribution and habitats. This species has been found to occur only in Chiang Mai Province. (Thailand, Chiang Mai Province, Doi Saket District, Huai Hong Khrai Royal Development Study Centre, 445 m a.s.l., 18°52'"N, 99°13'"E). All specimens were collected from dry dipterocarp forest (Likhitrakaen et al. 2021).

Remarks. Based on specimens described by Likhitrakarn et al. 2021, deposited in the CUMZ (holotype CUMZ-Zeph0001, paratypes CUMZ-Zeph0002).

Zephronia phrain Likhitrakarn & Golovatch, 2021

Figures 1E, F; 5; 6

Zephronia phrain Likhitrakarn & Golovatch, 2021 in Likhitrakarn et al. 2021: 19.

Material examined. Thailand – Tak Province • 2 ♂♂ 2 ♀♀; Mae Sot District, Phawor Shrine; 16°46'16.8"N, 98°41'13"E; 694 m a.s.l.; October 2016; S. Panha, R. Srisonchai, C. Sutcharit, W. Siriwut leg.

Description of some characters for a population in Tak Province. ***Body length*:** Length in male 29.0–31.0 mm (holotype 33.5 mm), female 30.0–33.0 mm; head 5.5 mm; thoracic shield 5.5–6.0 mm; anal shield 9.5–10.5 mm.

***Body width*:** Width in male 16.5 mm (holotype 18.2 mm), female 16.5–17.0 mm; head 8.0–9.0 mm; thoracic shield 15.0–16.0 mm; anal shield 14.0–15.5 mm.

***Body height*:** Height in male 10.0 mm (holotype 11.2 mm), female 10.0–11.0 mm; thoracic shield 9.0–10.5 mm; tergite 9.5–11.0 mm.

Color (Fig. 1E, F): Specimens in life with brown or dark brown; head, antennae and collum, thoracic shield, paratergites, anal shield and legs brown or dark brown; anterior margins of thoracic shield, of tergites and of anal shield dark brown contrasting

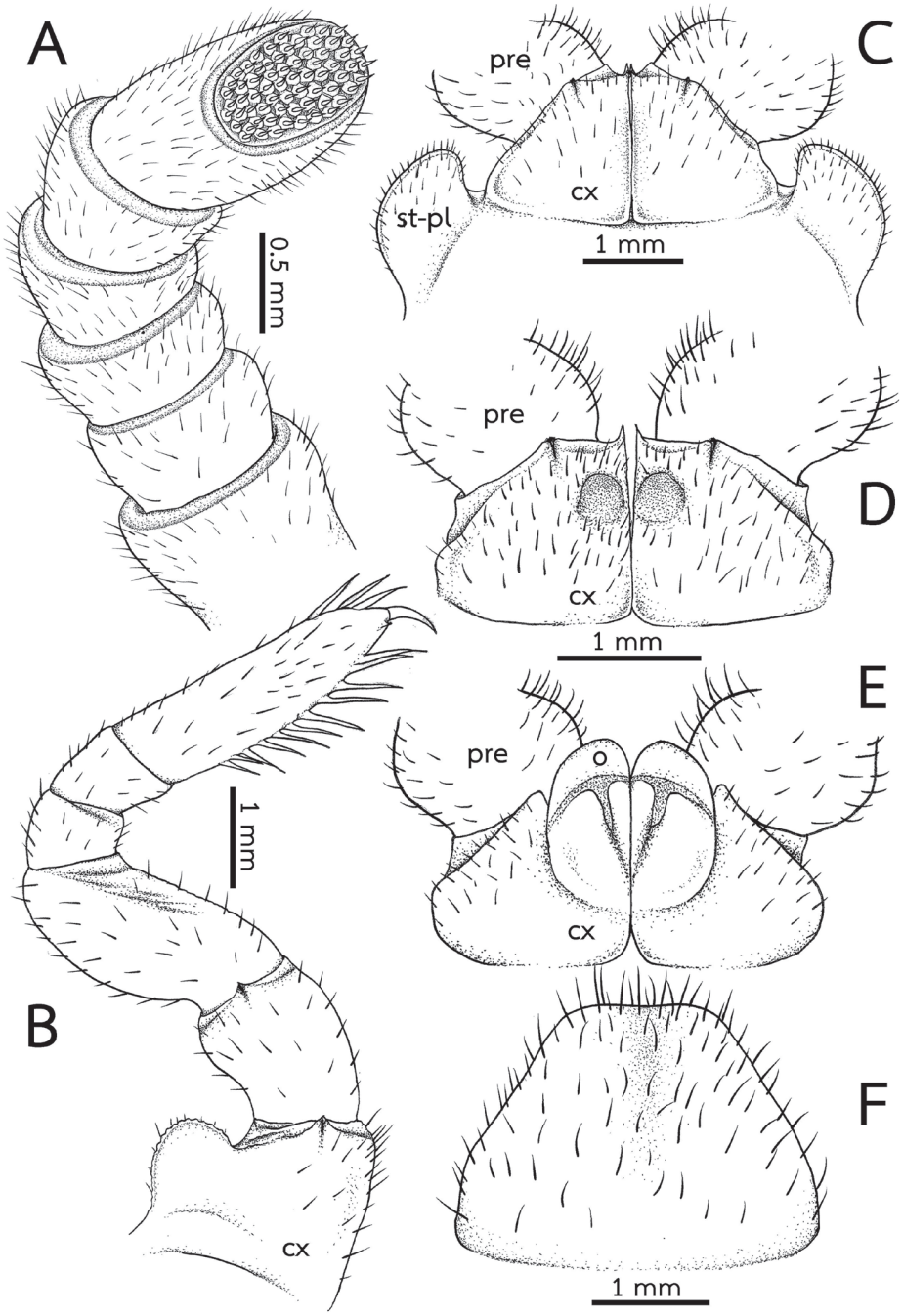

Figure 5. *Zephronia phrain* **A–D** male specimen from Phawor Shrine, Tak Province **E, F** female **A** right antenna, ventral view **B** the ninth left leg, posterior view **C** first coxae with stigmatic plates, posterior view **D** coxae of second legs with gonopores, posterior view **E** coxae and prefemur of second legs with vulvae, posterior view **F** subanal plate, ventral view. Abbreviations: cx = coxa, o = operculum, pre = prefemur, syn-cx = syncoxite, st-pl = stigmatic plate.

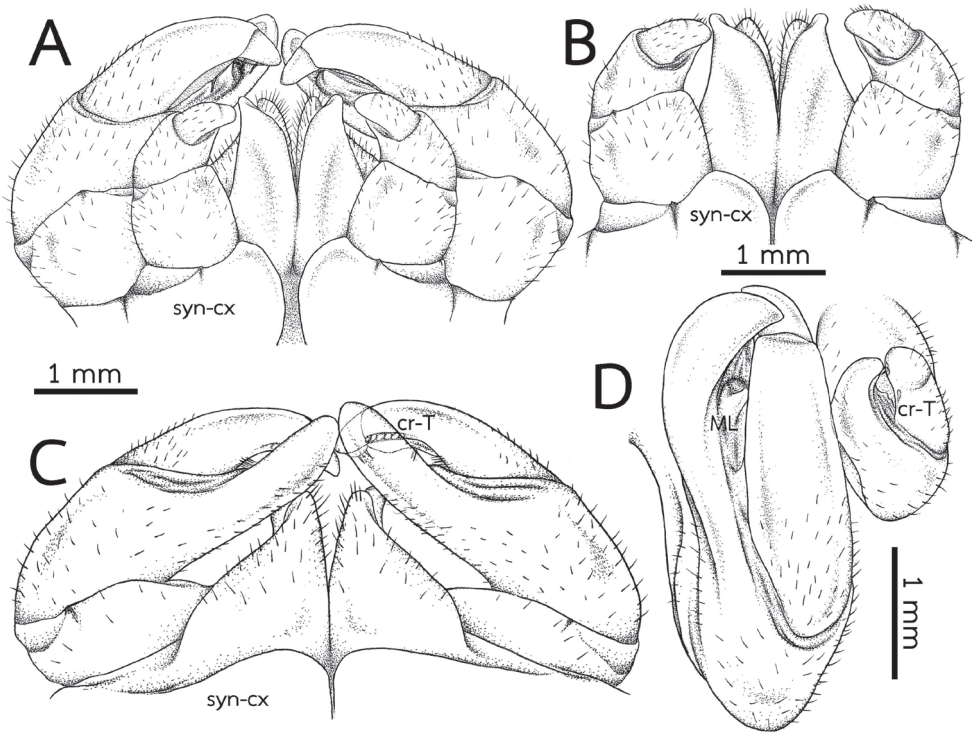

Figure 6. *Zephronia phrain*, male specimen from Phawor Shrine, Tak Province **A** telopods, anterior view **B** anterior telopod, anterior view **C** posterior telopod, posterior view **D** right anterior and posterior telopods, ventral view. Abbreviations: cr-T = crenulated teeth, cx = coxa, ML = membranous lobe, syn-cx = syncoxite.

with the posterior brown ones; setose part of thoracic shield with golden sheen. Color in alcohol after six years not changed.

Tergites (Fig. 1E, F): Quite shiny; surface glabrous, with sparse, tiny, inconspicuous pits; tip of paratergite of midbody tergites curved, directed posteroventrad; anterior half of lateral margin covered with long and conspicuous setae.

Legs (Fig. 5B): Leg-pairs 1 and 2 without apical spine. Leg-pair 1 with four ventral spines, leg-pair 2 with four or five ventral spines. Leg-pair 3 with seven or eight ventral spines and one or two apical spines. Leg-pair 4 with nine or ten ventral spines and two or three apical spines. Leg-pairs 5–19 with 9–11 ventral spines and 1–3 apical spines. Last two leg-pairs with eight or nine ventral spines, and one or two apical spines. In leg 9, femur ca. 1.7×, tarsus ca. 3.4× longer than wide. Length of tarsus > femur > prefemur > coxa > tibia ≥ postfemur. All podomeres densely setose. Coxa large, with dentate ridge marginally (coxal process). Coxal process absent in leg-pairs 1 and 2. Prefemur without teeth. Femur slightly extended mesally; mesal margin with very small, tiny, inconspicuous teeth.

Subanal plate (Fig. 5F): Trapeziform, undivided; central margin (tip) truncate, narrow; lateral margin straight. Densely setose.

Head, antenna, Tömösváry's organ, gnathochilarium, stigmatic plates, laterotergites, collum, thoracic shield, endotergum, anal shield, male sexual characters, anterior telopods, posterior telopods, and female sexual characters: Same as the original description in Likhitrakarn et al. 2021.

Distribution and habitats (Figs 15D, 16). Currently known to occur in northern Thailand (Chiang Mai and Tak provinces) in dry dipterocarp forest and from limestone areas. Observations made at Phawor Shrine found that most specimens were seen creeping on rocks, with some hiding in leaf litter. Notably, the specimens were found in syntopy with the dragon millipede (*Nagaxytes spatula* Srisonchai, Enghoff & Panha, 2018) at the same site (Srisonchai et al. 2018b).

Remarks. Based on observations of live specimens in the field, two color patterns were found, dark green in type specimens and brown/dark brown in the others from Tak Province (Fig. 2E, F; fig. 1C, D in Likhitrakarn et al. 2021).

A species described by Pocock (1890) from Myanmar (Thagatà, Mount Mooleyit, Kayah State), *Z. gestri* Pocock, 1890 occurs close to the type locality of this widespread species, but *Z. phrain* clearly differs from *Z. gestri* by being longer in body length (vs. shorter, ca. 14 mm), having a longer immovable finger or longer process of telopoditomere 2 (vs. shorter) and having a truncate/round central margin of subanal plate (vs. convex).

Based on material described by Likhitrakarn et al. 2021, deposited in the CUMZ (holotype CUMZ-Zeph0003, paratypes CUMZ-Zeph0004).

Zephronia viridisoma Rosenmejer & Wesener, 2021

Zephronia viridisoma Rosenmejer & Wesener, 2021 in Rosenmejer et al. 2021: 121.

Distribution and habitats. The type locality is in Thailand (Nakhon Si Thammarat Province, Sichon District, Khao Lark Waterfall, 9°03'"N, 99°47'"E). Khao Lark Waterfall = Khao Lak = near Si Khit Waterfall. The material was collected from a dense jungle in limestone areas (Rosenmejer et al. 2021).

Remarks. Only nine specimens have been collected and all were found to appear in a small area. This species can be regarded as endemic to southern Thailand.

Zephronia enghoffi sp. nov.

http://zoobank.org/033601FE-A945-445F-AE11-7CFEE3E05747
Figures 2A, B; 7; 8; 13C, D; 14B

Type material. ***Holotype*****:** Thailand – Khon Kaen Province • ♂; Tham Phaya Nakharat; 16°48'52"N, 101°57'16"E; 528 m a.s.l.; 21 July 2020; R. Srisonchai, C. Sutcharit leg.; CUMZ-Zeph0005. ***Paratypes*****:** Thailand – Khon Kaen Province • 4 ♂♂ 3 ♀♀; same locality as holotype; CUMZ-Zeph0006 • 2 ♀♀; same Province, Chum Pae District, Tham Poo Lup; 16°49'45.4"N, 101°59'7.6"E; 346 m a.s.l.; 10 October 2014; R.

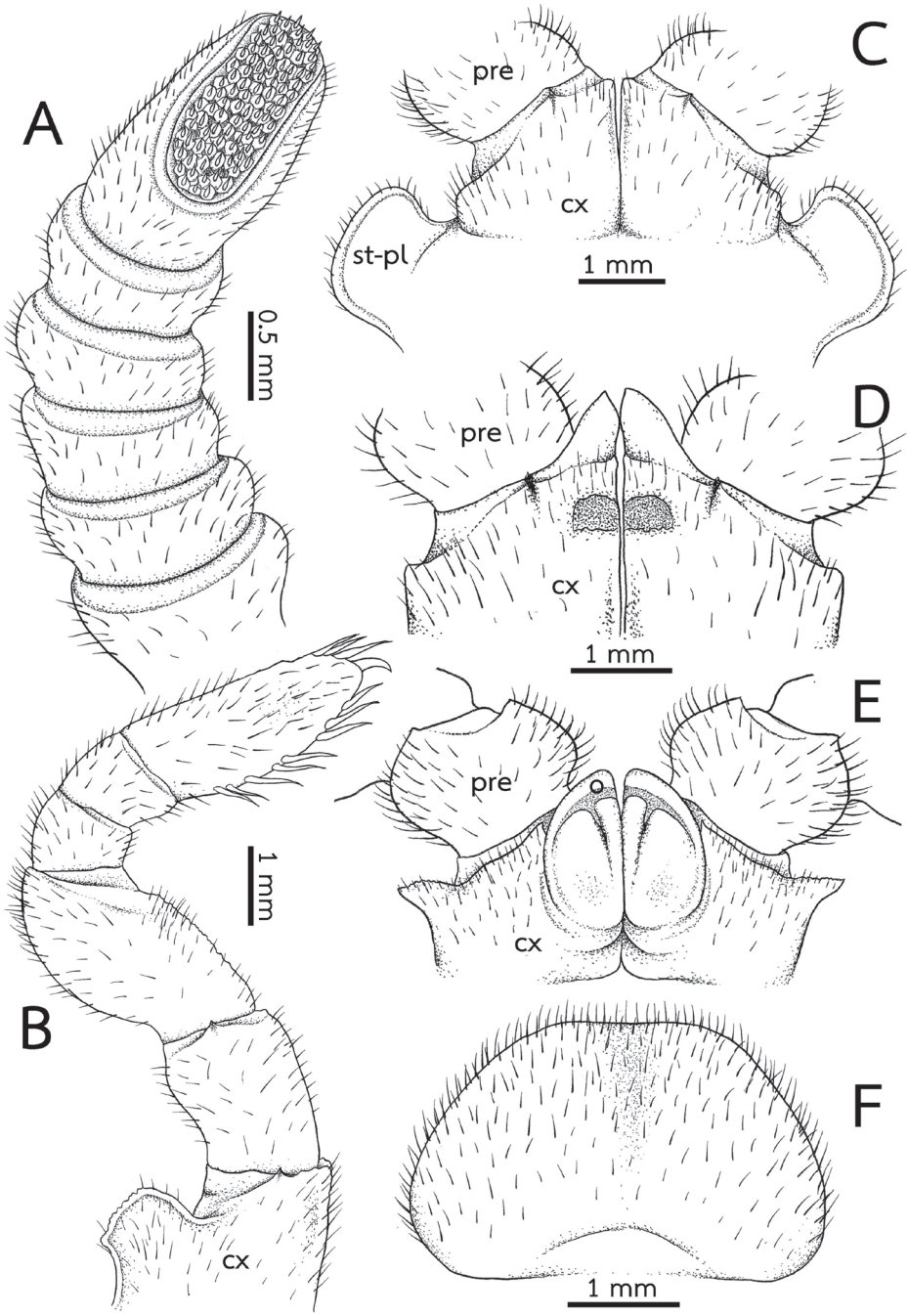

Figure 7. *Zephronia enghoffi* sp. nov. **A–D** male holotype (CUMZ-Zeph0005) **E, F** female paratypes (CUMZ-Zeph0006) **A** right antenna, ventral view **B** the ninth left leg, posterior view **C** First coxae with stigmatic plates, posterior view **D** coxae of second legs with gonopores, posterior view **E** coxae and prefemur of second legs with vulvae, posterior view **F** subanal plate, ventral view. Abbreviations: cx = coxa, o = operculum, pre = prefemur, syn-cx = syncoxite, st-pl = stigmatic plate.

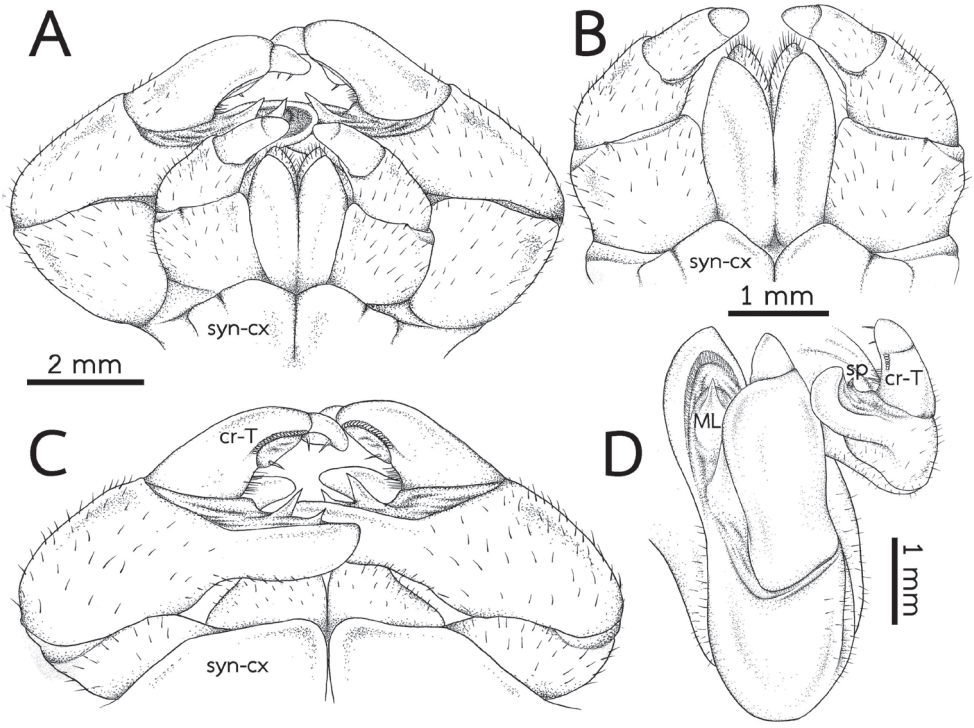

Figure 8. *Zephronia enghoffi* sp. nov., male holotype (CUMZ-Zeph0005) **A** telopods, anterior view **B** anterior telopod, anterior view **C** posterior telopod, posterior view **D** right anterior and posterior telopods, ventral view. Abbreviations: cr-T = crenuations/teeth, cx = coxa, ML = membranous lobe, sp = sclerotized process, syn-cx = syncoxite.

Srisonchai, C. Sutcharit leg.; CUMZ-Zeph0006. **Further specimens, not paratypes:** Thailand – Loei Province • 1 ♂ 2 ♀♀; Wang Saphung District, Pak Puan Arboretum; 17°21'20"N, 101°44'59"E; 316 m a.s.l.; 10 October 2014; R. Srisonchai, C. Sutcharit leg.; CUMZ-Zeph0006.

Etymology. This species is named after Henrik Enghoff from Natural History Museum of Denmark, University of Copenhagen, Denmark, the Danish myriapodologist who initiated an important research step on millipede studies for Thailand.

Diagnosis. A member of *Zephronia* s. s. in which the position of Tömösváry's organ located next to the aberrant ommatidia, not inside the antennal groove. Adult body length medium, > 29 mm, usually ca. 32 mm, up to 36 mm; body brown or dark brown, inner surface (underside) of anal shield with a single locking carina on each side, and leg-pair 2 of male coxa with a long membranous lobe at mesal margin. Similar in these respects to *Z. golovatchi* sp. nov., but differs from this species by the following combination of characters; antenna short, leg-pair 2 of female coxa apico-mesally with large and conspicuous coxal ridge, operculum of vulva regularly rounded and narrow in posterior view, mesal margin of operculum tapering apically, central margin (tip) of subanal plate shallowly concave, process of

telopoditomere 2 of anterior telopod quite long and equal in length to the combination of telopoditomeres 3+4, and immovable finger telopoditomere 2 of posterior telopod (process of telopoditomere 2) equal in length to movable finger (consisting of telopoditomeres 3 and 4).

Description. ***Body length*****:** Length in male 29.0–33.0 mm (holotype 31.0 mm), female 30.0–36.0 mm; head 4.5–5.5 mm; thoracic shield 5.5–7.0 mm; anal shield 11.0–11.5 mm.

Body width**:** Width in male 16.0–18.5 mm (holotype 18.0 mm), female 16.0–19.0 mm; head 9.0–10.0 mm; thoracic shield 16.0–18.0 mm; anal shield 14.0–17.0 mm.

Body height**:** Height in male 10.0–12.0 mm (holotype 11.0 mm), female 10.0–13.0 mm; thoracic shield 10.0–12.0 mm; tergite 10.0–13.0 mm.

Color (Fig. 2A, B): Specimens in life with light brown to brown color; antennae dark brown; head, thoracic shield, tergites, paratergites and basal part of legs brown; posterior margin of tergites dark brown; a few apical podomeres greenish brown. Color in alcohol after 8 months not changed.

Head**:** Wide and stout, subtrapeziform; anterior part of head with dense and long setae; central part of head glabrous; posterior part of head with dense and short setae. Labrum with a single tooth at anterior margin. Each eye with 90–100 ommatidia. Aberrant ocellus located near antennal groove (at upper part of groove).

Antenna (Fig. 7A): Short and stout, with rounded joints; length 3.5–4 mm; reaching backward to tarsus of legs 2 or 3. Lengths of antennomeres 6 > 5 > 4 = 3 = 2 = 1. Antennomere 6 densely setose, sensilla basiconica surrounding apical disc. Last antennomere thickened and flattened, strongly widened apically, axe-shaped. Shape of antennae sexually dimorphic; thickened, widened apically and slightly flattened in male, in female cylindrical. Apical disc with ca. 75 apical cones. No sclerotized ridge between antennal socket and ommatidia.

Tömösváry's organ**:** Separated from ommatidium, located on a brim between ommatidia and antennal socket, smaller in diameter than an individual ommatidium.

Gnathochilarium**:** Ventral surface with setae, other structures typical of the order. Mandibles not dissected.

Stigmatic plates (Fig. 7C): First stigmatic plate subtriangular; apex rounded, broad, expanded apically then becoming a fanlike; curved towards coxa 1.

Laterotergites**:** Laterotergite 1 narrow, projecting into a sharp tip. Laterotergite 2 larger than laterotergite 1, tip weakly extended, with a round projection.

Collum**:** Surface glabrous, except for anterior margins near rim with isolated and long setae.

Thoracic shield**:** Surface as those of tergites, covered with small setae, each seta located in a tiny pit; shallow groove wide anterolaterally, with very long setae.

Tergites (Fig. 2A, B): Quite shiny; surface densely setose, visible in normal vision; entirely covered by short setae, each locating in tiny pits; tip of paratergite of midbody tergites curved, directed posteroventrad.

Endotergum (Figs 13C, D, 14B): Posterior margin flat, regular. Inner section (inner area) with setiferous tubercles or setae. Middle section (middle area) with a single row of elliptical cuticular impressions, distance between impressions longer than in-

dividual diameter. Bristles arranged in two rows, tip of the longest bristles extended beyond posterior margin or reaching to posterior margin.

***Anal shield*:** Sexually dimorphic, in female very large and strongly rounded, in male slightly more rectangular. Outer surface covered by tiny and dense setae locating in small pits, similar to those of tergites. Inner surface (underside) covered by long setae; with a single, black, and long locking carina, half as long as length of last laterotergite.

Legs (Fig. 7B): Leg-pairs 1 and 2 without apical spine. Leg-pairs 1 with 2 ventral spines, leg-pair 2 with four ventral spines. Leg-pair 3 with 5–7 ventral spines and one apical spine. Leg-pair 4 with 8–11 ventral spines, and one or two apical spines. Leg-pairs 5–19 with 8–10 ventral spines and 1–3 apical spines. Last two leg-pairs with 7–10 ventral spines and one or two apical spines. In leg 9, femur ca. 1.5×, tarsus ca. 2.3× longer than wide. Length of tarsus ≥ femur > prefemur > coxa > tibia ≥ postfemur. All podomeres densely setose. Coxa large, with dentate ridge marginally (coxal process). Coxal process absent in leg-pairs 1 and 2 (except for female leg-pair 2). Leg-pair 2 of female coxa apico-mesally with large, conspicuous coxal ridge, directed laterad. Leg-pair 2 of male coxa with membranous lobe at mesal margin; lobe large and long, projecting ventrad. Prefemur without teeth. Femur rather short and stout, slightly extended mesally, mesal margin with 5–7 small teeth.

Subanal plate (Fig. 7F): Subsemicircular, undivided, wide; central margin (tip) shallowly concave, broad; lateral margin slightly convex. Densely setose.

Male sexual characters (Fig. 7D): Gonopore quite large, covered with a single, undivided, subsemicircular, sclerotized plate.

Anterior telopods (Fig. 8A, B, D): Telopodite with four telopoditomeres; all telopoditomeres sparsely setose, except for the apical part of telopoditomere 3 and all parts of telopoditomere 4 without setae. First telopoditomere rectangular, slightly large and stout, broader than telopoditomeres 2–4. Telopoditomere 2 large. Process of telopoditomere 2 equal in length to the combination of telopoditomeres 3 and 4; visible in posterior view; curved and slender, 1.5X longer than wide, twice as long as telopoditomere 4; tip bent and round, directed anteriad, close to the basal part of telopoditomere 4. Margin towards telopoditomere 3 with a membranous area carrying a sclerotized process (sp), conspicuous, short, apically with sharp tip. Telopoditomere 3 with six small crenulated teeth (cr-T) in ventral side. Telopoditomere 4 short and stout, conspicuous, straight; tip round, directed mesad; with two prominent sclerotized spines in posterior side.

Posterior telopods (Fig. 8A, C, D): Telopodite with four telopoditomeres; telopoditomeres 1 and 2 on both sides covered with sparse setae, except for immovable finger part; telopoditomere 3 at base of both inner margin and outer margin with a few setae; telopoditomere 4 without setae. First telopoditomere stout and broad, half as long as telopoditomere 2. Telopoditomere 2 slender, immovable finger (process of telopoditomere 2) as long as movable finger (consisting of telopoditomeres 3 and 4). Immovable finger long and slender, wide, 2.5× as long as wide, not curved, tip directed mesad; at margin with several semi-circular rows of sclerotized spots. Margin towards

movable finger with two conspicuous membranous lobes, triangular, inner lobe bigger and longer than outer one. Telopoditomere 3 slender, quite long, slightly expanded distad, slightly curved, thrice as long as telopoditomere 4; with a long and sclerotized spine located on a large, swollen, membranous lobe; posterior part with a row of 17–19 crenulated teeth (cr-T). Telopoditomere 4 short and stout, 1.5× longer than wide; at inner margin with a large, conspicuous, swollen, membranous lobe and two evident sclerotized spines.

Female sexual characters (Fig. 7E): Vulva large, covering ca. 2/3 coxa, located at mesal side, extending mesally to basal third of prefemur. Operculum regularly rounded, narrow in posterior view; mesal margin not protruding.

Distribution and habitats (Figs 15B, C, 16). All specimens were collected from limestone habitats (in dry dipterocarp forest). Known only from three sites in limestone mountain ranges of Khon Kaen and Loei provinces.

Remarks. With regard to the morphological characters of coxae 2 in both male and female, this species exhibits the remarkable shape in which the male has a very long membranous lobe (Fig. 7D) and the female displays conspicuous coxal ridges apico-mesally (Fig. 7E). Moreover, the surface of tergites covered with conspicuous setae/hairy in *Z. enghoffi* sp. nov. is more distinctive than in the other two new species (Fig. 2A, B).

Zephronia golovatchi sp. nov.

http://zoobank.org/8033D6ED-BAE9-4347-851D-8B2C7B147FE5
Figures 2C, D; 9; 10; 13E, F; 14C

Type material. ***Holotype*****:** Thailand – Nakhon Ratchasima Province • ♂; Pak Chong District, Khao Yai National Park, Khao Luk Chang; 14°31'49.6"N, 101°21'32"E; 410 m a.s.l.; 26 April 2009; N. Likhitrakarn, C. Sutcharit, W. Siriwut leg.; CUMZ-Zeph0007. ***Paratypes*****:** Thailand – Nakhon Ratchasima Province • 1 ♂ 4 ♀♀; same locality as holotype; CUMZ-Zeph0008.

Etymology. The species is named for our highly esteemed colleague Sergei I. Golovatch (Zoological Museum, State University of Moscow, Russia), one of the most productive millipede taxonomists, who encouraged all new and young myriapodologists in Thailand.

Diagnosis. Adult body length medium to large > 29 mm, usually 35 mm, up to 37 mm; body brown or dark brown, marginal bristles of endotergum extending over posterior margin, inner surface (underside) of anal shield with a single locking carina on each side, and leg-pair 2 of male coxa with membranous lobe at mesal margin. Similar in these respects to *Z. enghoffi* sp. nov., but differs from this species by the following combination of characters: antenna long; operculum of vulva regularly rounded and broad in posterior view; mesal margin of operculum not tapering apically; central margin (tip) of subanal plate divided by a conspicuous mesal constriction, process of telopoditomere 2 of anterior telopods shorter than telopoditomere 3; telopoditomere 3 of anterior telopods with 2 or 3 crenulated teeth; immovable finger telopoditomere

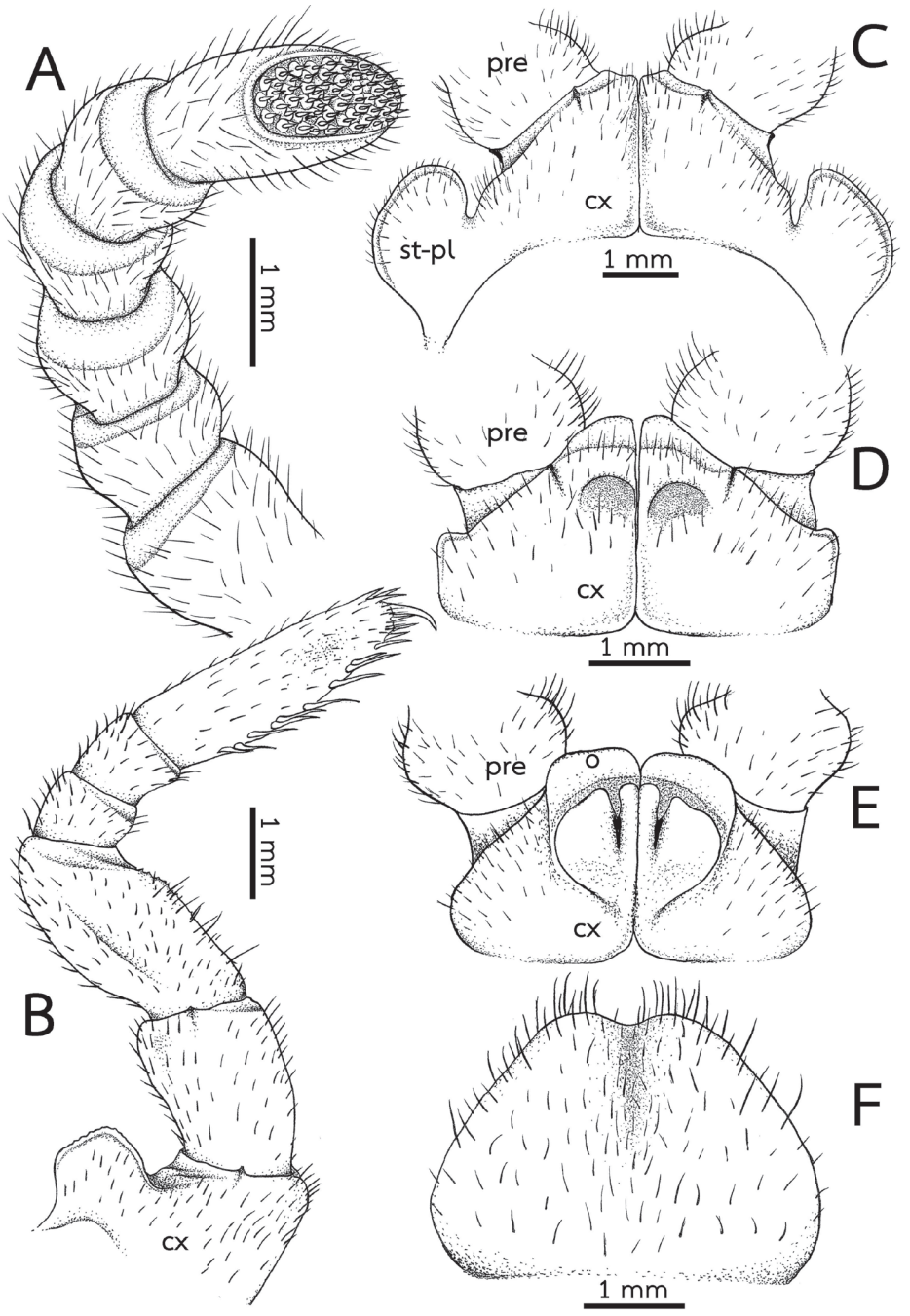

Figure 9. *Zephronia golovatchi* sp. nov. **A–D** male holotype (CUMZ-Zeph0007) **E, F** female paratypes (CUMZ-Zeph0008) **A** right antenna, ventral view **B** the ninth left leg, posterior view **C** first coxae with stigmatic plates, posterior view **D** coxae of second legs with gonopores, posterior view **E** coxae and prefemur of second legs with vulvae, posterior view **F** subanal plate, ventral view. Abbreviations: cx = coxa, o = operculum, pre = prefemur, syn-cx = syncoxite, st-pl = stigmatic plate.

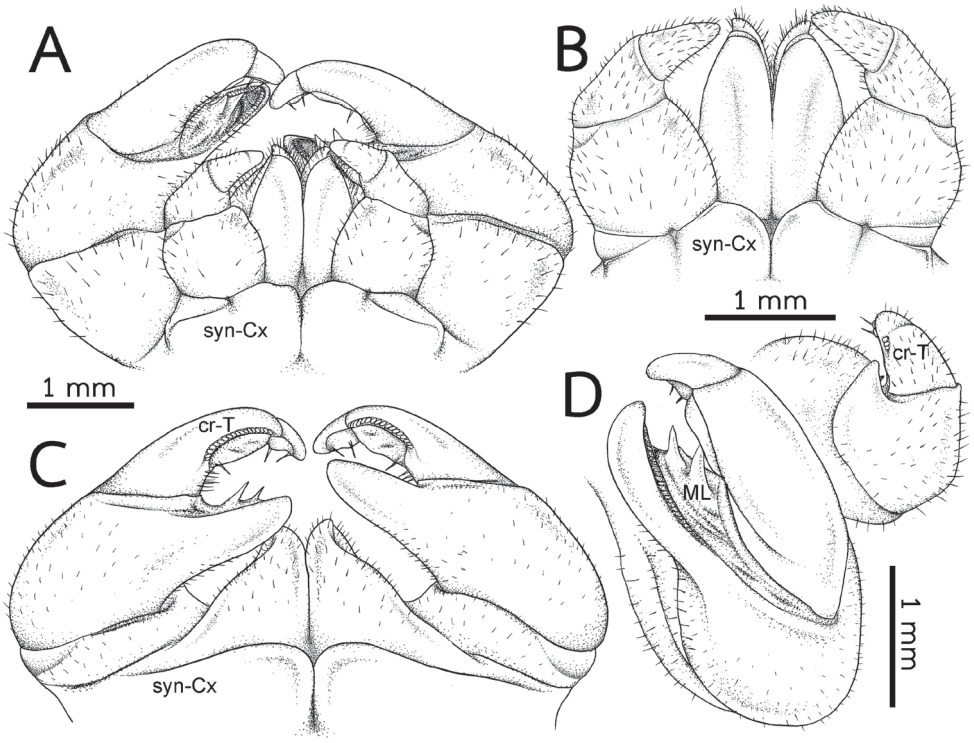

Figure 10. *Zephronia golovatchi* sp. nov., male holotype (CUMZ-Zeph0007) **A** telopods, anterior view **B** anterior telopod, anterior view **C** posterior telopod, posterior view **D** right anterior and posterior telopods, ventral view. Abbreviations: cr-T = crenulated teeth, cx = coxa, ML = membranous lobe, syn-cx = syncoxite.

2 of posterior telopod (process of telopoditomere 2) shorter than movable finger (consisting of telopoditomeres 3 and 4).

Description. ***Body length*:** Length in male 35.0–36.5 mm (holotype 35.0 mm), female 35.0–37.0 mm; head 5.5–7.5 mm; thoracic shield 5.0–6.0 mm; anal shield 10.5–11.5 mm.

***Body width*:** Width in male 19.0–21.0 mm (holotype 20.0 mm), female 19.0–22.0 mm; head 10.0–11.0 mm; thoracic shield 17.5–20.5 mm; anal shield 16.0–18.5 mm.

***Body height*:** Height in male ca 11.0 mm (holotype 11.0 mm), female 11.0–12.0 mm; thoracic shield 9.0–10.5 mm; tergite 10.0–11.5 mm.

Color (Fig. 2C, D): Specimens in life with brown color; antennae dark brown; head, collum, thoracic shield, tergites, paratergites, anal shield and legs brown; posterior margin of tergites dark brown. Color in alcohol after 13 years changed to pale brown.

***Head*:** Wide and stout, subtrapeziform; anterior part of head with dense and long setae; central part of head with sparse and long setae; posterior part of head with dense and short setae. Labrum with a single tooth at anterior margin. Each eye with ca. 90–100 ommatidia. Aberrant ocellus located inside antennal groove (at upper part of groove).

Antenna (Fig. 9A): Quite long and stout, with rounded joints; length ca. 5 mm; reaching backward to tarsus of legs 3 or 4. Lengths of antennomeres 6 > 5 = 4 = 3 =

2 = 1. Antennomere 6 densely setose, sensilla basiconica surrounding apical disc. Last antennomere thickened and flattened, strongly widened apically, axe-shaped. Shape of antennae sexually dimorphic; thickened, widened apically and slightly flattened in male, in female cylindrical. Apical disc with 90–100 apical cones. No sclerotized ridge between antennal socket and ommatidia.

***Tömösváry's organ*:** Not distinctly separated from ommatidium, located closely to anterior margin of ommatidia, equal in size to an individual ommatidium.

***Gnathochilarium*:** Ventral surface with setae, other structures typical of the order. Mandibles not dissected.

Stigmatic plates (Fig. 9C): First stigmatic plate subtriangular; apex rounded, broad; slightly projecting towards coxa 1.

***Laterotergites*:** Laterotergite 1 narrow, projecting into a sharp tip. Laterotergite 2 broader than laterotergite 1, tip slightly extended, with round projection.

***Collum*:** Surface glabrous, except for anterior margins near rim with isolated and long setae.

***Thoracic shield*:** Surface as those of tergites, covered with inconspicuous and small setae, each seta located in tiny pits; shallow groove wide anterolaterally, with very long setae.

Tergites (Fig. 2C, D): Quite dull; surface entirely covered by short setae, visible by normal vision; each seta locating in tiny pits; anterior margin densely setose; posterior margin sparsely setose; tip of paratergite in midbody slightly curved, directed posteroventrad.

Endotergum (Figs 13E, F, 14C): Posterior margin flat, regular. Inner section (inner area) with a few setiferous tubercles or setae. Middle section (middle area) with a single row of small, conspicuous, elliptical cuticular impressions; distance between impressions longer than individual diameter; with a row of conspicuous ridges between bristles and impressions. Bristles arranged in two rows, tip of the longest bristles extended beyond posterior margin or reaching to posterior margin.

***Anal shield*:** Sexually dimorphic, in female very large and weakly bell-shaped, in male slightly bell-shaped. Outer surface pubescent, similar to those of tergites; setae small and very short locating in tiny pits; anterior margin densely setose, posterior margin sparsely setose. Inner surface (underside) covered by setae; with a single, black, very long, locking carina, ca. 1/3 as long as length of last laterotergite.

Legs (Fig. 9B): Leg-pairs 1 and 2 without apical spine. Leg-pair 1 with two ventral spines, leg-pair 2 with four or five ventral spines. Leg-pair 3 with 7–9 ventral spines and one or two apical spines. Leg-pair 4 with 9–11 ventral spines and one or two apical spines. Leg-pairs 5–19 with 8–12 ventral spines and 1–3 apical spines. Last two leg-pairs with 9–11 ventral spines and one or two apical spines. In leg 9, femur ca. 1.7×, tarsus ca. 3.2× longer than wide. Length of tarsus > femur > prefemur > coxa > tibia ≥ postfemur. All podomeres densely setose. Coxa large, with dentate ridge marginally (coxal process). Coxal process absent in leg-pairs 1 and 2. Prefemur without teeth. Femur extended mesally, mesal margin with 7–9 conspicuous teeth.

Subanal plate (Fig. 9F): Trapeziform, divided by a conspicuous mesal constriction; central margin (tip) strongly concave, narrow; lateral margin straight. Densely setose.

Male sexual characters (Fig. 9D): Gonopore large, covered with a single, undivided, subsemicircular, sclerotized plate.

Anterior telopods (Fig. 10A, B, D): Telopodite with four telopoditomeres; telopoditomeres 3 and 4 often clearly divided by conspicuous suture, some specimens inconspicuous; all telopoditomeres sparsely setose, except for process of telopoditomere 2 with no setae. First telopoditomere rectangular, large, stout. Telopoditomere 2 slender. Process of telopoditomere 2 short, shorter than telopoditomeres 3; visible in posterior view; tip curved, blunt and narrow, directed anteromesad, close to middle part of telopoditomere 3. Margin towards telopoditomere 3 with a membranous area carrying a sclerotized process (sp); a process inconspicuous, short, tip quite sharp. Telopoditomere 3 with two or three crenulated teeth (cr-T), conspicuous. Telopoditomere 4 very short and stout, inconspicuous; tip round, directed mesad; with two small, conspicuous, sclerotized spines in posterior side.

Posterior telopods (Fig. 10A, C, D): Telopodite with four telopoditomeres; telopoditomeres 1 and 2 on both sides sparse setose, except for apical part of immovable finger (process of telopoditomere 2); telopoditomere 3 at base of inner margin with conspicuous setae, but none for outer margin; telopoditomere 4 without setae. First telopoditomere large, wide, as long as wide. Telopoditomere 2 large, immovable finger (process of telopoditomere 2) relatively shorter than movable finger (consisting of telopoditomeres 3 and 4). Immovable finger slender, twice as long as wide, slightly curved, tip directed anteroventrad; at margin with several semi-circular rows of sclerotized spots, conspicuous. Margin towards movable finger with two membranous lobes, conspicuous and long, conical, inner lobe bigger and longer than outer one, tip sharp. Telopoditomere 3 very long and slender, tapering apically, strongly curved, thrice as long as telopoditomere 4; with a long and sclerotized spine located on a large, swollen, membranous lobe; posterior part with a row of 17 or 18 crenulated teeth (cr-T). Telopoditomere 4 slender, 2× longer than wide; at inner margin with a large, conspicuous, swollen, membranous lobe and with two evident sclerotized spines; tip curving mesodorsad.

Female sexual characters (Fig. 9E): Vulva large, covering ca. 2/3 coxa, located at mesal side, extending mesally to basal third of prefemur. Operculum regularly rounded, margin straight, mesal margin not protruding.

Distribution and habitats (Fig. 16). Known only from the type locality. All specimens have been taken from limestone habitats and were found walking on top of decayed wood or hiding under leaf litter.

Remarks. This species has thin membranous lobe on male coxae 2 (Fig. 9D), but this lobe seems to be shorter than that of *Z. enghoffi* sp. nov. (Fig. 7D).

Zephronia panhai sp. nov.

http://zoobank.org/127730AA-2FEC-49F1-B3F9-412C216E7F53
Figures 2E, F; 11; 12; 13G, H; 14D, E

Type material. ***Holotype*****:** Thailand • ♂; Phetchaburi Province, Tha Yang District, Wat Khao Khachiu; 12°57'42.7"N, 99°54'49.9"E; 22 m a.s.l.; 17 August 2019; R. Srisonchai, C. Sutcharit, W. Siriwut leg.; CUMZ-Zeph0009. ***Paratypes*****:** Thailand – Phetch-

aburi Province • 8 ♂♂ 6 ♀♀; same locality as holotype; CUMZ-Zeph0010 • 1 ♂; same data as holotype; NHMD • 1 ♂; same data as holotype; ZMUM • 1 ♂; same data as holotype; ZRC. **Further specimens, not paratypes:** Thailand – Phetchaburi Province • 3 ♂♂ 2 ♀♀; Khao Yoi District, Wat Puangmali (Wat Tham Khao Ego); 13°18'45.3"N, 99°47'5.1"E; 22 m a.s.l.; 8 September 2016; R. Srisonchai, C. Sutcharit, W. Siriwut leg.; CUMZ-Zeph0010 • 1 ♂ 2 ♀♀; Rachaburi Province, Pak Tho District, Wat Buri Ratchawanaram; 13°22'45"N, 99°47'6"E, 26 m a.s.l.; 14 November 2019; R. Srisonchai, C. Sutcharit, W. Siriwut leg.; CUMZ-Zeph0010 • 2 ♂♂ 4 ♀♀; Kanchaburi Province, Mueang District, Wat Tham Mangkorn Thong; 13°59'8.2"N, 99°31'2.9"E; 46 m a.s.l.; 3 September 2017; R. Srisonchai, C. Sutcharit, W. Siriwut leg.; CUMZ-Zeph0010.

Etymology. The species name recognizes the great professor and a long-time mentor to the authors, Somsak Panha (Chulalongkorn University Museum of Zoology, Thailand).

Diagnosis. Differs from all congeners by the combination of the following characters; grey body color, adult body length ca. 21 mm, tergites covered by conspicuous setae, long setae on tergites extending over the posterior margin (Figs 13G, 14D), marginal bristles of endotergum not extending over posterior margin, margin of operculum on vulva slightly concave and slightly invaginated medially, telopoditomere 3 of anterior telopods with conspicuous crenulated teeth and telopoditomere 3 of posterior telopods with a row of 11or 12 crenulated teeth.

Description. ***Body length*****:** Length in male 19.0–22.0 mm (holotype 20.0 mm), female 20.0–23.0 mm; head 4.0 mm; thoracic shield 4.0–4.5 mm; anal shield 6.0–7.5 mm.

Body width**:** Width in male 10.0–11.5 mm (holotype 10.0 mm), female 10.0–12.0 mm; head 6.0–7.0 mm; thoracic shield 10.0–11.0 mm; anal shield 9.5–10.5 mm.

Body height**:** Height in male 7.0–7.5 mm (holotype 7.0 mm), female 7.0–7.5 mm; thoracic shield 6.0–7.0 mm; tergite 6.5–7.5 mm.

Color (Fig. 2E, F): Specimens in life with light grey; head, antennae and collum greenish grey; thoracic shield, tergites and anterior part of anal shield grey; paratergites, posterior margins of tergites and posterior part of anal shield greyish brown. Color in alcohol after two years not changed.

Head**:** Wide and stout, subtrapeziform; anterior part of head with dense and long setae; central part of head with sparse and long setae; posterior part of head with dense and short setae. Labrum with a single tooth at anterior margin. Each eye with ca. 70 ommatidia. Aberrant ocellus located near antennal groove (at upper part of groove).

Antenna (Fig. 11A): Short and stout, with rounded joints; length ca. 3 mm; reaching backward to tarsus of leg 2. Lengths of antennomeres 6 > 5 = 4 = 3 = 2 = 1. Antennomere 6 densely setose, sensilla basiconica surrounding apical disc. Last antennomere thickened and flattened, strongly widened apically, axe-shaped. Shape of antennae sexually dimorphic; thickened, widened apically and slightly flattened in male, in female cylindrical. Apical disc with ca. 50 apical cones. No sclerotized ridge between antennal socket and ommatidia.

Tömösváry's organ**:** Separated from ommatidia, located on a brim between ommatidia and antennal socket, smaller in diameter than an individual ocellus.

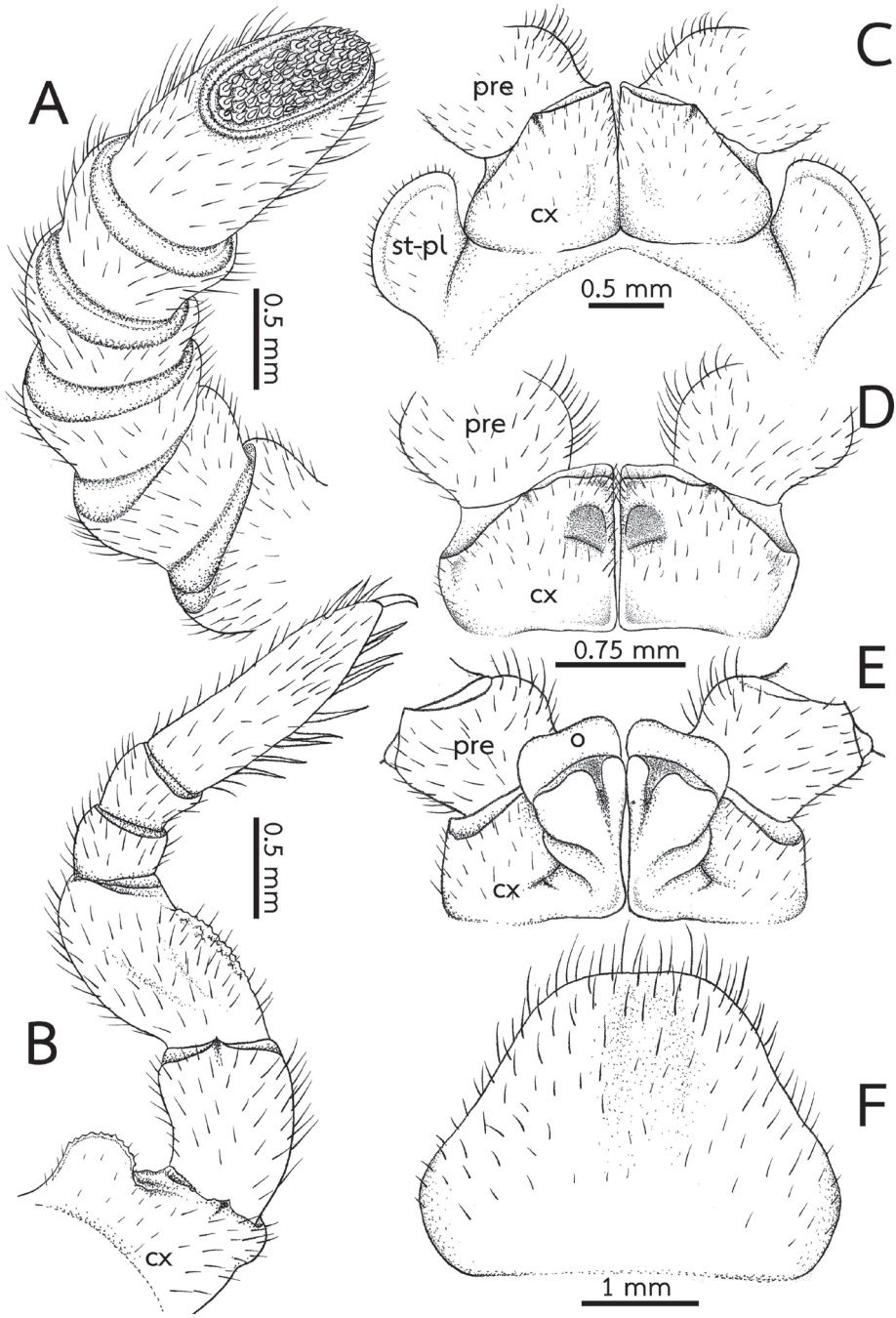

Figure 11. *Zephronia panhai* sp. nov. **A–D** male holotype (CUMZ-Zeph0009) **E, F** female paratypes (CUMZ-Zeph0010) **A** right antenna, ventral view **B** the ninth left leg, posterior view **C** first coxae with stigmatic plates, posterior view **D** coxae of second legs with gonopores, posterior view **E** coxae and prefemur of second legs with vulvae, posterior view **F** subanal plate, ventral view. Abbreviations: cx = coxa, o = operculum, pre = prefemur, syn-cx = syncoxite, st-pl = stigmatic plate.

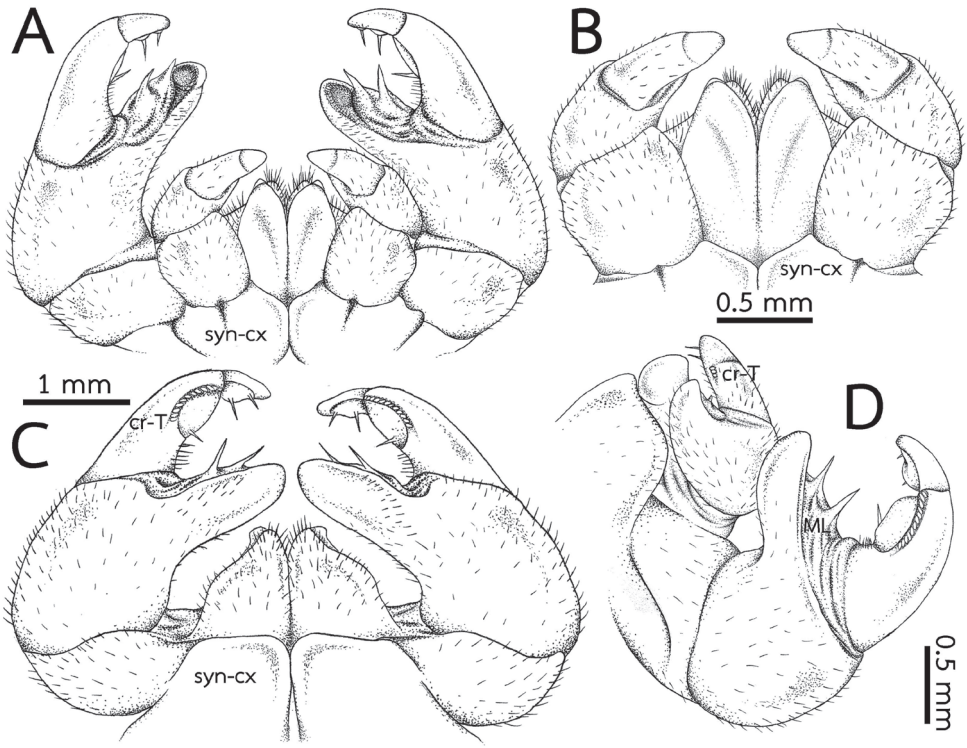

Figure 12. *Zephronia panhai* sp. nov., male holotype (CUMZ-Zeph0009) **A** telopods, anterior view **B** anterior telopod, anterior view **C** posterior telopod, posterior view **D** right anterior and posterior telopods, ventral view. Abbreviations: cr-T = crenulated teeth, cx = coxa, ML = membranous lobe, sp = sclerotized process, syn-cx = syncoxite.

***Gnathochilarium*:** Ventral surface with setae, other structures typical of the order. Mandibles not dissected.

Stigmatic plates (Fig. 11C): First stigmatic plate subtriangular; apex rounded, broad; straight towards coxa 1.

***Laterotergites*:** Laterotergites 1 and 2 narrow, projecting to a sharp tip.

***Collum*:** Surface with very long setae in both anterior and posterior margins, setae located in pits.

***Thoracic shield*:** Surface as those of tergites, covered with tiny setae; shallow groove with long setae, slightly broad at anterolateral margin.

Tergites (Fig. 2E, F): Quite dull; surface densely setose, easily seen by normal vision; with numerous and short setae, each locating in tiny pits; tips of paratergites of midbody tergites weakly curved, directed posteroventrad.

Endotergum (Figs 13G, H, 14D, E): Posterior margin flat, regular; tip of setae. Inner section (inner area) with a few setiferous tubercles or setae. Middle section (middle area) with a single row of conspicuous, elliptical cuticular impressions; distance between im-

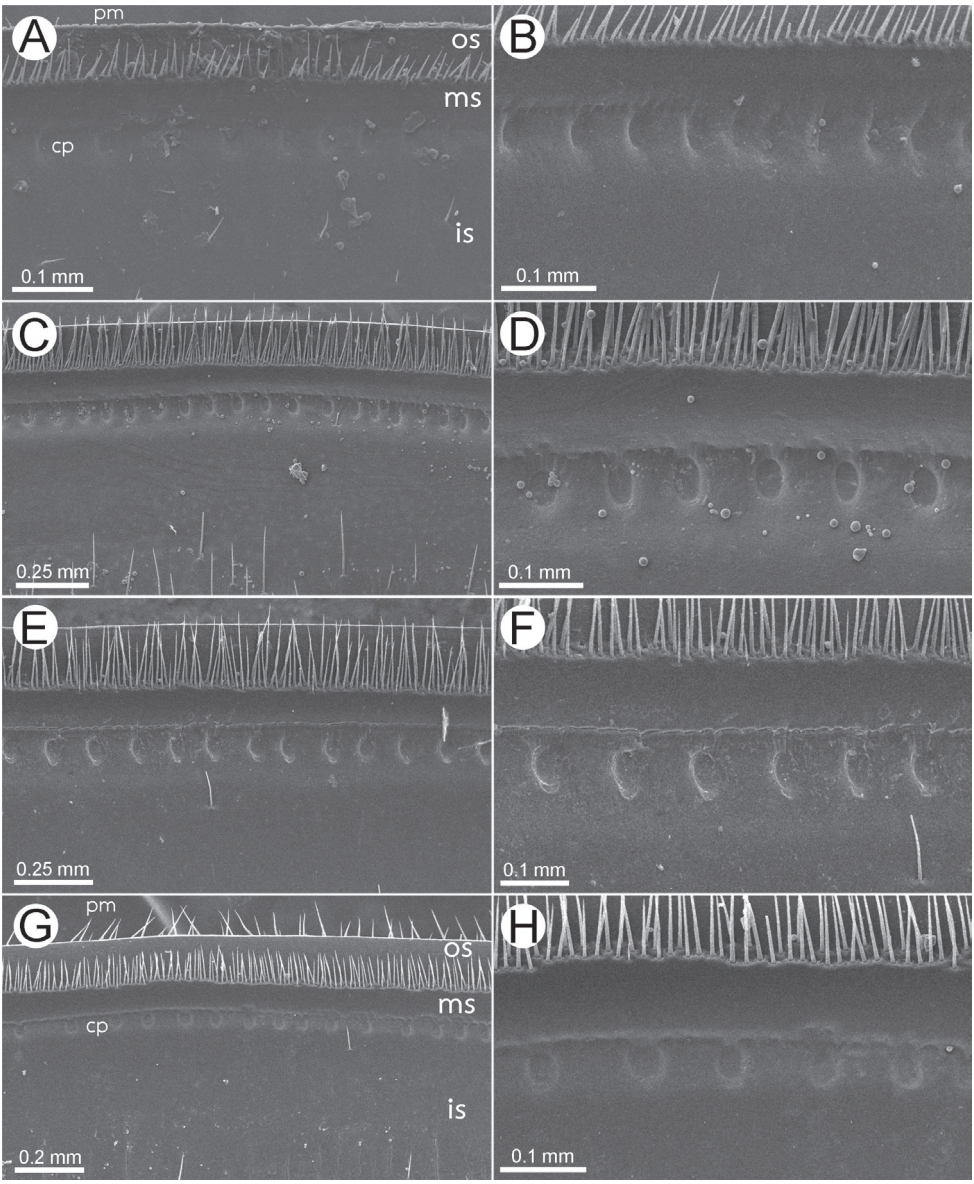

Figure 13. SEM of endoterga of body ring 7, all from ventral views **A, B** *Zephronia siamensis* Hirst, 1907 **C, D** *Zephronia enghoffi* sp. nov. **E, F** *Zephronia golovatchi* sp. nov. **G, H** *Zephronia panhai* sp. nov. Abbreviations: cp = cuticular impression, ms = middle section, is = inner section, os = outer section, pm = posterior margin.

pressions longer than individual diameter. Bristles arranged in two rows, tip of the longest bristles not extended beyond posterior margin or not reaching to posterior margin.

***Anal shield*:** Sexually dimorphic, in female weakly bell-shaped, in male strongly bell-shaped. Outer surface pubescent, setae small and very short, similar to those of

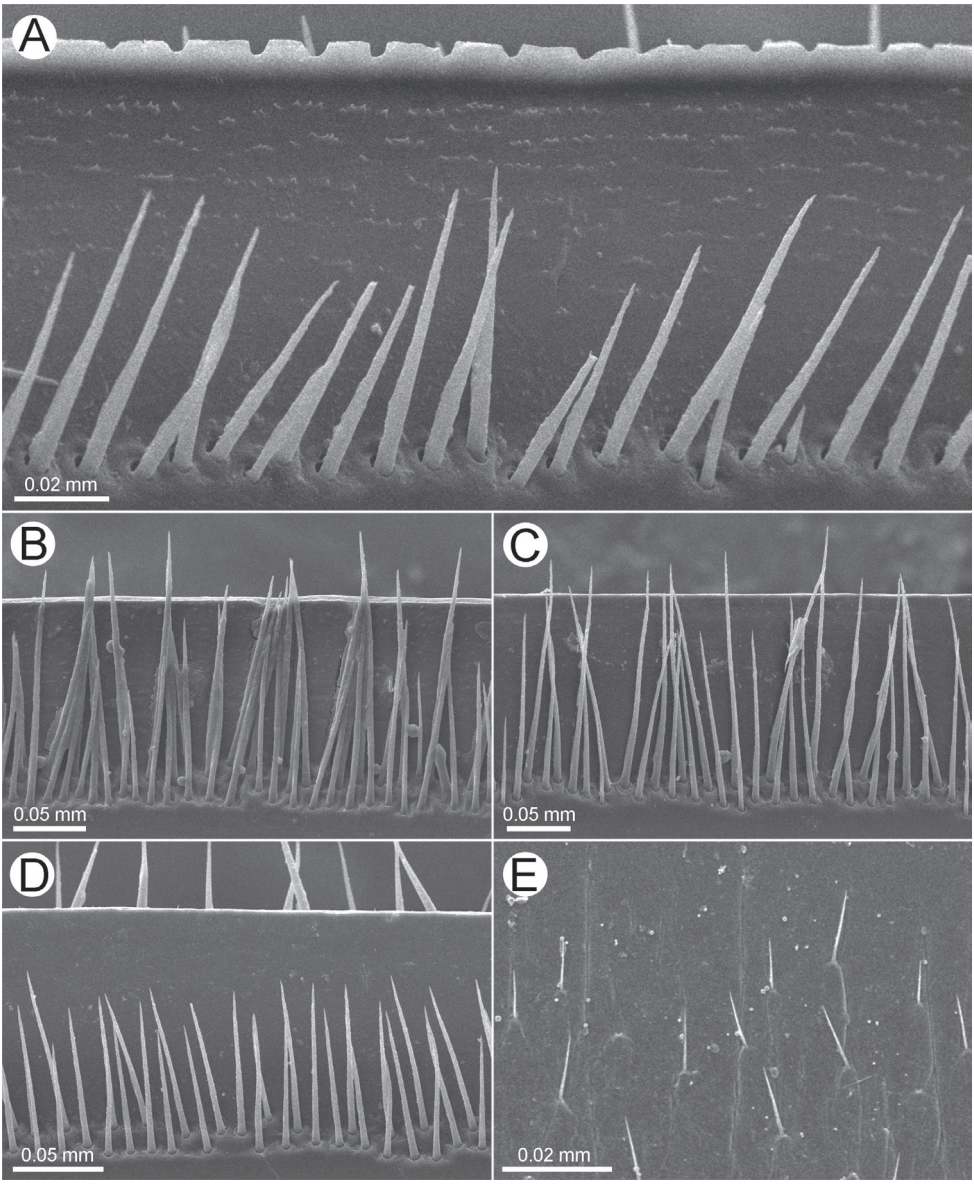

Figure 14. SEM of endoterga in body ring 7, all from ventral views **A** *Zephronia siamensis* Hirst, 1907 **B** *Zephronia enghoffi* sp. nov. **C** *Zephronia golovatchi* sp. nov. **D** *Zephronia panhai* sp. nov. **E** inner area of endotergum in *Zephronia panhai* sp. nov.

tergites. Inner surface (underside) covered by setae; with a single locking carina, half as long as length of last laterotergite.

Legs (Fig. 11B): Leg-pairs 1 and 2 without an apical spine. Leg-pair 1 with two or three ventral spines, leg-pair 2 with four ventral spines. Leg-pair 3 with six ventral spines and one apical spine. Leg-pair 4 with 7–9 ventral spines and 1–3 apical spines.

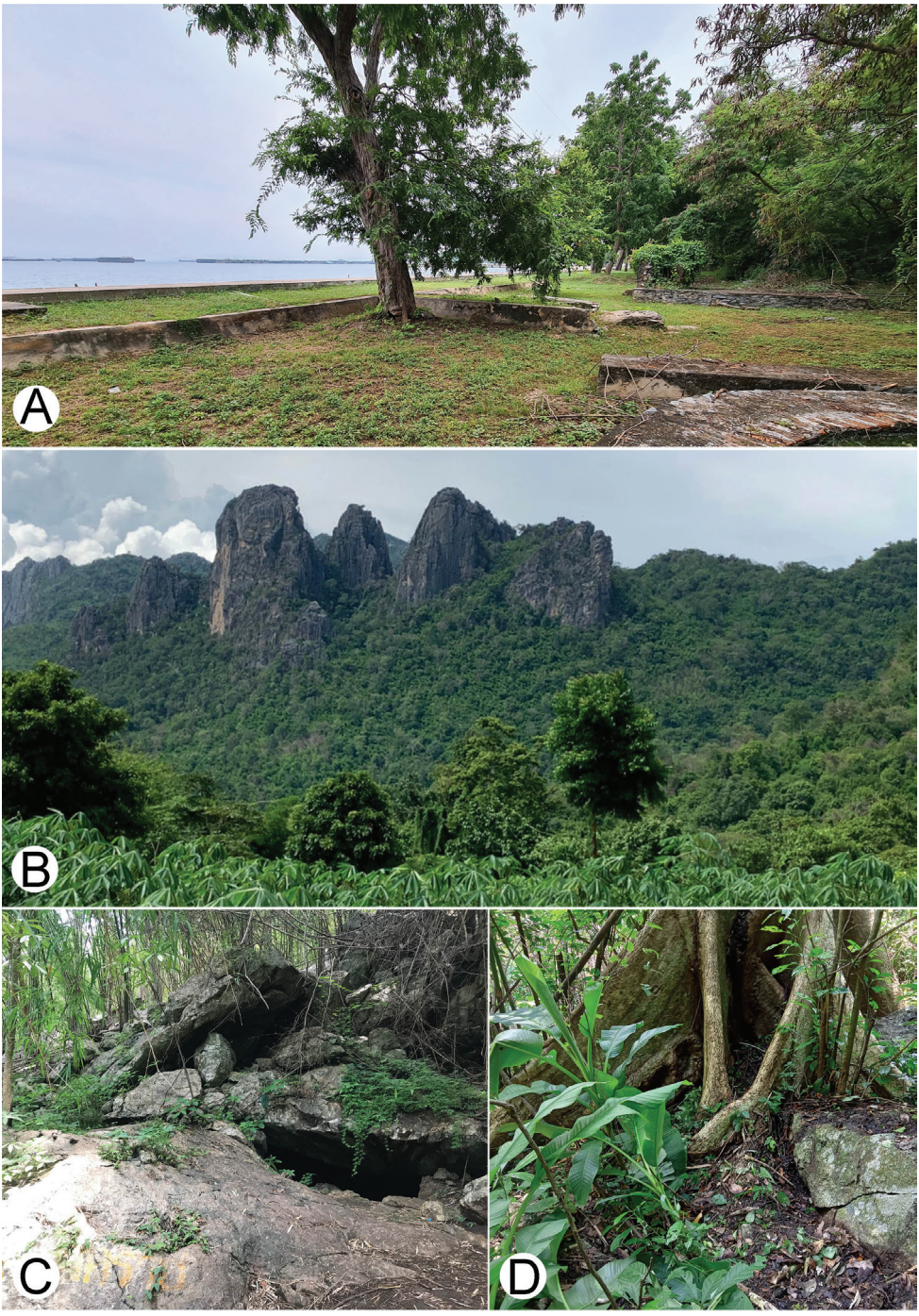

Figure 15. Limestone habitats of some *Zephronia* spp. **A** type locality of *Zephronia siamensis* (Koh Srichang, Chonburi Province) **B, C** type locality of *Zephronia enghoffi* sp. nov. (Tham Phaya Nakharat, Khon Kaen Province) **D** Habitat of *Zephronia phrain* at Phawor shrine, Tak Province.

Leg-pairs 5–19 with 7–11 ventral spines and 1–3 apical spines. Last two leg-pairs with eight or nine ventral spines and one or two apical spines. In leg 9, femur 1.4×, tarsus 3.5× longer than wide. Length of tarsus > femur > prefemur > coxa > tibia ≥ postfemur. All podomeres densely setose. Coxa large, with dentate ridge marginally (coxal process). Coxal process absent in leg-pairs 1 and 2. Prefemur without teeth. Femur quite short and stout, slightly extended mesally; mesal margin with 7 or 8 conspicuous teeth, long, conical shape.

Subanal plate (Fig. 11F): Trapeziform, undivided; central margin (tip) slightly rounded, narrow; lateral margin slightly concave. Densely setose.

Male sexual characters (Fig. 11D): Gonopore large, covered with a single, undivided, triangular, sclerotized plate.

Anterior telopods (Fig. 12A, B, D): Telopodite with four telopoditomeres; telopoditomeres 3 and 4 clearly divided by a conspicuous suture; all telopoditomeres sparsely setose, except for telopoditomeres 4 without setae. First telopoditomere rectangular, broad, 1.5× longer than wide. Telopoditomere 2 stout. Process of telopoditomere 2 quite short, subequal in length to telopoditomeres 3; visible in posterior view, but partly seen mesally in anterior view; tip curved and well-rounded, directed mesad, close to basal part of telopoditomere 4. Margin towards telopoditomere 3 with a membranous area carrying a sclerotized process (sp); a process conspicuous, but very short, tip quite sharp. Telopoditomere 3 with three crenulated teeth (cr-T), conspicuous. Telopoditomere 4 very short and stout, conspicuous; tip round, directed mesad; with two small, sclerotized spines in posterior side.

Posterior telopods (Fig. 12A, C, D): Telopodite with four telopoditomeres; telopoditomeres 1 and 2 on both sides with sparse setae, except for apical part of immovable finger (process of telopoditomere 2); telopoditomere 3 at base of inner margin with conspicuous setae, but none for outer margin; telopoditomere 4 without setae. First telopoditomere stout and narrow, ca. half as long as telopoditomere 2. Telopoditomere 2 large, immovable finger (process of telopoditomere 2) relatively shorter than movable finger (consisting of telopoditomeres 3 and 4). Immovable finger slender, twice as long as wide, strongly curved, tip directed anteroventrad; at margin with several conspicuous semi-circular rows of sclerotized spots. Margin towards movable finger with two membranous lobes, conspicuous long, triangular, inner lobe bigger and longer than outer one, tip sharp. Telopoditomere 3 very long and slender, tapering apically, curved, thrice as long as telopoditomere 4; with a long and sclerotized spine located on a large, swollen, membranous lobe; posterior part with a row of 11–12 crenulated teeth (cr-T). Telopoditomere 4 slender, 2× longer than wide; at inner margin with a large, conspicuous, swollen, membranous lobe and with two evident sclerotized spines; tip curving mesad.

Female sexual characters (Fig. 11E): Vulva large, covering ca. 2/3 coxa, located at mesal side, extending mesally to basal third of prefemur. Operculum regularly rounded, margin slightly concave, mesal margin not protruding.

Distribution and habitats (Fig. 16). The new species is known from Phetchaburi, Ratchaburi, and Kanchanaburi provinces. All specimens were collected from limestone habitats.

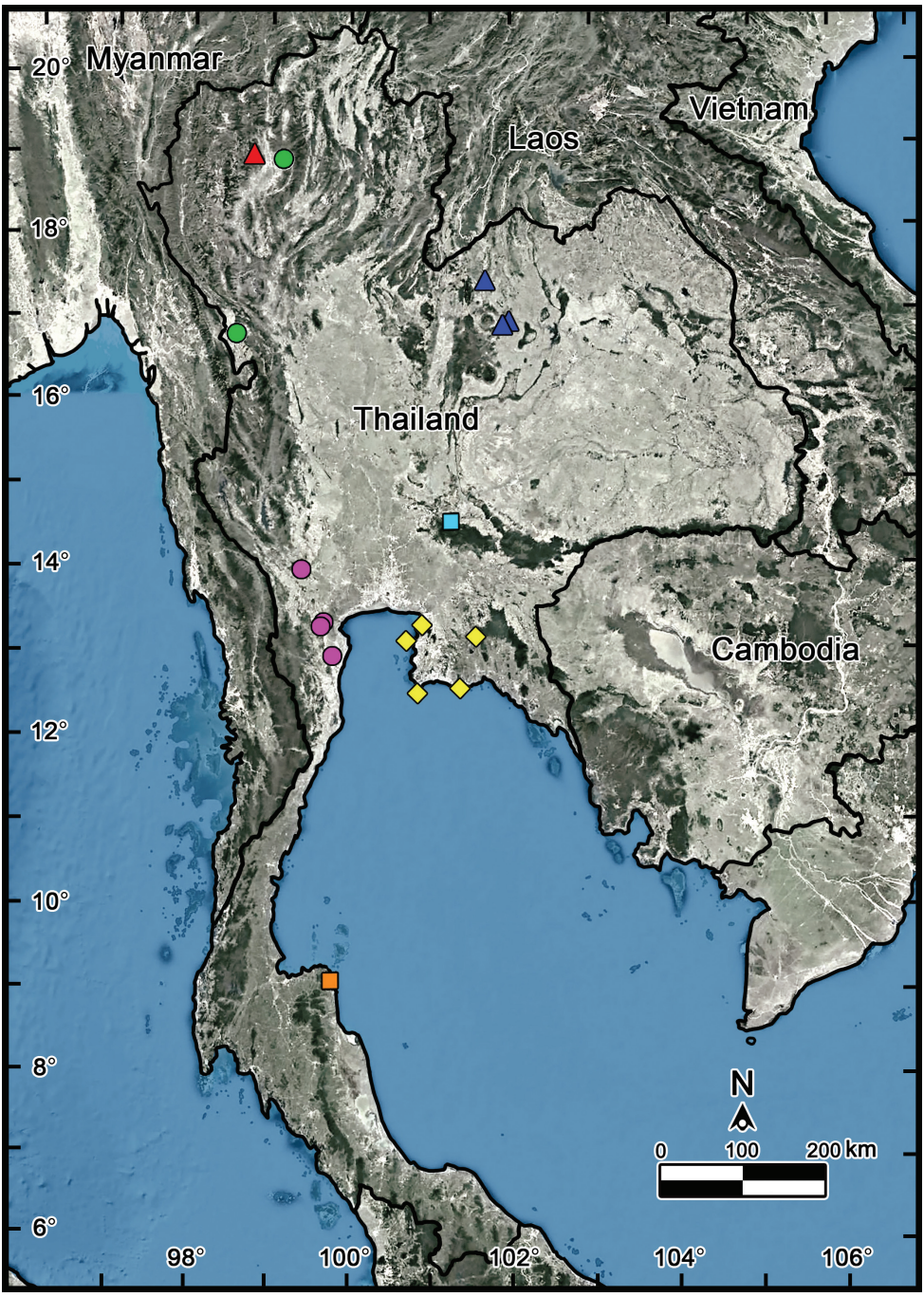

Figure 16. Known distribution of *Zephronia* spp. in Thailand. Red triangle = *Zephronia lannaensis*; green circle = *Zephronia phrain*; blue triangle = *Zephronia enghoffi* sp. nov.; sky blue square = *Zephronia golovatchi* sp. nov.; purple circle = *Zephronia panhai* sp. nov.; yellow diamond = *Zephronia siamensis* Hirst, 1907; orange square = *Zephronia viridisoma*.

Remarks. At the field collecting site, grey living specimens blended in perfectly with the brownish grey rock or leaf litter, making it difficult to find the animals. All specimens were infested by tiny, engorged, white, phoretic deutonymphs of an unidentified mite. The mite can often be found especially on the ventral part of the body such as antennal sockets and coxae, and could easily be discerned. The distribution of *Z. viridescens* from Dawei, Myanmar (Tavoy, Lower Burma – Moti Ram), is quite close to where the new species is distributed. However, *Z. panhai* sp. nov. differs from it by having a shorter body length ca. 21 mm (vs. longer, ca. 32 mm) and telopoditomeres 3 and 4 of anterior telopod distinctly separated (vs. indistinctly separated).

Unconfirmed species recorded for Thailand

Zephronia cf. *viridescens* Attems, 1936

Zephronia viridescens Attems, 1936: 180; Jeekel 2001: 22.
Zephronia cf. *viridescens* – Wongthamwanich et al. 2012b: 913; Sukteeka and Thanee 2015: 18.

Distribution and habitats. Originally, this species was reported from Tavoy, Lower Burma (Moti Ram) by Attems (1936) (= Dawei, Tenasserim).

Remarks. Although ecological studies by Wongthamwanich et al. (2012b), and Sukteeka and Thanee (2015) have reported '*Zephronia* cf. *viridescens*' from northern and northeastern Thailand, these works do not provide clear and unique characters for the species, and the specimens are not available for re-examination. The original description by Attems (1936) clearly stated that one of the diagnostic characters of *Z. viridescens* is its greenish body color. These contrast with the '*viridescens*' material examined by Wongthamwanich et al. (2012b: fig. 4) and Sukteeka and Thanee (2015: fig. 2), which display a distinct brownish body color. Not only can the brown color be used to discriminate *Z. viridescens* from Thai '*viridescens*' material, but the distribution is remarkably different. *Z. viridescens* was originally described from Dawei in Myanmar while '*viridescens*' specimens have been recorded to inhabit the northern and northeastern regions of Thailand. It seems likely that the '*viridescens*' specimens belong to another species and are distinct from all other known species. Therefore, further systematics study based on fresh specimens from northern and northeastern Thailand is necessary in order to confirm the existence of *Z. viridescens* in Thailand. At this moment, we thus exclude this nominal species from the Thai millipedes.

Key to the confirmed species of *Zephronia* in Thailand

1 Entire body grey (Fig. 2E, F). Setae on tergites very long, extending over the posterior margin (Figs 13G, 14D) ..... ***Z. panhai* sp. nov.**
– Body brown or green or partly green (not grey) (Figs 1, 2A–D). Setae on tergites short, not extending over the posterior margin (Fig. 13A, C, E) **2**

2 Second coxa in male with conspicuous membranous lobe (Figs 7D, 9D) ...**3**
– Second coxa in male without membranous lobe, inconspicuous (Figs 3D, 5D)....**4**
3 Female vulval operculum regularly rounded, narrow in posterior view (Fig. 7E). Subanal plate subsemicircular, central margin (tip) shallowly concave (Fig. 7F) ..... ***Z. enghoffi* sp. nov.**
– Female vulval operculum regularly rounded, margin straight and wide (Fig. 9E). Subanal plate trapeziform, with a conspicuous mesal constriction, central margin (tip) strongly concave (Fig. 9F).....***Z. golovatchi* sp. nov.**
4 Process of telopoditomere 2 of anterior telopod long, almost equal in length to the combination of telopoditomeres 3 and 4 (Fig. 6D). Inner section of endoterga with numerous setiferous setae..... .....***Z. phrain* Likhitrakarn & Golovatch, 2021**
– Process of telopoditomere 2 of anterior telopod short, subequal in length to telopoditomere 3 (Fig. 4B, C). Inner section of endoterga with a few setiferous setae or without setae (Fig. 13A).....**5**
5 Surface of tergites glabrous. Endoterga: tip of the longest bristles extended beyond posterior margin or extending over posterior margin. Female vulva with a large and pointed operculum, conspicuously protruded ....***Z. viridisoma* Rosenmejer & Wesener, 2021**
– Surface of tergites with setae or hairy (Fig. 1C). Endoterga: tip of the longest bristles not extended beyond posterior margin or not extending over posterior margin (Figs 13A, 14A). Operculum of female vulva not pointed, regularly rounded (Fig. 3E) **6**
6 Body green or partly green (Fig. 1A–D). Tergites with two brown patches locating at almost middle part of anterior half (Fig. 1A, B). Endoterga: posterior margin not flat, 'rectangle-wavy' margin (Fig. 14A); middle section with a single row cuticular impressions, conspicuous (Fig. 13B) ....***Z. siamensis* Hirst, 1907**
– Entire body brown. Tergites without color patch on middle part of anterior half, all brown. Endoterga: posterior margin flat; middle section without a row cuticular impressions, inconspicuous..... .....***Z. lannaensis* Likhitrakarn & Golovatch, 2021**

Discussion

The exploration of the millipede fauna in Thailand has uncovered a hitherto unknown diversity among the genus *Zephronia*. With the three new species described herein, the Thai giant pill-millipede genus *Zephronia* currently contains seven species that promote the number in the genus to 47 species in total. Considering the recorded species of *Zephronia* in Thailand, all can be found in small distribution area, although two of them (*Z. panhai* sp. nov. and *Z. siamensis*) have been shown to have somewhat

wider ranges. However, they still occupy less than approximately 300 km^2 along the mountain ranges in the North and also gulf of Thailand in the East (Fig. 16). This pattern is also marked in *Sphaerobelum* species (*S. aesculus* Rosenmejer & Wesener, 2021 (Rosenmejer et al. 2021)) by its occurrence at 160 km east of the type locality.

The species boundaries of *Zephronia* have been mostly based on several morphological features (Wongthamwanich et al. 2012a; Semenyuk et al. 2018; Wesener 2019). The most distinctive characteristics of the three species compared to the congeners can be seen especially in endoterga, anterior telopod and posterior telopod. The use of combinations of characters as being utilities for species discrimination in this study is congruent with previous taxonomic works (Golovatch et al. 2012; Wesener 2016, 2019; Semenyuk et al. 2018, 2020; Likhitrakarn et al. 2021). Furthermore, based on the observations in the field, the live specimens of some species can be easily distinguished from other congeners by their bright body color as presented in *Z. panhai* sp. nov. (Fig. 2E, F), *Z. phrain* (Fig. 1E, F) as well as in *Z. siamensis* (Fig. 1A–D). Based on the combination of several morphological traits plus the live body color, we can confirm that the species boundaries are within *Zephronia.*

As the two recognized groups of *Zephronia* have been proposed based on the location of Tömösváry's organ (Wesener 2019; Semenyuk et al. 2020; Likhitrakarn et al. 2021), the three new species exhibit all of the unique characters that are in agreement with its placement in *Zephronia* s. s. The group previously harbored nine species, viz., *Z. dawydoffi* Attems, 1953, *Z. konkakinhensis* Semenyuk et al., 2020, *Z. lannaensis* Likhitrakarn & Golovatch, 2021, *Z. montis* Semenyuk et al., 2020, *Z. ovalis* Gray, 1832, *Z. phrain* Likhitrakarn & Golovatch, 2021, *Z. siamensis* Hirst, 1907, *Z. viridescens* Attems, 1936, and *Z. viridisoma* Rosenmejer & Wesener, 2021. Unfortunately, the lack of genetic data prevents a conclusive phylogenetic comparison to other closely related species of the genus at this point. It will be necessary to continue with studies on this group, collecting new material as well as re-examining previously collected material in combination with molecular works. In this way, the systematics within the genus or closely related genera may be elucidated and improved.

The preceding records of the genus, without regarding the three newly described species, were recorded only from northern and eastern parts of Thailand. The central and southern areas of Thailand, which are the intermediate zone between the Malay Peninsula and the upper region of mainland Southeast Asia, had no records of the genus so far. Our finding of these three species fills the gaps in the distribution and confirms the genus *Zephronia* across Thailand. Further collecting in unexplored areas in several parts of mainland Southeast Asia, especially Cambodia, Laos, and Thailand, will probably reveal many new, remarkable species.

Acknowledgements

The authors would like to thank the National Park Departments, the Plant Genetic Conservation Project under the Initiative of Her Royal Highness Maha Chakri Sirindhorn and Center of Excellence on Biodiversity for the permission and enable us for

the field trips in several restricted/remote areas. This research project was financially supported by the young researcher development project of Khon Kaen University and the Academic Affairs Promotion Fund, Faculty of Science, Khon Kean University, Fiscal year 2021 (RAAPF) for RS, and also partially supported by the TRF Strategic Basic Research BDG 6080011 (2017–2019) to CS and NL. We also thank the members of the Animal Systematics Research Unit for kind help in the field collecting. Special thanks go to Ting Hui Ng (ZRC) for English revision. The very useful comments that beneficially improved the manuscript from the referees are gratefully acknowledged.

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ZooKeys 1067: 57–82 (2021)
doi: 10.3897/zookeys.1067.72779
https://zookeys.pensoft.net

RESEARCH ARTICLE

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Behningiidae and Potamanthidae (Insecta, Ephemeroptera) in Thailand

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Academic editor: L. Pereira-da-Conceicoa | Received 9 August 2021 | Accepted 29 September 2021 | Published 29 October 2021

http://zoobank.org/8DB9C8FE-9DF7-438D-92BA-4B40E81F5DE1

Citation: Kwanboon S, Sartori M, Boonsoong B (2021) Behningiidae and Potamanthidae (Insecta, Ephemeroptera) in Thailand. ZooKeys 1067: 57–82. https://doi.org/10.3897/zookeys.1067.72779

Abstract

The aim of this study is to review the family Behningiidae and Potamanthidae in Thailand. Two genera and three species of Behningiidae are recognised: *Protobehningia merga* Peters & Gillies, 1991, *Behningia baei* McCafferty & Jacobus, 2006, and *Behningia nujiangensis* Zhou & Bisset, 2019, which is newly reported from Thailand. The egg structure of *B. nujiangensis* is described for the first time using scanning electron microscopy. The larva of *P. merga* is redescribed and its distribution is expended northward with a new record from Chiang Mai province. Two genera and five species of Potamanthidae are identified: *Potamanthus formosus* Eaton, 1892, *Rhoenanthus magnificus* Ulmer, 1920 (new record for Thailand), *Rhoenanthus obscurus* Navás, 1922, *Rhoenanthus distafurcus* Bae & McCafferty, 1991, and *Rhoenanthus speciosus* Eaton, 1881. Our morphological evidence is supported by COI data for the family Potamanthidae. Diagnostic characters, distributions, and keys are presented for the larvae of all known species of Thai behningiid and potamanthid mayflies.

Keywords

Biodiversity, COI, egg, mayfly, new record

Introduction

The Behningiidae is a small mayfly family represented by three extant genera (*Behningia* Lestage, 1930, *Dolania* Edmunds & Traver, 1959, and *Protobehningia* Tshernova, 1960) and one fossil genus (*Archaeobehningia* Tshernova, 1977) (Hubbard 1994). Members of the Behningiidae are known as tuskless burrowing mayflies for their sand-dwelling behaviour (Miller et al. 2018). To date, seven species have been described, and three of them have been documented in the Oriental region (two species from Thailand and one species from China) (Zhou et al. 2019). *Behningia baei* McCafferty & Jacobus, 2006 and *Protobehningia merga* Peters & Gillies, 1991 have been described from Thailand and to date have only been reported from the type localities (Peters and Gillies 1991; Parnrong et al. 2002; McCafferty and Jacobus 2006). Only larval exuviae of *P. merga* are known (Peters and Gillies 1991).

The family Potamanthidae is widely distributed throughout the Holarctic and Oriental regions and accounts for 25 species worldwide. In Southeast Asia, seven species in two genera and four subgenera have been reported (Nguyen and Bae 2004). Bae and McCafferty (1991) recognised subgenera within *Potamanthus* and *Rhoenanthus*, and we followed this classification in the present study. The known species in Thailand are *Potamanthus* (*Potamanthodes*) *formosus* Eaton, 1982, *Rhoenanthus* (*Rhoenanthus*) *distafurcus* Bae & McCafferty, 1991, *Rhoenanthus* (*Rhoenanthus*) *speciosus* Eaton, 1881, and *Rhoenanthus* (*Potamanthindus*) *obscurus* Navás, 1922 (Bae and McCafferty 1991; Parnrong et al. 2002).

In this study, we review the species of Behningiidae and Potamanthidae in Thailand, and we provide the first records of *B. nujiangensis* Zhou & Bisset, 2019 and *R. magnificus* Ulmer, 1920. We also redescribe the larva of *P. merga*, and we present the first description of the egg structure of *B. nujiangensis*. A distribution map of Thai behningiid and potamanthid mayflies is also provided.

Materials and methods

The specimens were collected from streams and rivers in Thailand and were preserved in absolute ethanol. Measurements (in mm) and photographs were taken using a Nikon SMZ800 and ZEISS Stemi 305 stereoscopic microscope. For scanning electron microscopy (SEM), specimens (head, legs, labrum, labium, labial palp, glossa, paraglossa, and eggs) were dried in a critical point dryer (CPD7501) and coated with gold (Sputter Coater SC7620). The specimens were observed and photographed with an FEI Quanta 450 SEM. The final plates were prepared with Adobe Photoshop CC 2020. The material is deposited in the collection of the Zoological Museum at Kasetsart University in Bangkok, Thailand (**ZMKU**). The distribution map was constructed using the Simple Mapper website (http://www.simplemappr.net) and GPS coordinates.

Molecular methods

Each specimen was dissected for DNA extraction using a genomic DNA purification kit (NucleoSpin, Macherey-Nagel, Germany) following the manufacturer's protocol. A fragment of the mitochondrial cytochrome oxidase I (COI) was amplified using the primers LCO1490 and HCO2198 (Folmer et al. 1994). The polymerase chain reaction (PCR) conditions and procedure were as described by Gattolliat et al. (2015). The PCR products were purified using a Gel and PCR Clean-up Kit (NucleoSpin, Macherey-Nagel, Germany) and were sequenced by ATGC Co., Ltd (Thailand). The Kimura-2-parameter distances were calculated using the MEGA X program (Kumar et al. 2018). A phylogenetic tree was analysed by the maximum likelihood (ML) method and the Tamura 3-parameter protocol was performed with MEGA X using the likelihood-ratchet method with 1,000 bootstrap replicates. Nucleotide sequences obtained in this study have been deposited in the GenBank database (Table 1). Other analysed mayfly sequences, obtained from the Barcode of Life Data System (BOLD), were *Dolania americana* (**BIT011-04**), *Potamanthus formosus* (**THMAY125-12**), and *Rhoenanthus* cf. *magnificus* (**THMAY127-12, THMAY128-12**).

Taxonomy

Order Ephemeroptera Hyatt & Arms, 1891
Family Behningiidae Motas & Bacesco, 1937
Genus *Behningia* Lestage, 1930

***Behningia baei* McCafferty & Jacobus, 2006**
Figures 7, 9

Materials examined. None.

Diagnosis. The larvae of *Behningia baei* McCafferty & Jacobus, 2006 can be distinguished from other *Behningia* species based on the following characteristics: i) labrum deeply emarginate in a V or U shape at anteromedian margin, ii) labial palp I without concavity on outer margin, iii) labial palp II less than 50% length of labial palp III, iv) tarsus of foreleg as long as tibia and v) coxa of hind leg less than 60% as long as femur.

Distribution. Phitsanulok province**.**

Remark. The larvae of *B. baei* were originally described by McCafferty and Jacobus (2006) and collected from Phitsanulok province (Thailand). In this study, we attempted to collect specimens at the type locality (Klong Nam Kub, Ban Khok Phakwan), but no specimens were found during our fieldwork. However, the habitat of the type locality of *B. baei* is suitable for behningiid larvae, consisting of wadeable, widely flooded rivers with fine sandy bottoms and braided channels (Fig. 7).

Table 1. List of the sequenced specimens.

Species	Code	Collection locality	Collector	Date	GenBank accession number
Protobehningia merga	PM01CM	Chiang Mai	B. Boonsoong	13 Nov 2020	MW792224
Potamanthus formosus	PF01NA	Nan	B. Boonsoong	28 Nov 2020	MZ453438
	PF02KN	Kanchanaburi	S. Kwanboon	11 Jul 2019	MZ453439
	PF03CR	Chiang Rai	S. Kwanboon	6 Mar 2021	MZ436659
	PF04CR	Chiang Rai	S. Kwanboon	5 Mar 2021	MZ436660
Rhoenanthus magnificus	RM01NA	Nan	S. Kwanboon	10 Mar 2018	MZ436661
	RM04NA	Nan	B. Boonsoong	28 Nov 2020	MZ436662
	RM05CR	Chiang Rai	S. Kwanboon	6 Mar 2021	MZ436663
	RM06CR	Chiang Rai	S. Kwanboon	7 Mar 2021	MZ436664
R. obscurus	RO02FCM	Chiang Mai	S. Kwanboon	15 Nov 2020	MZ436665
	ROO7CM	Chiang Mai	S. Kwanboon	15 Nov 2020	MZ436666
R. distafurcus	RD01NA	Nan	B. Boonsoong	28 Nov 2020	MZ436667
	RD02NA	Nan	B. Boonsoong	28 Nov 2020	MZ436668
	RD03KN	Kanchanaburi	B. Boonsoong	15 Oct 2015	MZ436669
	RD04RB	Ratchaburi	B. Boonsoong	19 Apr 2016	MZ436670

Behningia nujiangensis Zhou & Bisset, 2019

Figures 1A, 2–4, 9

Materials examined. 2 mature larvae, Thailand, Chiang Mai province, Mae Tang district, Tard Luang Waterfall, 19°01'27.5"N, 98°51'17.1"E, 18.IX.2011, P. Sritipsak leg. deposited in ZMKU.

Diagnosis. The larvae of *Behningia nujiangensis* Zhou & Bisset, 2019 can be separated from those of other *Behningia* species based on the following characteristics: i) labrum shallowly emarginate at anteromedian margin (Fig. 2A), ii) molar areas of mandible with a small apical spine (Fig. 2B), iii) galea-lacinia of maxilla elongated and slender (Fig. 2C), iv) labial palp 3-segmented, segment II as long as segment III (Fig. 2D), v) tarsus of forelegs about 40% the length of tibia (Fig. 3A, B), vi) middle and hind legs with coxa as long as femur (Fig. 3C, D).

Egg (dissected from mature larva). Length 1.62–1.73 mm, width 1.09–1.26 mm (n = 13); oval (Fig. 4A); with massive amounts of fibrous adhesive material localised at the polar and equatorial regions of the egg (Fig. 4B); chorion densely and finely punctutated, with a weakly developed pentagonal reticulation, circular in shape and convex in the middle (Fig. 4C); funnelform micropyle in the centre of circular accumulations of adhesive material only at the equatorial zone (Fig. 4D).

Distribution. Chiang Mai province**.**

Remark. The larvae of *B. nujiangensis* were originally described by Zhou et al. (2019) and collected from China (Nujiang river, Yunnan province, upper Salween river). In Thailand, the samples were collected from the Tard Luang waterfall (fine sandy habitat) in 2011, and specimens were deposited but only identified to the genus level (Dr. Akekawat Vitheepradit, Department of Entomology, Kasetsart University). In this study, we re-examined and identified the specimens. We attempted to collect specimens from the same microhabitat near the Tard Luang waterfall; however, unfortunately, no specimens were found.

Figure 1. Habitus of larvae **A** *Behningia nujiangensis* Zhou & Bisset, 2019 **B** *Protobehningia merga* Peters & Gillies, 1991.

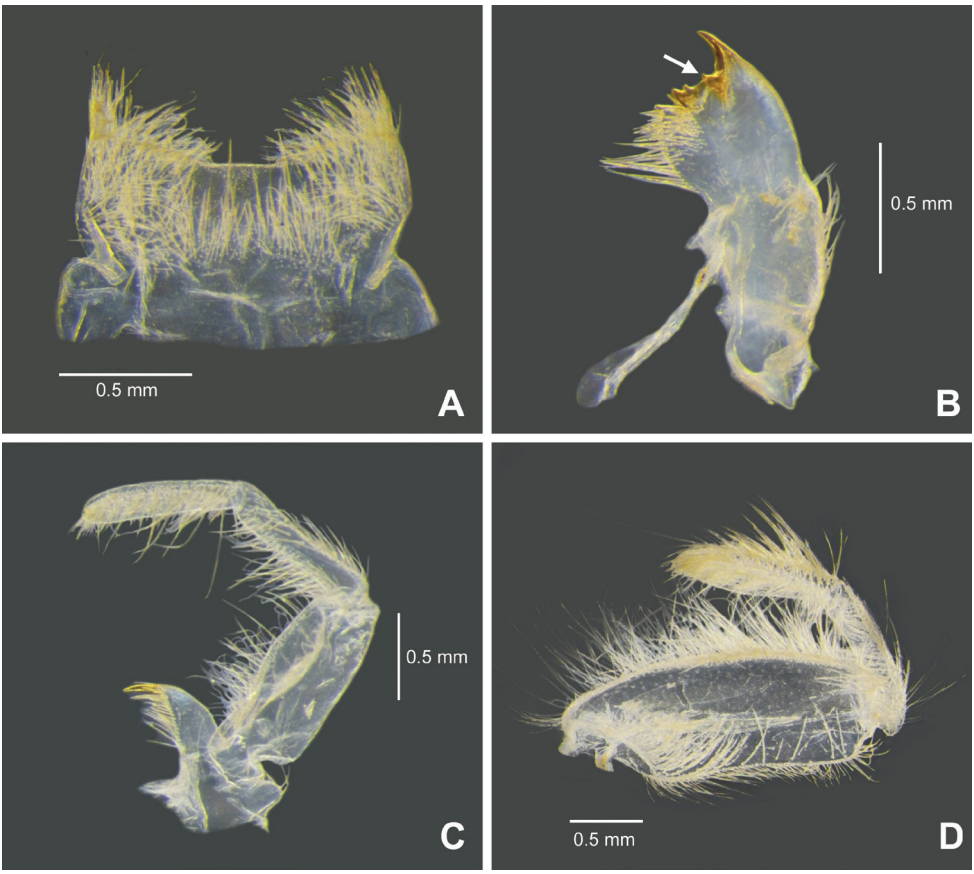

Figure 2. *Behningia nujiangensis* Zhou & Bisset, 2019, larval morphology **A** labrum **B** left mandible (ventral view, arrow indicated small spine) **C** left maxilla (ventral view) **D** left labial palp (ventral view).

Genus *Protobehningia* Tshernova & Bajkova, 1960

Protobehningia merga Peters & Gillies, 1991

Figures 1B, 5, 6, 8, 9

Materials examined. 2 larvae, deposited in ZMKU, Thailand, Chiang Mai province, Mae Chaem district, Mae Chaem river, 18°30'46.0"N 98°21'22.6"E, 475 m, 5.X.2019, B. Boonsoong leg., 1 larva, same data, 13.XI.2020, B. Boonsoong leg. (ZMKU).

Re-description of larva. Larva (in alcohol, Fig. 1B) Body length 7.2 mm without cerci; cerci 2.7 mm. Body pale yellowish.

Head. Anterior margin not projecting, front with densely short goldish setae standing out on the head (Fig. 1B, 5A). Black eyes on dorsolateral margin; ocelli almost white, inner margin of ocelli black in front of compound eye. Antennae at lateral margin of head. Labium extending the entire anterior margin of head, with long setae; labial palp 3-segmented, surface of labial palp covered with rows of long

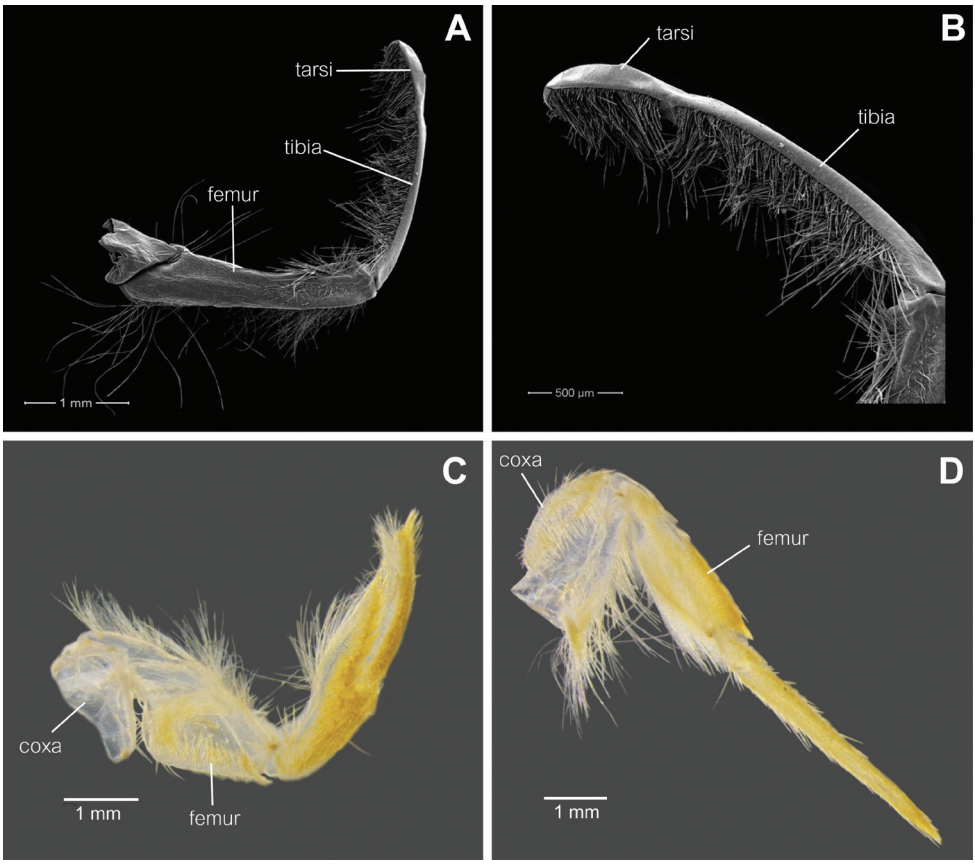

Figure 3. *Behningia nujiangensis* Zhou & Bisset, 2019, larval morphology **A** foreleg **B** closer view of tibia and tarsi of foreleg **C** middle leg **D** hind leg.

blunt setae, base of second palp segment with the longest setae, first segment longer than other segments (Fig. 5B), glossae and paraglossae with numerous (>20) setae (Fig. 5C). Left mandible and right mandible strong and dentated, mostly similar to *P. asiatica*. Maxillary palpi 3-segmented, maxilla base extending, apex narrow with terminal tooth.

Thorax. Colour pale yellowish. Forelegs flattened, with large broad coxae, flat femur, small claws (Fig. 6A), tarsi fused with tibiae (Fig. 6B), outer margin with long row of setae, short setae present at inner margin. Midleg and hindleg tarsus and tibia not fused (Fig. 6C, D), hindleg with strong claw, curved, thorn-like in shape.

Abdomen. Similar in colour to head and thorax, abdominal segments elongated and convex, with short straight setae at lateral margin, lateral margin of abdominal segment I–IX with flat projections spine-like in shape. Gill present on segment I–VII, plumose shape, first gill filament single (Fig. 5D); gills II–VII double, upper branch of each gill shorter than lower one. Three caudal filaments fringed with short pale setae, length of median filament as long as lateral filaments.

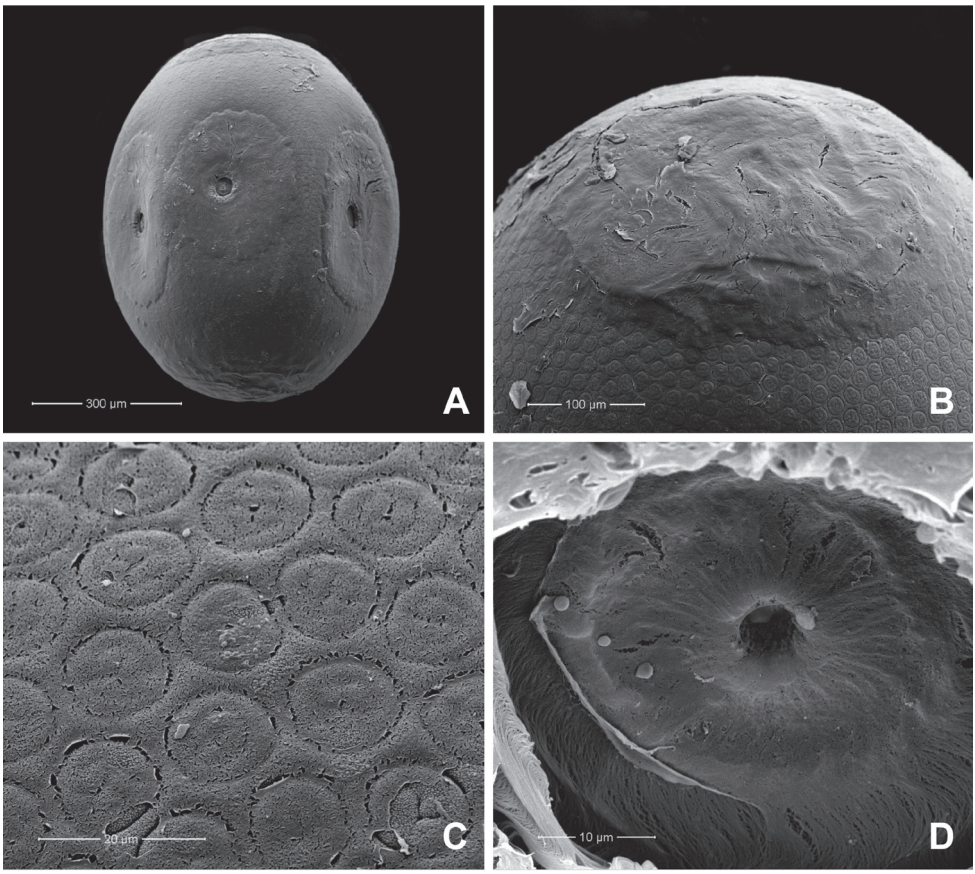

Figure 4. *Behningia nujiangensis* Zhou & Bisset, 2019, SEMs of egg structures **A** general outline of egg **B** polar cap **C** chorion surface **D** micropyle.

Diagnosis. The larvae of *Protobehningia merga* Peters & Gillies 1991 can be distinguished from those of *P. asiatica* based on the following characteristics: i) glossae and paraglossae with more than 20 setae on the ventral surface, ii) maxillary palp segment II 2/3 the length of segment I, each maxillary palp segment completely divided, but segments II and III indistinct (Peters and Gillies 1991).

Distribution. Kanchanaburi and Chiang Mai provinces.

Biological aspects. In general, the larvae of behningiid mayflies are rarely collected. In this study, the larvae (middle instar) were found in October (turbidity from flooding, Fig. 8A) and November in a river in Chaing Mai province, whereas Peters and Gillies (1991) found the exuviae and imago during December in Kanchanaburi province (western Thailand). The specimens were collected from the Mae Chaem river, which is submontane and bordered by farmland and residential areas (Fig. 8A). The

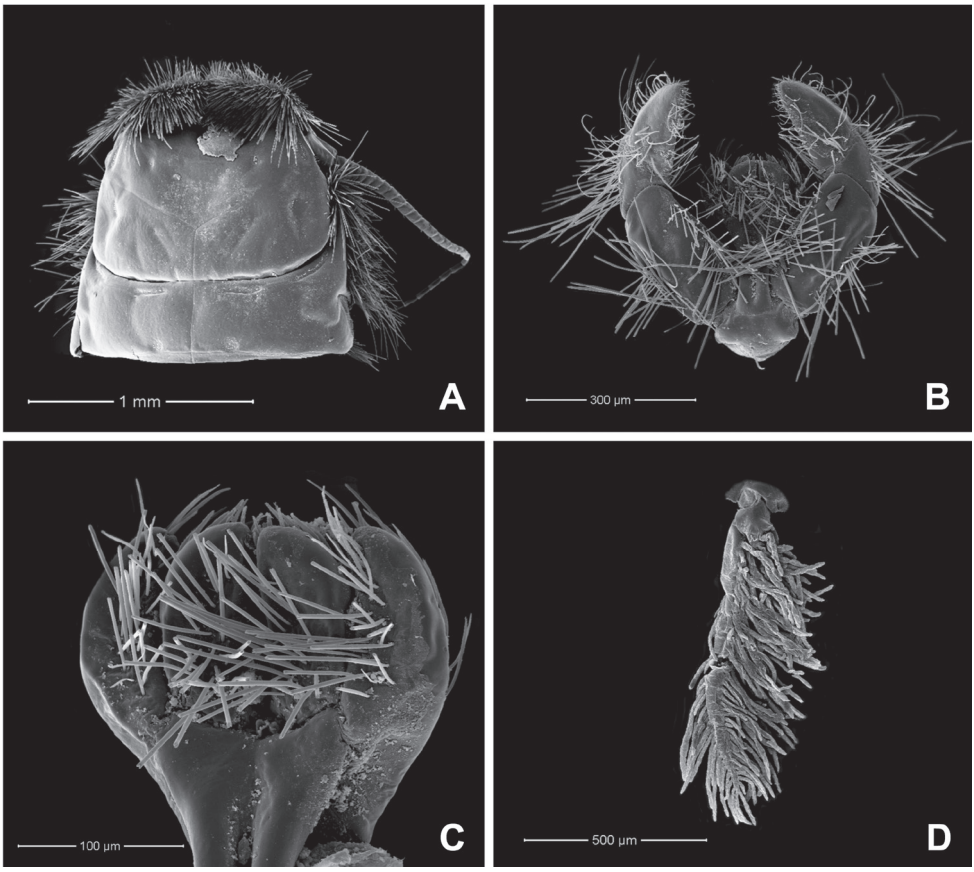

Figure 5. *Protobehningia merga* Peters & Gillies, 1991, larval morphology **A** overview of head **B** labium (ventral view) **C** glossa & paraglossae (ventral view) **D** gill I.

substrates were covered with fine- and coarse-grained sand (Fig. 8C). The larvae of *P. merga* were collected using an aquatic net in a fine sandy habitat, where the depth of the sandy bottom was more than 50 cm and near the littoral zone (Fig. 8B, D). The larvae were usually found together with those of the oligoneuriid mayfly, *Chromarcys magnifica* Navás, 1932 and the gomphid dragonfly, *Paragomphus capricornis* Förster, 1914.

Remarks. Only two species of *Protobehningia* are known in the world: *Protobehningia asiatica* Tshernova & Bajkova 1960 and *Protobehningia merga* Peters & Gillies 1991. Peters and Gillies (1991) used larval exuviae of *P. merga* for comparison with *P. asiatica*, but they did not give a more detailed description of the larval stage. The labium structures of our specimens are similar to those of the larval exuviae described by Peters and Gillies (1991). Our new record also expands the geographic distribution of *P. merga* to northern Thailand.

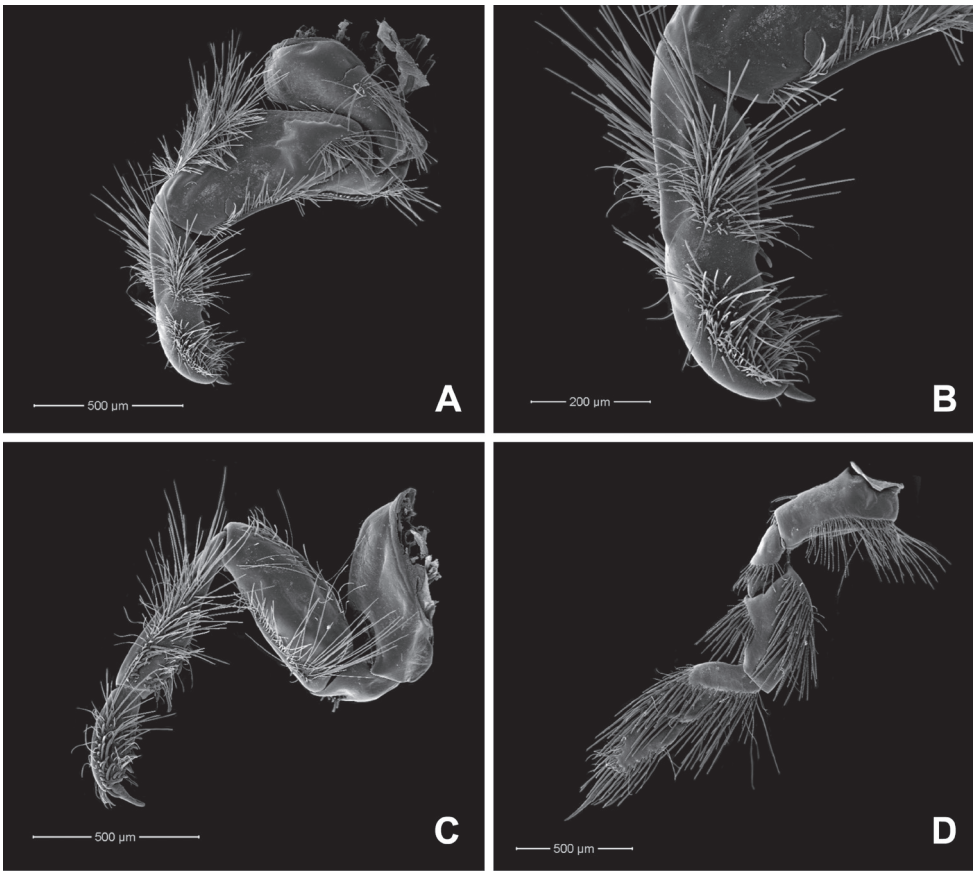

Figure 6. *Protobehningia merga* Peters & Gillies, 1991, larval morphology **A** foreleg **B** closer view of tibia and tarsi of foreleg **C** middle leg **D** hind leg.

Key to genera and species of Behningiidae in Thailand

(adapted from Zhou et al. 2019)

1 Tarsi of forelegs not fused to tibiae (Fig. 3A); tibiae of hind legs reduced (Fig. 3D).....***Behningia*, 2**

– Tarsi of forelegs fused to tibiae (Fig. 6B); tibiae of hind legs not reduced (Fig. 6D); glossae and paraglossae with more than 20 long stout setae on the ventral surface (Fig. 5C).....***Protobehningia, P. merga***

2 Medio-anterior emargination of labrum deep (McCafferty and Jacobus 2006, fig. 1); coxa of hind leg less than 60% as long as femur (McCafferty and Jacobus 2006, fig. 7).....***Behningia baei***

– Medio-anterior emargination of labrum very shallow (Fig. 2A); coxa of hind leg as long as femur (Fig. 6D) .....***Behningia nujiangensis***

Figure 7. Habitats of *Behningia baei* McCafferty & Jacobus, 2006 larva **A** Klong Nam Kub stream (March 2021) **B** microhabitat.

Figure 8. Habitats of *Protobehningia merga* Peters & Gillies, 1991 larva **A** Mae Chaem wadeable river (October 2019) **B** sampling method **C** sandy bottom river (November 2020) **D** microhabitat.

Family Potamanthidae Klapalek,1909
Genus *Potamanthus* Pictet, 1843
Subgenus *Potamanthodes* Ulmer, 1920

***Potamanthus* (*Potamanthodes*) *formosus* Eaton, 1892**
Figures 10A, 11A, 14, 15

Materials examined. 1 larva, Thailand, Chanthaburi province, Makham district, Ban Pa Rim Tarn homestay, 12°51'00.0"N, 102°12'17.1"E, 5.X.2019, B. Boonsoong leg. (ZMKU); 2 larvae, Kanchanaburi province, Huai Pak Kok, 14°39'34.4"N, 98°32'02.3"E, 175 m, 11.VII.2019, S. Kwanboon leg. (ZMKU); 2 larvae, Chiang Rai province, Huai Kang Pla waterfall, 20°05'21.6"N, 99°46'47.8"E, 519 m, 5.III.2021, S. Kwanboon leg. (ZMKU); 4 larvae, Chiang Rai province, Klong Mae Salong, 20°09'52.0"N, 99°40'06.8"E, 6.III.2021, S. Kwanboon leg. (ZMKU); 1 larva, Nan province, Ban Ratsadonsamakkhi, 18°52'23.4"N, 100°49'54.1"E, 59 m, 28.XI.2020, B. Boonsoong leg.

Diagnosis. The larvae of *Potamanthus formosus* Eaton, 1892 can be distinguished from those of other *Potamanthus* (*Potamanthodes*) species based on the following characteristics: i) dorsal forefemora with simple stout setae (Fig. 11A), ii) a subapical cluster

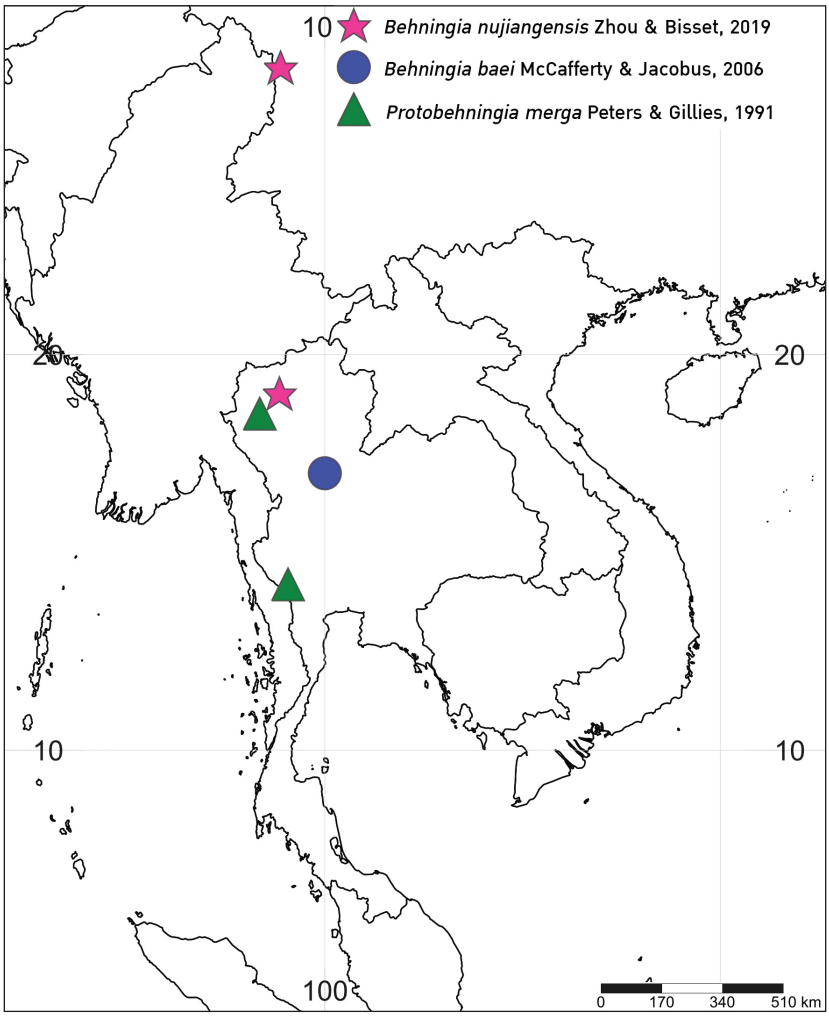

Figure 9. Distribution map of the family Behningiidae in Thailand.

of setae on the foretibia, iii) short mandibular tusk (0.10–0.23× length of the head) (Fig. 10A), and iv) relatively small body length.

Distribution. Chanthaburi, Kanchanaburi, Nan, and Chiang Rai provinces.

Remark. The adult of *P. formosus* was described by Eaton (1892) based on materials from Myanmar. Imanishi (1940) described the species *Potamanthus kamonis* based on imaginal and larval materials from Japan, and *P. kamonis* was synonymized with *P. formosus* by Uéno (1969). *Potamanthus formosus* is widely distributed in East Asia and Southeast Asia (China, Japan, South Korea, Malaysia, Vietnam, Myanmar, and Thailand). In the present study, the specimens were found in eastern, western, and northern Thailand, so *P. formosus* is the most widespread potamanthid in Thailand (Fig. 14).

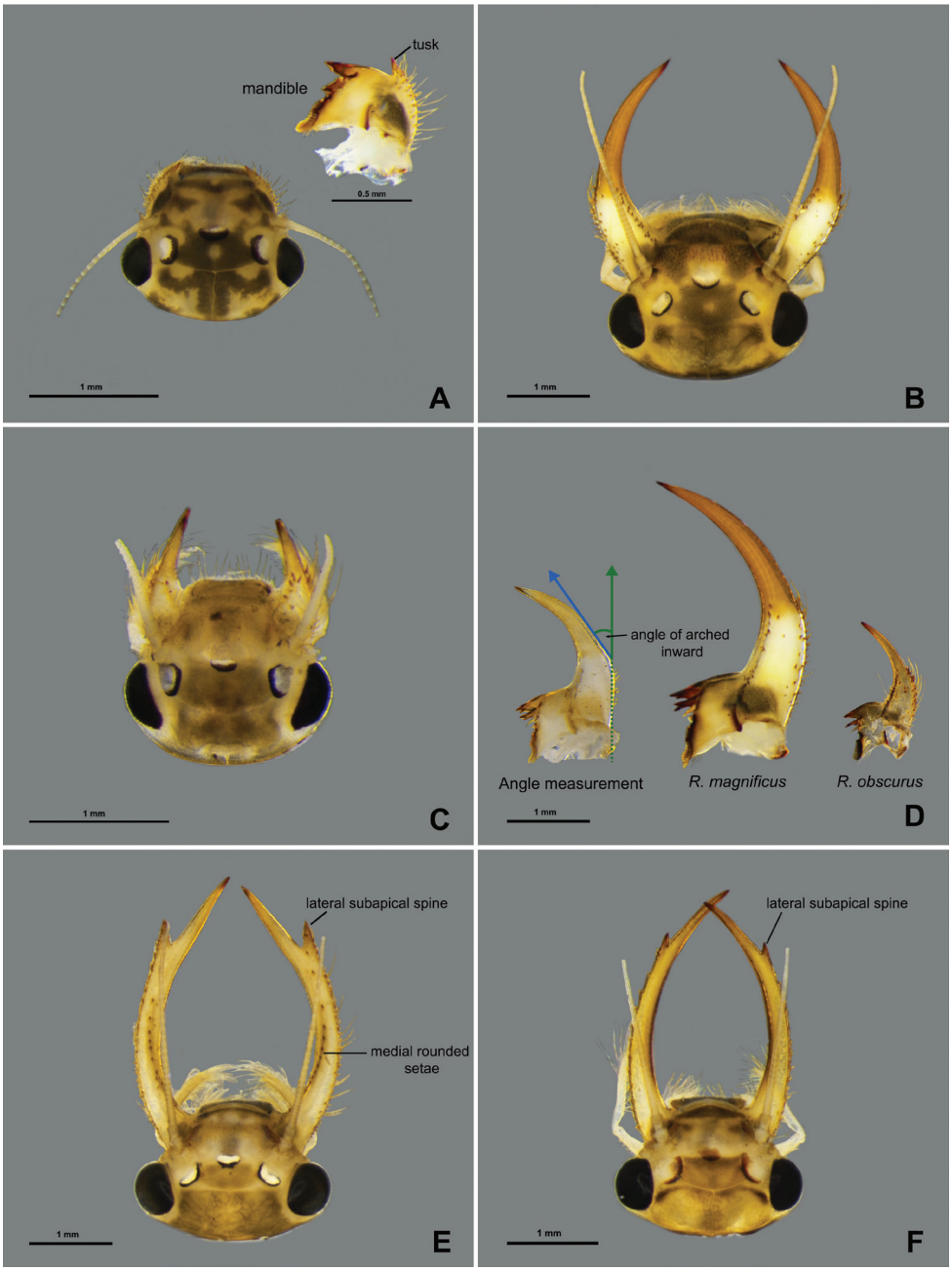

Figure 10. Larval morphology (head and mandibular tusk) **A** *Potamanthus formosus* Eaton, 1892 **B** *Rhoenanthus magnificus* Ulmer, 1920 **C** *R. obscurus* Navás, 1922 **D** angle measurement of mandibular tusk **E** *R. distafurcus* Bae & McCafferty, 1991 **F** *R. speciosus* Eaton, 1881.

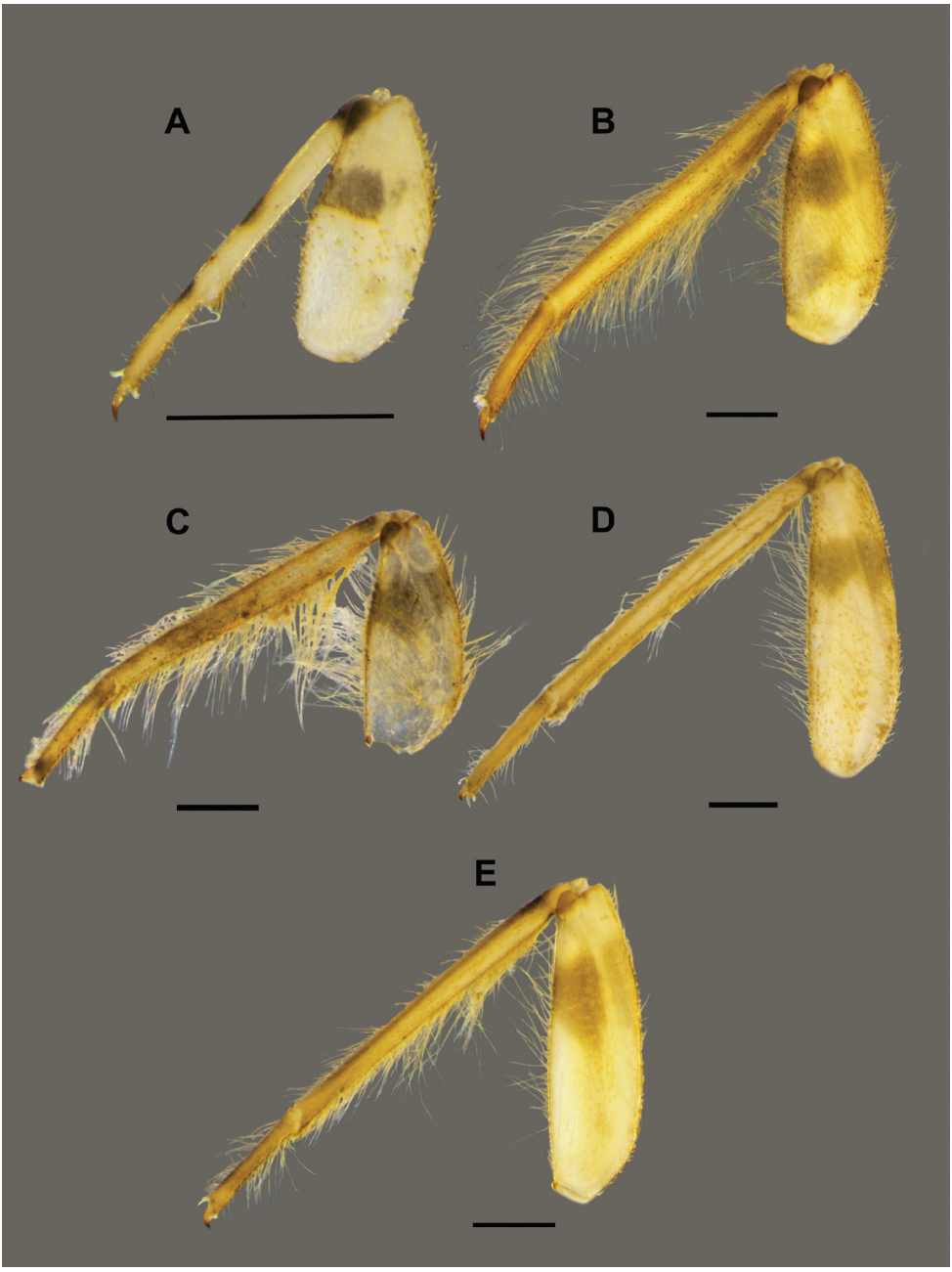

Figure 11. Larval morphology (foreleg) **A** *Potamanthus formosus* Eaton, 1892 **B** *Rhoenanthus magnificus* Ulmer, 1920 **C** *R. obscurus* Navás, 1922 **D** *R. distafurcus* Bae & McCafferty, 1991 **E** *R. speciosus* Eaton, 1881. Scale bar: 1 mm.

Figure 12. Habitus of larva of *Rhoenanthus magnificus* Ulmer, 1920.

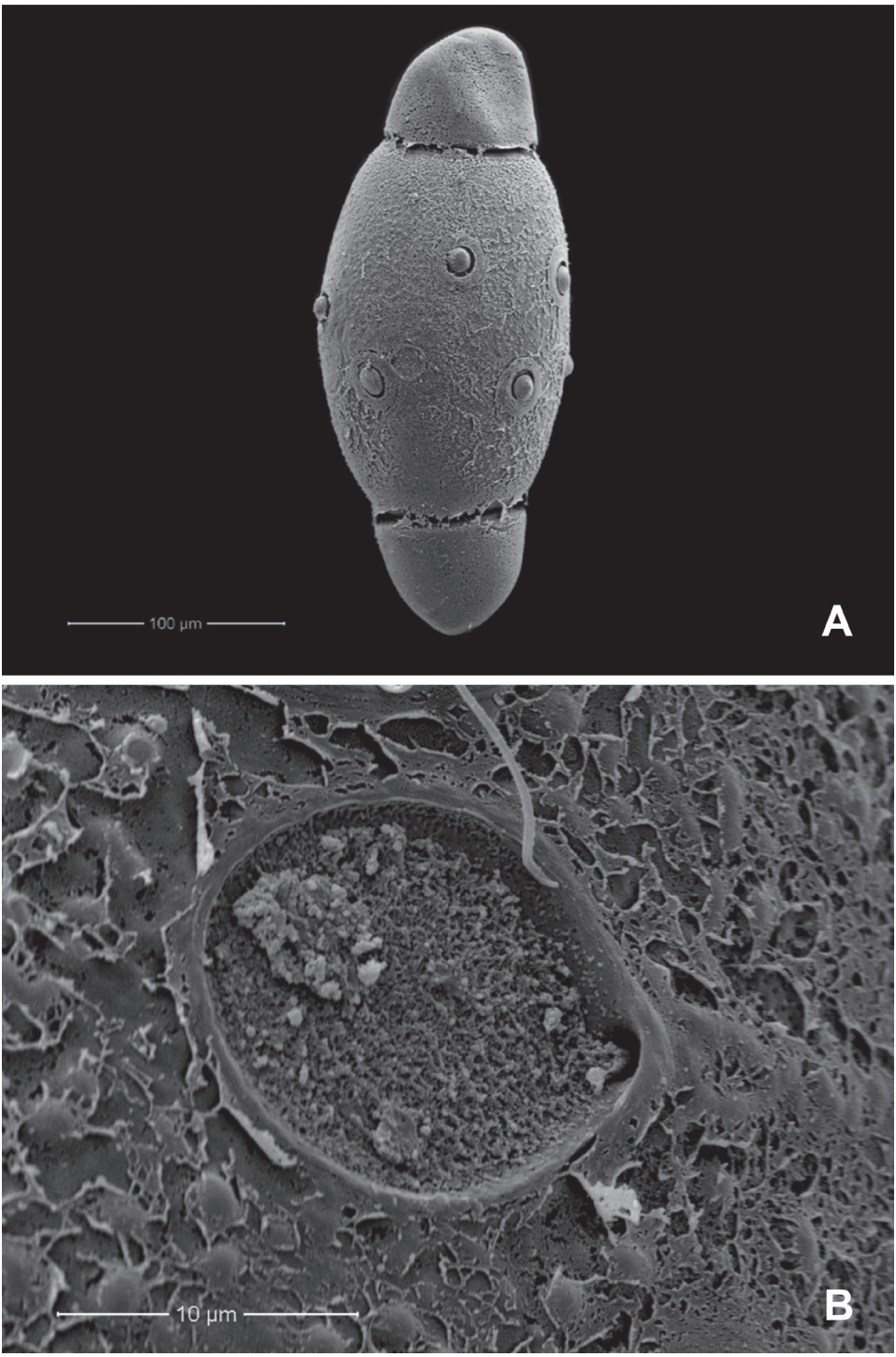

Figure 13. SEMs of egg structures of *Rhoenanthus speciosus* Eaton, 1881 **A** general outline of egg **B** micropyle.

Genus *Rhoenanthus* Eaton, 1881
Subgenus *Potamanthindus* Lestage, 1930

Rhoenanthus (*Potamanthindus*) *magnificus* Ulmer, 1920
Figures 10B, D, 11B, 12, 14, 15

Materials examined. 5 larvae, Thailand, Chiang Mai province, Chiang Dao, Mae Na, 19°19'13.08"N, 98°53'25.98"E, 742 m, 11.III.2016, B. Boonsoong leg. (ZMKU); 8 larvae, Loel province, Nam Thob ranger station, 17°15'36.5"N, 101°34'52.9"E, 338 m, 20.III.2016, B. Boonsoong leg. (ZMKU); 1 larva, Nan province, Bo Kluea district, Sapan waterfall, 19°11'25.8"N, 101°11'56.3"E, 800 m, 28.XI.2020, B. Boonsoong leg; 2 larvae, Nan province, Bo Kluea district, Lamer resort, 19°09'08.8"N, 101°09'17.0"E, 28.XI.2020, S. Kwanboon leg; 3 larvae, Nan province, Bo Kluea district, Mae Nam Wa stream, 19°16'22.6" N 101°10'48.2" E, 848 m, 26.XI.2019, B. Boonsoong leg; 7 larvae, Chiang Rai province, Mueang district, Mae Kon stream, 19°51'46.1"N, 99°39'04.7"E, 534 m, 6.III.2021, S. Kwanboon leg; 2 larvae, Chiang Rai province, Mueang district, Mae Kon stream, Pong Phrabat waterfall, 20°00'41.8"N, 99°48'15.1"E, 470 m, 7.III.2021, S. Kwanboon leg.

Diagnosis. The larvae of *Rhoenanthus magnificus* (Fig.12) can be distinguished from those of other *Rhoenanthus* (*Potamanthindus*) species based on the following characteristics: i) large body size (18–21 mm), ii) mandibular tusks arched inward about 33–34° (angle measurement as shown in Fig. 10D), iii) length of the mandibular tusks ca 1.4× length of head, and iv) length of the foretibiae ca 1.5× length of the forefemora and about 2.9× length of the foretarsi (Fig. 11B) (Nguyen and Bae 2004).

Distribution. Chiang Mai, Chiang Rai, Loei, and Nan provinces.

Remark. The larva of *R. magnificus* was originally described by Nguyen and Bae (2004) from material collected in northern and central Vietnam. The species is known from southern China and Vietnam. In the present study, we found this species in streams of several provinces (Fig. 14).

Rhoenanthus (*Potamanthindus*) *obscurus* Navás, 1922
Figures 10C, D, 11C, 14, 15

Materials examined. 1 female imago (reared) and 1 male imago (reared), Thailand, Chiang Mai province, Mae Ping river, Elely Cafe, 19°04'08.4"N, 98°56'28.8"E, 15.XI.2020, S. Kwanboon leg. (ZMKU)**.**

Diagnosis. The larvae of *Rhoenanthus obscurus* can be distinguished from those of other *Rhoenanthus* (*Potamanthindus*) species based on the following characteristics: i) medium-sized body (12–17 mm), ii) mandibular tusks arched inward about 28° (angle measurement as shown in Fig. 10D), iii) length of mandibular tusks ca 0.7–0.8× length of the head, and iv) length of foretibiae ca 1.32–1.49× length of the forefemora

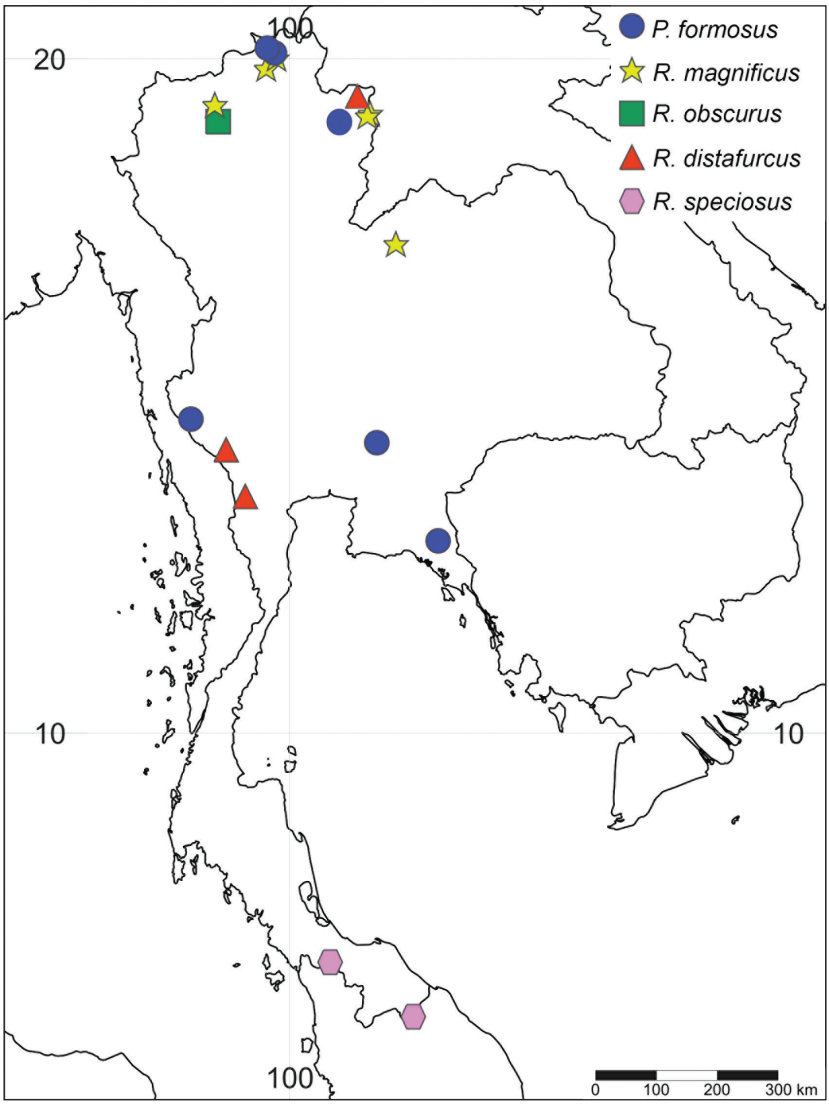

Figure 14. Distribution map of the family Potamanthidae in Thailand.

and about 2.55–3.02× length of the foretarsi (Fig. 11C) (Bae and McCafferty 1991; Nguyen and Bae 2006).

Distribution. Chiang Mai province.

Remark. The larva of *R. obscurus* was originally described by Gose (1969) as *Potamanthus* sp. TPA and collected from Thailand (Chantaburi province). Bae and McCafferty (1991) redescribed the larva with material from Mae Ping river, Chiang Mai province. In this study, we found this species in the same river as in the previous study. Our specimens were reared in the laboratory and successfully raised to the imago stage.

Subgenus *Rhoenanthus* Eaton, 1881

Rhoenanthus (*Rhoenanthus*) *distafurcus* Bae & McCafferty, 1991

Figures 10E, 11D, 14, 15

Materials examined. 1 larva, Thailand, Kanchanaburi province, Sai Yok district, Pueng Wahn Resort, 14°12'08.9"N, 99°03'36.0"E, 15.X.2015, B. Boonsoong leg; 2 larvae, Ratchaburi province, Suan Phueng district, Pha Chi river, 13°30'57.3"N, 99°20'40.1"E, 19.IX.2016, B. Boonsoong leg; 1 larva, Nan province, Bo Kluea district, Sapan waterfall, 19°11'25.8"N, 101°11'56.3”E, 800 m, 28.XI.2020, B. Boonsoong leg.

Diagnosis. The larvae of *Rhoennanthus distafurcus* can be distinguished from those of other *Rhoenanthus* (*Rhoenanthus*) species based on the following characteristics: i) subapical spine of the mandibular tusk well developed laterally (Fig. 10E), with a simple, short spine, ii) 16–20 medial rounded setae on mandibular tusk (Fig. 10E) iii) length of the mandibular tusks ca 1.7–1.9× length of head, iv) length of foretibiae ca 1.19–1.25× length of the forefemora and about 2.5–2.8× length of the foretarsi, (v) leg with colour marking as in Fig. 11D, and vi) lack of bipectinated setae on the mandible (Soldan and Puthz 2000).

Distribution. Kanchanaburi, Ratchaburi, and Nan provinces.

Remark. Bae and McCafferty (1991) described *R. distafurcus* based on imaginal specimens from Thailand, India, and Vietnam. The larva of *R. distafurcus* was described by Soldan and Puthz (2000) based on specimens from Vietnam. In Thailand, a male adult of this species was found in Khao Yai National Park (Bae and McCafferty 1991). In the present study, larval specimens of this species were found in western and northern Thailand.

Rhoenanthus (*Rhoenanthus*) *speciosus* Eaton, 1881

Figures 10F, 11E, 13, 14

Materials examined. 5 larvae, Thailand, Narathiwat province, Klong Aika Ding stream, 5°47'45.9"N, 101°50'05.5"E, 22.IV.2018, B. Boonsoong leg.

Diagnosis. The larvae of *Rhoenanthus speciosus* can be distinguished from those of other *Rhoenanthus* (*Rhoenanthus*) species based on the following characteristics: i) lateral subapical spine of the mandibular tusk present (Fig. 10F), ii) absence of medial rounded setae on the mandibular tusk, iii) length of the mandibular tusks ca 1.7–2.3× length of the head, iv) length of the foretibiae ca 1.2–1.23× length of the forefemora and about 2.72–2.82× length of the foretarsi, v) leg with colour marking as in Fig. 11E, and vi) 4 or 5 bipectinated lateral setae on the mandibles (Bae and McCafferty 1991).

Egg (dissected from mature larva). Oval; with two large conical polar caps, (Fig. 13A); chorion with numerous scattered tubercles, with knob-terminated coiled threads at the equatorial zone; tagenoform micropyle; sperm guide circular (Fig. 13B).

Distribution. Narathiwat and Songkla provinces.

Remark. The larvae of *Rhoenanthus speciosus* were reported by Bae and McCafferty (1991) based on specimens from Indonesia and Malaysia. Parnrong et al. (2002) reported this species from Songkhla province (southern Thailand). In the present study, we found the larva of this species in the nearby Narathiwat province. The distribution of *R. speciosus* seems to be restricted to the south of the Isthmus of Kra, as was found for another mayfly species, *Prosopistoma wouterae* (Boonsoong & Sartori, 2019). These findings constitute the northern limit of the known distribution of this species.

Key to genera and species of Potamanthidae in Thailand

(adapted from Bae and McCafferty 1991; Nguyen and Bae 2006)

1 Mandibular tusks subequal to, or longer than 1/2 length of head (Fig. 10C, E, F) ..... ***Rhoenanthus*, 2**

– Mandibular tusks shorter than 1/2 length of head (Fig. 10A) .... ***Potamanthus*, subgenus *Potamanthodes*, *P. formosus***

2 Mandibular tusks with lateral subapical spine, appearing apically forked .... **subgenus *Rhoenanthus*, 3**

– Mandibular tusks without lateral subapical spine, not appearing apically forked ..... **subgenus *Potamanthindus*, 4**

3 Mandibular tusks with large lateral subapical spine with 16–20 medial rounded setae (Fig. 10E) ..... ***R. distafurcus***

– Mandibular tusks with small lateral subapical spine, without medial rounded setae (Fig. 10F) ..... ***R. speciosus***

4 Mandibular tusks strongly convergent and abruptly curved inward about 33–34° (Fig. 10D), length of the mandibular tusks ca 1.4× length of head (Fig. 10B) ..... ***R. magnificus***

– Mandibular tusks strongly convergent and abruptly curved inward about 28° (Fig. 10D), length of the mandibular tusks ca 0.7–0.8× length of head (Fig. 10C) ..... ***R. obscurus***

Molecular analysis

The partial sequence of the mitochondrial COI gene (658 bp) of *P. merga* (MW792224) found in Thailand was analysed and compared with the sequence of *Dolania americana* (BIT011-04) from BOLD. However, there is no available sequence for the genus *Behningia*. The intergeneric genetic distance between these two genera was 22.39%, as determined by the Kimura 2-parameter (K2P) model. For Potamanthidae, the phylogenetic tree of the ML analysis is shown in Figure 15 and depicts four clearly separated clades delineating four species. No sequence of *Rhoenanthus speciosus* are included due to unsuccessful DNA extraction. Analysis of the K2P genetic distance to confirm the species delimitation revealed that the intraspecific genetic distances vary between 0.2–5.4%, whereas the interspecific distances are high, ranging from 14–20% (Table 2). The lowest interspecific distance value was found between *R. magnificus* and *R. obscurus* (14%), which share close morphological characters.

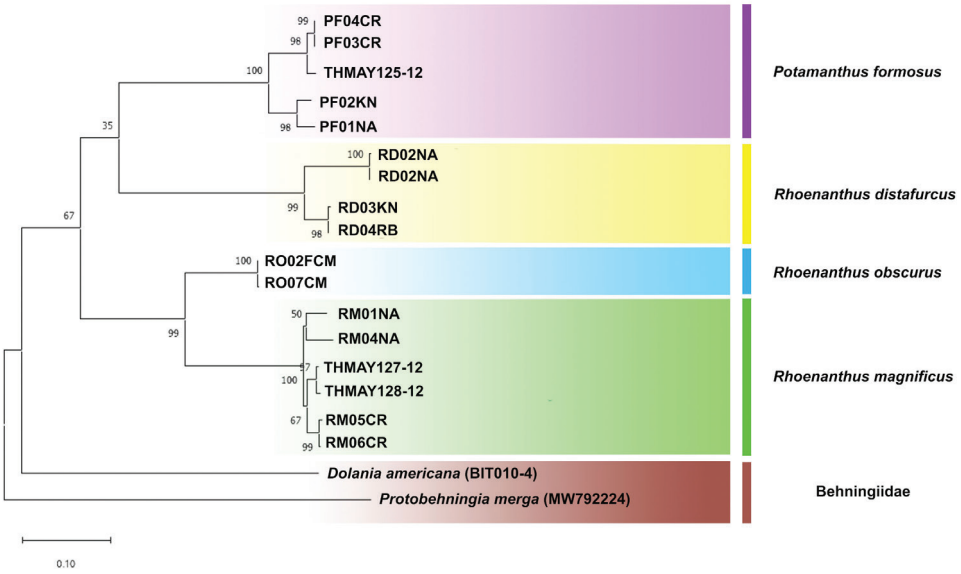

Figure 15. The COI phylogenetic construction based on the maximum likelihood (ML) analysis of family Potamanthidae in Thailand.

Table 2. Pairwise genetic distances (COI) between species of Potamanthidae using the Kimura 2-parameter.

		1	2	3	4
1	*Potamanthus formosus*	–			
2	*Rhoenanthus obscurus*	0.171–0.190	–		
3	*Rhoenanthus magnificus*	0.181–0.212	0.125–0.158	–	
4	*Rhoenanthus distafurcus*	0.177–0.198	0.171–0.196	0.182–0.210	–

Discussion

The discovery of an additional species of *Behningia* in Thailand reveals the high diversity of the behningiid mayflies in the country. The presence of *B. nujiangensis* was confirmed based on morphological evidence according to Zhou et al. (2019) and McCafferty and Jacobus (2006). In the present study, larvae of *B. nujiangensis* were collected from a stream in Chiang Mai province, whereas Zhou et al. (2019) described the species from the Nujiang river (China, upper Salween river), a short section of the river that flows through northern Thailand (Fig. 9). The habitat of *B. nujiangensis* is restricted to sandy bottoms in streams or rivers. The larval exuviae and imagoes of *P. merga* were known only from a river in Kanchanaburi province (western Thailand) by Peters and Gillies (1991). In addition, larvae of *P. merga* were collected from the Mae Chaem river, Chiang Mai province (northern Thailand). This a second report and a new distribution record for this species. The eggs of the genus *Behningia* are the largest known among mayflies, with *B. nujiangensis* reaching more than 1 mm in length. The length of eggs of *Behningia lestagei* (0.9–1 mm) and *Dolania americana* (0.7–0.8 mm) were reported by Keffermul-

ler (1959) and Koss and Edmunds (1974). The egg structure of *B. nujiangensis* is similar to that of *Behningia lestagei*. The position of adhesive material differs between *Behningia* and *Dolania*. However, the egg of *Protobehningia* is still unknown.

The presence of *R. magnificus* in Thailand was confirmed based on the morphological characters proposed by Nguyen and Bae (2004). This species is a new record in Thailand. In this study, the larvae of *R. magnificus* were collected from streams and rivers, where they were often found at the interface of small stones and finer substrate (sand and gravel) in the slow current streams, as previously reported by Nguyen and Bae (2004). Our results allow us to conclude that five valid species of the family Potamanthidae exist in Thailand, as supported by morphological and molecular analyses.

Conservation issues of the Behningiidae

The larvae of Behningiidae are restricted to fine sandy habitats (Peters and Gillies 1991; McCafferty and Jacobus 2006; Park et al. 2019; Zhou et al. 2019). The habitat of *Behningia tshernovae* Edmunds & Traver, 1959 in Korea is restricted to fine sand streams, and high-quality water is needed for its survival (Park et al. 2019). *Behningia ulmeri* is a very rare and extremely endangered European lowland species. In Poland, it may have become extinct as well, and any protective measures there would seem useless (Bauernfeind and Soldán 2012). Among the Thai behningiid mayflies, *B. baei* was found in the Klong Namkub (Phitsanoluk province) in 2002 and *B. nujiangensis* in the Tard Luang waterfall (Chiang Mai province) in 2011, whereas *Protobehningia merga* was found in the Khwae Noi river (Kanchanaburi province) in 1987 and has not been found again in re-samplings. Thai streams and rivers are altered by channel alterations, dam constructions, and sand harvesting. The sandy habitats have gradually decreased in Thailand, and this has threatened the survival of sand-dwelling organisms, including behningiid mayflies. The conservation of fine sandy habitat is, therefore, required to protect this extremely specialized psammophilous fauna.

Acknowledgements

This research is funded by Kasetsart University through the Graduate School Fellowship Program. We are most grateful to Assistant Professor Dr Akekawat Vitheepradit and Mr Prabsuek Sritipsak (Department of Entomology, Faculty of Agriculture, Kasetsart University) for kindly provide specimens for this study. This research has been supported by the Centre of Excellence on Biodiversity (BDC) Office of Higher Education Commission (BDC-PG2-161004). This research was approved by the Institutional Animal Care and Use Committee, Faculty of Science, Kasetsart University, Thailand under Project number ACKU61-SCI-028**.** We would like to thank the Department of Zoology and the Faculty of Science at Kasetsart University in Bangkok for their assistance and use of their facilities.

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ZooKeys 1067: 83–92 (2021)
doi: 10.3897/zookeys.1067.72596
https://zookeys.pensoft.net

RESEARCH ARTICLE

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A new species of *Petta* (Annelida, Pectinariidae), with comments on *Petta assimilis* McIntosh, 1885

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Academic editor: Andrew David | Received 5 August 2021 | Accepted 24 September 2021 | Published 29 October 2021

http://zoobank.org/EA5DA7C4-3688-4FAC-8D83-BA7D20F4F84A

Citation: Zhang J, Hutchings P (2021) A new species of *Petta* (Annelida, Pectinariidae), with comments on *Petta assimilis* McIntosh, 1885. ZooKeys 1067: 83–92. https://doi.org/10.3897/zookeys.1067.72596

Abstract

The genus *Petta* Malmgren, 1866 is a small and poorly known genus of the annelid family Pectinariidae Quatrefages, 1866. A previous revision of the genus found that the type material of the species *P. assimilis* McIntosh, 1885 had been lost. While searching for material from the type locality, we were able to examine material from a similar area but collected in much shallower water from off South Africa which represents another undescribed species of *Petta*. The new species, *Petta brevis* **sp. nov.**, is described and compared to *P. assimilis* McIntosh, 1885, and a revised key to all species in the genus is provided.

Keywords

Indian Ocean, new species, Polychaeta, Pectinariidae, taxonomy

Introduction

Pectinariidae Quatrefages, 1866 is a small family of terebelliform polychaetes easily recognized by their characteristic ice cream cone shaped tubes made of sand grains cemented with mucus, and large opercular paleae. They typically inhabit soft sediments and use their buccal tentacles to sort organic particles in the sediment and carry them

to the mouth (Hutchings 2000). Currently, this family includes five genera and 65 recognized species (Hutchings et al. 2021).

The genus *Petta* Malmgren, 1866 is characterised by having: cephalic veil completely free from the operculum, with the margins either smooth or bearing several lappets and having a pair of ear-shaped lobes adjacent to the dorsal side of the veil; operculum semi-circular with smooth dorsal and lateral margins and a traverse row of numerous stout paleae on the ventral margin; two pairs of comb-like branchiae; seventeen pairs of notopodia on segments 5–21, with capillaries, and neuropodia from segment 7 or 8; neurochaetae as avicular uncini, with crest with transverse rows of progressively shorter teeth; scaphe not clearly separated from posterior body segments, with six pairs of distinct triangular lobes on the lateral margins and a vestigial anal flap. Species of *Petta* are distinguished by the number of pairs of scaphal hooks, by the presence or absence of an anal cirrus, by the numbers and shape of ventro-lateral lobes on segment 2 and 3, and by the number of pairs of neuropodia (Nogueira et al. 2019; Zhang et al. 2019). A revision of the genus, consisting of six species, by Zhang et al. (2019) found that the holotype of *P. assimilis* McIntosh, 1885, collected of South Africa during the "Challenger Expedition" , which had been lodged in the Natural History Museum, London, had been lost (Muir, pers. comm.), so they just provided a brief description based on McIntosh's original one. Subsequently, we had the opportunity to examine some material described by Branch (1994) as *P. assimilis*, collected from fairly close to the type locality south of South Africa (Fig. 1), but no detailed morphological description was provided. McIntosh described his single specimen from a depth of 2926 m, whereas Branch (1994) recorded the species at 360–376 m. Considering the limited data on the depth distributions of other species of *Petta*, there are no records of species occurring over such a depth range. The material reported by Branch (1994) and fixed in formalin, also has a different arrangement of anterior ventral pads, so we have described it as a new species, *P. brevis* sp. nov. Hopefully, additional material will be collected from a similar depth and location as that of *P. assimilis* so that a neotype can be designated at a later stage, as the original description lacks details regarding characters that Zhang et al. (2019) suggested are important for distinguishing species in this genus. Ideally, any additional material collected of *Petta brevis* sp. nov. from the type locality will be fixed in a way that can be used for molecular studies.

Material and methods

Five specimens were examined from 46°59'45"S, 38°00'39"E, at depths of 360–376 m, between Marion and Prince Edward Island south of South Africa. The holotype was stained with methyl green for photography using a Canon EOS 7D camera with a Macro EF 100 mm lens and a Spot Flex CCD 15.2 fitted on a Leica MZ16 Stereo microscope at the Australian Museum, Sydney. The software Helicon Focus 5.3 was used for focus stacking. Another specimen from the same sample was dehydrated in ethanol, critical point dried, coated with 20 nm of gold and examined under a JEOL JSM-6480

Scanning Electron Microscope (SEM) at Macquarie University, Sydney. Terminology follows that of Hutchings et al. (2019). Data on the holotype are given, with the variations of the other material, all designated as paratypes, given in parentheses in the case of complete specimens. All material is deposited in Iziko Museums of South Africa (formerly South African Museum, Cape Town).

Results

***Petta brevis* sp. nov.**
http://zoobank.org/BFEB135F-5072-4841-B65B-0F31C5F512D7
Figs 1–3

Petta assimilis – Branch 1994: 15 (Prince Edward Island). – Zhang et al. 2019: 311–312. Not *P. assimilis* McIntosh, 1885

Type material. ***Holotype*:** SAM A021260, from Station No MAD 39 FFF; 46°59'45"S, 38°00'39"E, depth 360–376 m, Marion and Prince Edward Island, South Africa, collected by bottom dredge, University Marion Island Survey, coll. 26 August 1987 by M. Branch.

***Paratypes*:** SAMC A094445, 1 specimen complete, prepared for SEM, and 3 incomplete specimens, with parts of body wall dissected and empty tubes. All paratypes collected from same location as holotype. All material fixed in formalin and then transferred to 70% alcohol.

Etymology. The specific epithet *brevis* is Latin for "shallow", which refers to the type locality of new species, collected in relatively shallow waters compared to *Petta assimilis*, which is known from a nearby area but in much deeper water.

Description. Holotype pale in colour except for golden paleae and sand grains visible through the body wall. Body cylindrical, tapering before scaphe (Figs 2A, B, 3A). Length 15 mm (20) including paleae and scaphe, maximum width 3 mm (3).

Cephalic veil semi-circular, free from operculum, with smooth lateral margins, distal (anterior) end thin, folded over with smooth margins (Fig. 2A–C). Pair of lateral ear-shaped lobes adjacent to dorsal side of cephalic veil (Fig. 2C). Buccal tentacles numerous, thick, with deep longitudinal grooves arising around buccal cavity (Figs 2B, C, 3C).

Operculum semi-circular, surface tessellated and slightly inflated, with lateral and dorsal margins slightly elevated but smooth (Figs 2A, D, 3C). Two rows of 13 pairs of golden coloured paleae, some broken but arranged in a fan shape, differing slightly in length, outer ones shorter and thinner than inner ones on each row, slightly curved dorsally, with blunt tips (Figs 2C, D, 3C).

First pair of tentacular cirri extending to about halfway along the outer paleae, slightly annulated with swollen base tapering to long thin tip arising from base of opercular margin and paleal ridge (Figs 2A–D, 3B, C). Pair of blunt-tipped triangular ventral lappets present just laterally to first pair of tentacular cirri (Figs 2C, 3A, B).

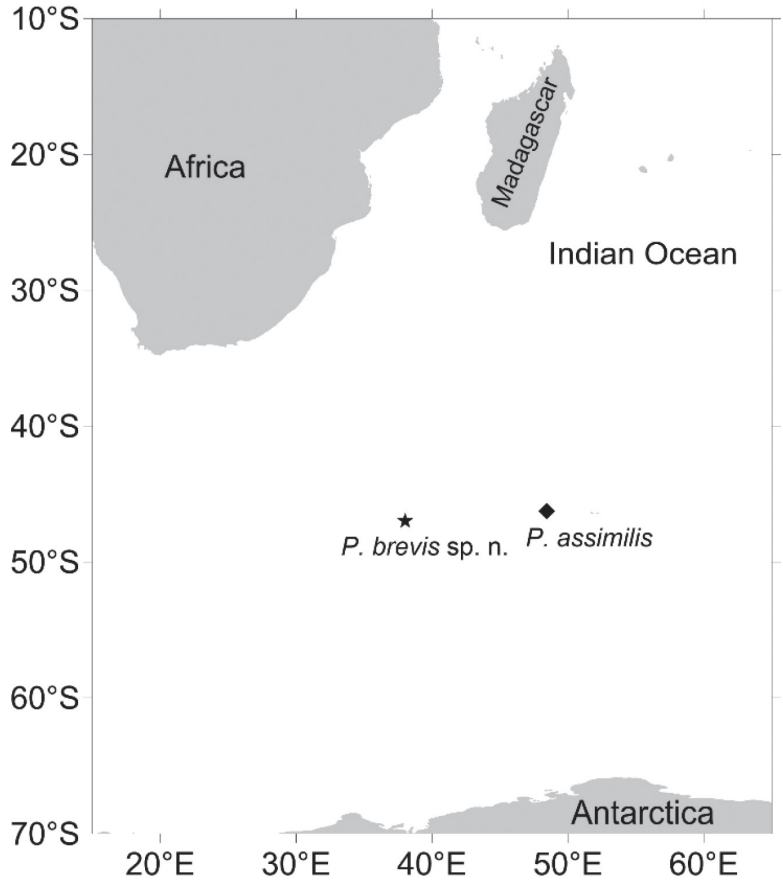

Figure 1. Type localities of *Petta brevis* sp. nov. and *Petta assimilis* McIntosh, 1885.

Second pair of tentacular cirri similar in length to first pair but thinner and with base less swollen than that of first pair (Figs 2A–D, 3B, C), inserted slightly dorsally on mid lateral connecting ridge of segment 2. Segment 2 with pair of broad ventro-lateral lobes separated by a broad and deep mid-ventral groove; each lobe with six pairs of triangular lappets, two mid ventral ones largest (Figs 2B, C, 3B, C).

Segments 3 and 4 with two pairs of similar-sized branchiae, those of segment 3 slightly displaced ventrally (Figs 2A, D, 3C). Each branchia with large basal hump and with about six loose, flat lamellae (Fig. 2D, E). Segment 3 with raised ventral ridge with pair of broad ventro-lateral lobes and pair of rectangular mid-ventral lobes, mid-ventral lobes with rounded margins (Figs 2C, 3B). Segment 4 with slightly raised ventral margins with slight mid ventral indentation, but ventral margins less glandular than those of segment 3 (Figs 2B, C, 3A, B). Pair of dorso-lateral pads small and smooth, arising from dorsal side of notopodia on segment 5 (Figs 2D, 3C), but distorted on segment 5 of holotype.

Discrete raised ventral glandular lobes (pads) on segments 2–7, decreasing in size and elevation posteriorly with slight mid-ventral indentation (Figs 2C, 3B).

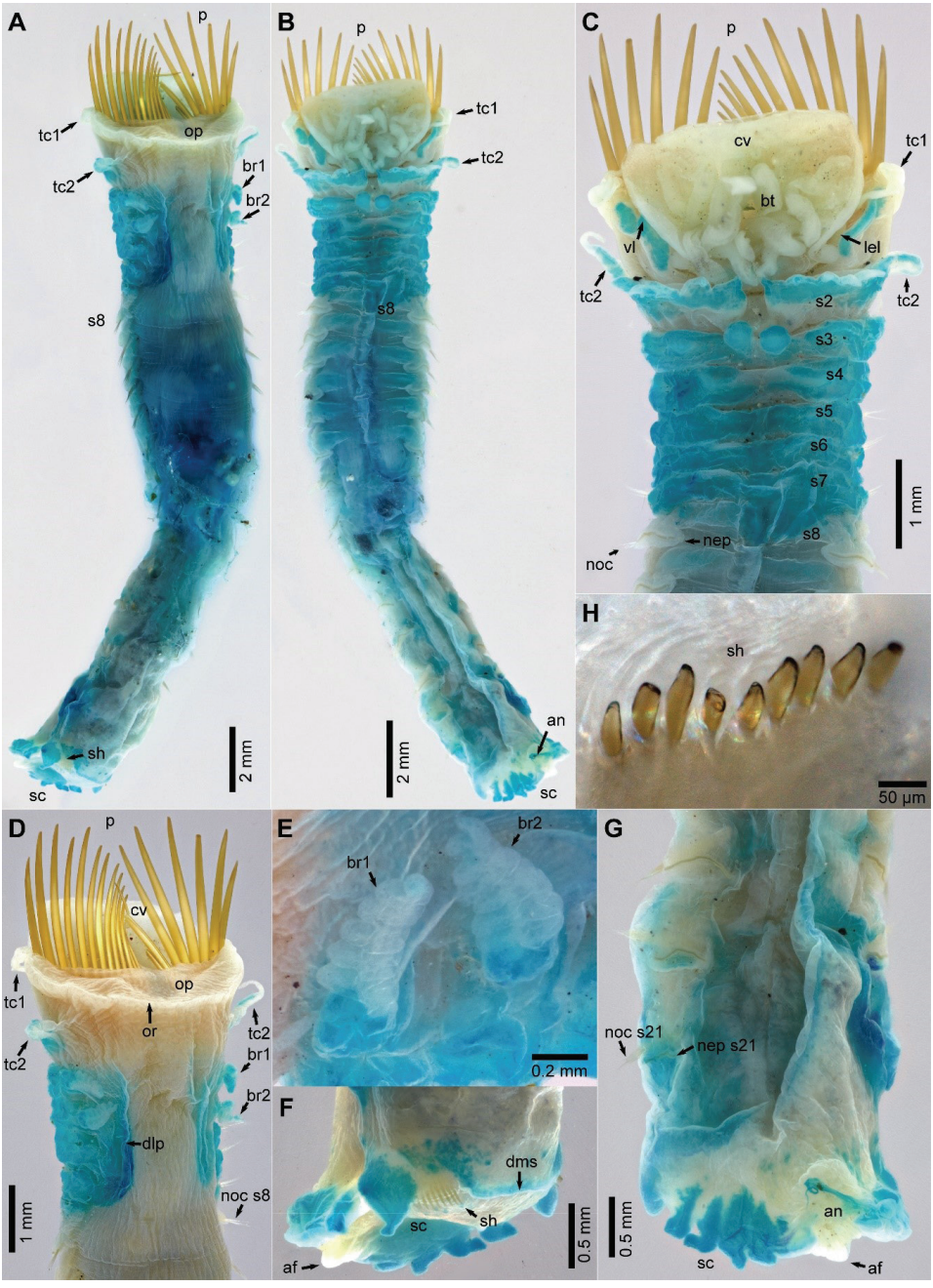

Figure 2. *Petta brevis* sp. nov., holotype (SAM-A021260) **A** dorsal view of whole body **B** ventral view of whole body **C** ventral view of anterior end **D** dorsal view of anterior end **E** close up of left branchiae **F** dorso-lateral view of posterior end **G** ventral view of posterior end **H** close up of scaphal hooks. Abbreviations: af, anal flap (plate); an, anus; br, branchiae; bt, buccal tentacles; cv, cephalic veil; dlp, dorso-lateral pad; dms, dorsal margin of scaphe; lel, lateral ear-shaped lobe; nec, neurochaetae; nep, neuropodium; noc, notochaetae; op, operculum; or, opercular rim; p, paleae; s, segment; sc, scaphe; sh, scaphal hooks; tc, tentacular cirri; vl, ventral lappet.

Notopodia of segment 1 with paleae, and notochaetae from segments 5–21 (17 pairs). Notopodia of segments 5–7 smaller and with smaller notochaetae (Figs 2D, 3C); notopodia of segments 8–13 relatively large with long chaetae; following notopodia decreasing posteriorly in size, length of notochaetae similarly decreasing. Notopodia with 2 rows of different capillary notochaetae; one with distal serrated wings, anterior surface covered with numerous minute spines from below wing to about mid-basal portion of chaeta; another tapering to acute tip without wings, anterior surface covered with numerous spines from mid-length to tip (Fig. 3E).

Neuropodia developed from segment 8 (Figs 2B, C, 3A, B), continuing to scaphal plate, with slightly raised tori. Neurochaetae (uncini) arranged in single transverse row on each torus. Uncinus with two main teeth, followed by several rows of numerous small teeth (Fig. 3F) and a large peg with blunt tip embedded into torus. Neuropodia of segment 21 with enlarged posterior lobe (Fig. 3A).

Scaphe long, ovoid, flattened dorsally, inconspicuous constriction on posterior segments. Lateral margins rolled dorsally, with six pairs of lobes; first pair largest, connected to dorsal margin of scaphe; posterior lobes narrow, triangular, almost of equal size; dorsal margin of scaphe smooth (Figs 2F, G, 3D). Anal flap triangular, without an anal cirrus. Scaphal hooks amber-coloured, left 9 and right 10 on holotype, arising from both sides of dorsal margin of scaphe, with blunt tips slightly curved dorsally (Fig. 2H).

Type of tube: with thin chitinous inner lining covered in small stones cemented together.

Variation. The paratypes consist of one complete specimen, prepared for SEM, and three anterior fragments with some parts of their body wall dissected and some empty incomplete tubes.

Remarks. *Petta brevis* sp. nov. is characterised by a cephalic veil with smooth margins, 13 pairs of paleae, 2 pairs of similar length tentacular cirri, segment 2 with pair of broad ventro-lateral lobes, each lobe with six pairs of triangular lappets, segment 3 with pair of ventro-lateral lobes, and rectangular mid ventral lobes, elongate scaphe not well separated from posterior body, lateral margin with six pairs of lobes, 9–10 pairs of blunt tipped scaphal hooks and smooth anal flap.

Petta brevis sp. nov. differs from *P. pusilla* Malmgren, 1866, which has the anterior margin of the cephalic veil with several lappets, in having a smooth margin to the cephalic veil, like all other species of *Petta*. The arrangement of lobes on segment 3 in *Petta brevis* sp. nov. differentiates it from *P. assimilis* McIntosh, 1885 and *P. investigatoris* Zhang, Hutchings & Kupriyanova, 2019, as these two species have lappets on the ventral lateral lobes of segment 3. The number of pairs of scaphal hooks also differs between species as well as the presence or absence of an anal cirrus: *P. pusilla* has 8 pairs of scaphal hooks and anal cirrus present; *P. pellucida* has 7 pairs of scaphal hooks and the presence/absence of anal cirrus was not stated; *P. tenuis* has 8 pairs of scaphal hooks and a long anal cirrus; *P. investigatoris* Zhang, Hutchings & Kupriyanova, 2019 and *P. williamsonae* Zhang, Hutchings & Kupriyanova, 2019 both have 9 pairs of scaphal hooks and long anal cirrus. For *P. assimilis*, no data on

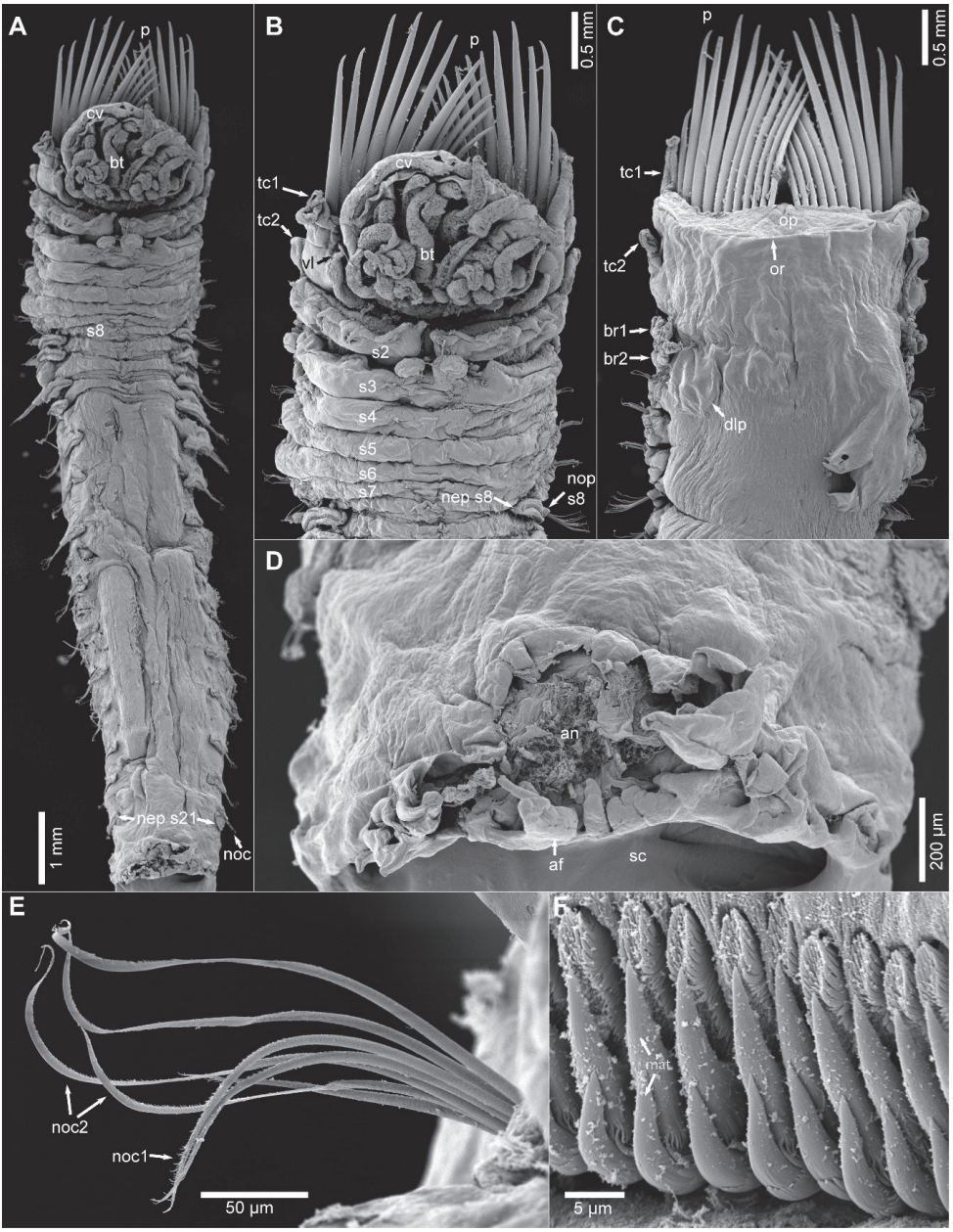

Figure 3. *Petta brevis* sp. nov., SEM of paratype (SAMC-A094445) **A** ventral view of whole body **B** ventral view of anterior end **C** dorsal view of anterior end **D** ventral view of posterior end with distorted scaphe **E** notochaetae **F** close up of uncini. Abbreviations: af, anal flap (plate); an, anus; br, branchiae; bt, buccal tentacles; cv, cephalic veil; dlp, dorso-lateral pad; mat, major teeth; nec, neurochaetae; nep, neuropodium; noc, notochaetae; nop, notopodium; op, operculum; or, opercular rim; p, paleae; s, segment; sc, scaphe; tc, tentacular cirri; vl, ventral lappet.

the number of pairs of hooks or whether an anal cirrus are present or not, was given, whereas *P. brevis* sp. nov. has 9 scaphal hooks on one side and 10 on the other and lacks an anal cirrus.

Discussion. McIntosh described *P. assimilis* from Station 147 (between Prince Edward and Kerguelen Islands), 46°16'S, 48°27'E, at a depth of 1600 fathoms (= 2926 m), and recorded the sediment as being diatom ooze. His description was focussed on how similar the new species was to the British representative of the genus, which he did not actually name, and he also compared the new species with *P. pusilla* Malmgren, 1866, which was described from the west coast of Sweden (Zhang et al. 2019). As no other species had been described from Europe when McIntosh described his species, one must assume that he was referring to an undescribed English species. McIntosh illustrated the ventral view and the scaphal plate (McIntosh 1885, plate XLVII, figs 8, 9) and the chaetae (plate XXVIA, figs 16–19) in a schematic way but gave no information as to the number of pairs of scaphal hooks present. Branch (1994) also collected a species of *Petta* from a similar area but in much shallower water and identified it as *P. assimilis*. As noted above, we found differences between the material collected by Branch, and therefore described it as a new species. Also, the review of the genus by Zhang et al. (2019) found that all species of *Petta* have very restricted depth ranges, which also supports our conclusion that *Petta brevis* sp. nov., although collected from a similar location as *P. assimilis* but at a much shallower depth, should be described as new.

Hartman (1967) also recorded *Petta assimilis* from off Cape Horn (1806–2013 m) and the Falkland Islands, 2452 m, South America. Comparing her description with that of McIntosh (1885), it is difficult to decide if Hartman's species is the same or yet another undescribed species of *Petta*. Certainly, the species recorded by Hartman differs from *Petta brevis* sp. nov. in terms of number of pairs of paleae and the structure of the branchiae. Although she stated that three pairs are present, the first is actually the second tentacular cirrus, and the scaphe has six pairs of triangular lobes, anal cirrus present, and 11 pairs of caudal spines that are distally slightly falcate. She mentioned that the anterior margins of segments 2 and 3 have 7 pairs of fimbriae, which on the figure (Hartman 1967, fig. 44A) equate to the ventro-lateral lobes. We suggest that the identity of Hartman's material cannot be determined at this stage. We also regard that *Petta assimilis* is an indeterminate species until material from much closer to the type locality becomes available and can be examined.

This study supports the findings of Zhang et al. (2019) that species of *Petta* are not common and are mainly reported from the deep sea, with some species only known from type material. It must be noted that deep sea habitats are relatively poorly sampled around the world; however, because tubes of pectinariids are very conspicuous, one would expect them to be recorded if present, which reinforces our belief that this family is not well represented in the deep sea. The only exception is *P. pusilla* Malmgren 1866, which has been recorded from many locations at depths of 15–200 m (see Zhang et al. 2019 for a complete list); however, we suggest that these records should be checked, as its geographical range is very large with

varying ecological conditions. Also, the holotype, which was examined by Zhang et al. (2019), differs from that given by Malmgren, which may have contributed to these widespread records.

Taxonomic key to genera of Pectinariidae and to all species of the genus *Petta* (modified from Zhang et al. 2019)

1 Opercular rim with cirri or lappets..... ***Amphictene***
– Opercular rim smooth **2**
2 Cephalic veil attached to lateral margin of operculum..... ***Lagis***
– Cephalic veil free from operculum **3**
3 More than one longitudinal row of major teeth on uncini ..... ***Pectinaria***
– One longitudinal row of major teeth on uncini..... **4**
4 Lateral and anterior margins of cephalic veil with numerous cirri or lappets; anal flap present; pair of dorso-lateral pads absent on segment 5 .... ***Cistenides***
– Lateral and anterior margins of cephalic veil smooth or only anterior margin with several lappets; anal flap vestigial; pair of dorso-lateral pads present on segment 5 ..... ***Petta*** **5**
5 Anterior margin of cephalic veil with several lappets ..... ***P. pusilla*** **Malmgren, 1866**
– Anterior margin of cephalic veil smooth **6**
6 Ventro-lateral lobes with continuous row of lappets on segment 3 7
– Ventro-lateral lobes smooth, without lappets on segment 3..... **8**
7 Anal flap without anal cirrus; ventro-lateral lobes with 4–5 lappets on segment 2..... ***P. assimilis*** **McIntosh, 1885**
– Anal flap with long anal cirrus; ventro-lateral lobes with 7–8 lappets on segment 2..... ***P. investigatoris*** **Zhang, Hutchings & Kupriyanova, 2019**
8 Scaphe distinctly separated by a constriction from posterior segments ..... ***P. williamsonae*** **Zhang, Hutchings & Kupriyanova, 2019**
– Scaphe not separated by a constriction from posterior segments **9**
9 Scaphal hooks 5–8..... **10**
– Scaphal hooks more than 9..... **11**
10 Scaphal hooks 7; lobes of segment 2 with pair of ventralmost cirri distinctly longer than other cirri; longer mid-ventral lobes on segment 3, cylindrical and distally rounded; neuropodia on segments 7–21..... ***P. pellucida*** **(Ehlers, 1887)**
– Scaphal hooks 5–8; cirri of lobes of segment 2 are all of even length; the mid-ventral lobes of segment 3 are spherical; neuropodia on segments 8–21 ..... ***Petta alissoni*** **Nogueira, Ribeiro, Carrerette & Hutchings, 2019**
11 Ventro-lateral lobes with 4–5 lappets on segment 2; scaphal hooks 11 ..... ***P. tenuis*** **Caullery, 1944**
– Ventro-lateral lobes with 6 lappets on segment 2; scaphal hooks 9–10 ..... ***P. brevis*** **sp. nov.**

Acknowledgements

This study was supported by the National Natural Science Foundation of China (Grant no. 41776172 and 42076129 to J.H. Zhang).

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ZooKeys 1067: 93–100 (2021)
doi: 10.3897/zookeys.1067.72419
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SHORT COMMUNICATION

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First description of the female of *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 (Araneae, Sparassidae)

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Academic editor: F. Martín Labarque | Received 31 July 2021 | Accepted 4 October 2021 | Published 29 October 2021

http://zoobank.org/08D154A5-217C-4B49-984A-BA752E006CC9

Citation: Gong L-J, Zhong Y (2021) First description of the female of *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 (Araneae, Sparassidae). ZooKeys 1067: 93–100. https://doi.org/10.3897/zookeys.1067.72419

Abstract

Sinopoda yichangensis Zhu, Zhong & Yang, 2020 was described from a single male from Qiaoliao Village, Hubei Province, China. To date, no additional specimens have been recorded. The female is reported for the first time from the type locality. Detailed morphological descriptions of the female, with photographs of living specimens and copulatory organs, are provided.

Keywords

Biodiversity, huntsman spiders, taxonomy, Yichang

Introduction

The genus *Sinopoda* Jäger, 1999 is the fourth largest genus of the family Sparassidae, with 133 species (World Spider Catalog 2021). To date, *Sinopoda* is distributed from high to low altitude in south, east, and southeast Asia, frequently co-distributed, some of which are located in caves. More than half of the known species were described based on a single sex in *Sinopoda*. From China, 71 species are known; among them, 19 species are only known from females and five only from males (World Spider Catalog

2021). *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 was described based on a single male specimen from Qiaoliao Village of Hubei Province, China (Zhu et al. 2020). Recently, new material containing both sexes were collected from the type locality. In addition, based on the similar body coloration patterns, we were able to match the females and males together.

Materials and methods

Specimens were examined and measured with a Leica M205C stereomicroscope. The points arising from the tegular appendages are listed as clock positions from the left bulb in ventral view. Male and female copulatory organs were examined and illustrated after dissection from the spider bodies; vulvae were cleared with Proteinase K. All photographs were taken with a Leica DFC450 digital camera attached to a Leica M205C stereomicroscope, with 10–20 photographs taken in different focal planes and combined using the image stacking software Leica LAS V4.8. Images were edited using Adobe Photoshop CC 2018.

Leg measurements are listed as: total length (femur, patella, tibia, metatarsus, tarsus). The number of spines is listed for each segment in the following order: prolateral, dorsal, retrolateral, ventral (in femora and patellae, ventral spines are absent, and the fourth digit is omitted in the spination formula). Abbreviations used in the text and figures are given below:

ALE anterior lateral eye;
AME anterior median eye;
AW anterior width of carapace;
C conductor;
CH clypeus height;
dRTA dorsal branch of RTA;
E embolus;
EA embolic apophysis;
FD fertilization duct;
FE femur;
GA glandular appendage;
LL lateral lobes;
LS lobal septum;
MS membranous sac;
Mt metatarsus;
OL opisthosoma length;
OW opisthosoma width;
Pa patella;
PI posterior incision of LL;
PL carapace length;
PLE posterior lateral eyes;
PME posterior median eyes;
Pp palp or palpus;
PP posterior part of spermathecae;
PW carapace width;
RTA retrolateral tibial apophysis;
SP spermophor;
ST subtegulum;
T tegulum;
Ta tarsus;
Ti tibia. I, II, III, IV – legs I to IV;
vRTA ventral branch of RTA;

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Taxonomy

Family Sparassidae Bertkau, 1872
Subfamily Heteropodinae Thorell, 1873
Genus *Sinopoda* Jäger, 1999

***Sinopoda yichangensis* Zhu, Zhong & Yang, 2020**
Figures 1–3

Sinopoda yichangensis Zhu, Zhong & Yang, 2020: 9, figs 4A–C, 5A–C, 6A, B (holotype male from Qiaoliao Village of Hubei Province, deposited in College of Life Science, Hubei University LJ-202001-ZY).

Material examined. 2♂, 3♀ (HUST 0002), Hubei Province, Yichang City, Wufeng County, Qiaoliao Village; 30.37°N, 110.54°E; alt. 986 m; 27.V. 2021, Yang Zhong leg.

Diagnosis. This species resembles *Sinopoda angulata* Jäger, Gao & Fei, 2002 (Zhu et al. 2020: fig. 2A–E) by palp with an embolus distally filiform, as long as the embolic apophysis, and epigyne with lateral lobes fused without visible seam, and anterior part of the internal duct system not visible in dorsal view (Fig. 2E, see dotted line). They can be distinguished from the latter by the following characters: 1, embolus arising from tegulum at 7- to 8-o'clock position in ventral view (6-o'clock position in *S. angulata*); 2, tip of embolic apophysis with blunt end (pointed in *S. angulata*); 3, female epigyne with lobal septum ~ 1/3 of epigynal width (~ 1/4 in *S. angulata*); 4, female vulva with internal duct system not touching (touching along median line in *S. angulata*) (Fig. 2E).

Description. Male. See Zhu et al. (2020).

Female. PL 6.2, PW 5.4, AW 3.5, OL 5.0, OW 3.3. Eyes and interdistances: AME 0.20, ALE 0.34, PME 0.19, PLE 0.33, AME-AME 0.25, AME-ALE 0.15, PME-PME 0.51, PME-PLE 0.62, AME-PME 0.53, ALE-PLE 0.64, CH AME 0.25, CH ALE 0.33. Spination: Palp: 131, 000, 2121, 1014; Fe: I–III 323, IV 321; Pa: I–IV 101; Ti: I 2026, III–IV 2226; Mt: I–II 1014, III–IV 3036. Measurements of palp and legs: Palp 7.1 (2.4, 1.4, 1.5, –, 1.8), I 16.9 (5.0, 2.6, 4.4, 3.4, 1.5), II 19.1 (5.6, 2.7, 4.9, 4.4, 1.5), III 16.2 (4.9, 2.4, 4.0, 3.5, 1.4), IV 17.4 (5.1, 2.0, 4.6, 4.2, 1.5). Leg formula: 2–4-1–3. Cheliceral furrow with three anterior and four posterior teeth, each furrow with 23 denticles (Fig. 3B). Copulatory organ as in diagnosis. Epigynal field wider than long, with short anterior muscle attachment bands, with one slit sensillum on each side close to the epigynal field. Glandular appendages short, extending only in anterior half of internal duct system. Internal duct system converging and strongly U-shaped. Fertilization ducts arising postero-laterally, curved. Membranous sac between fertilization ducts almost triangular (Fig. 2D, E). Coloration in ethanol: as in male, but slightly brighter (Fig. 3E, F).

Distribution. Known only from the type locality.

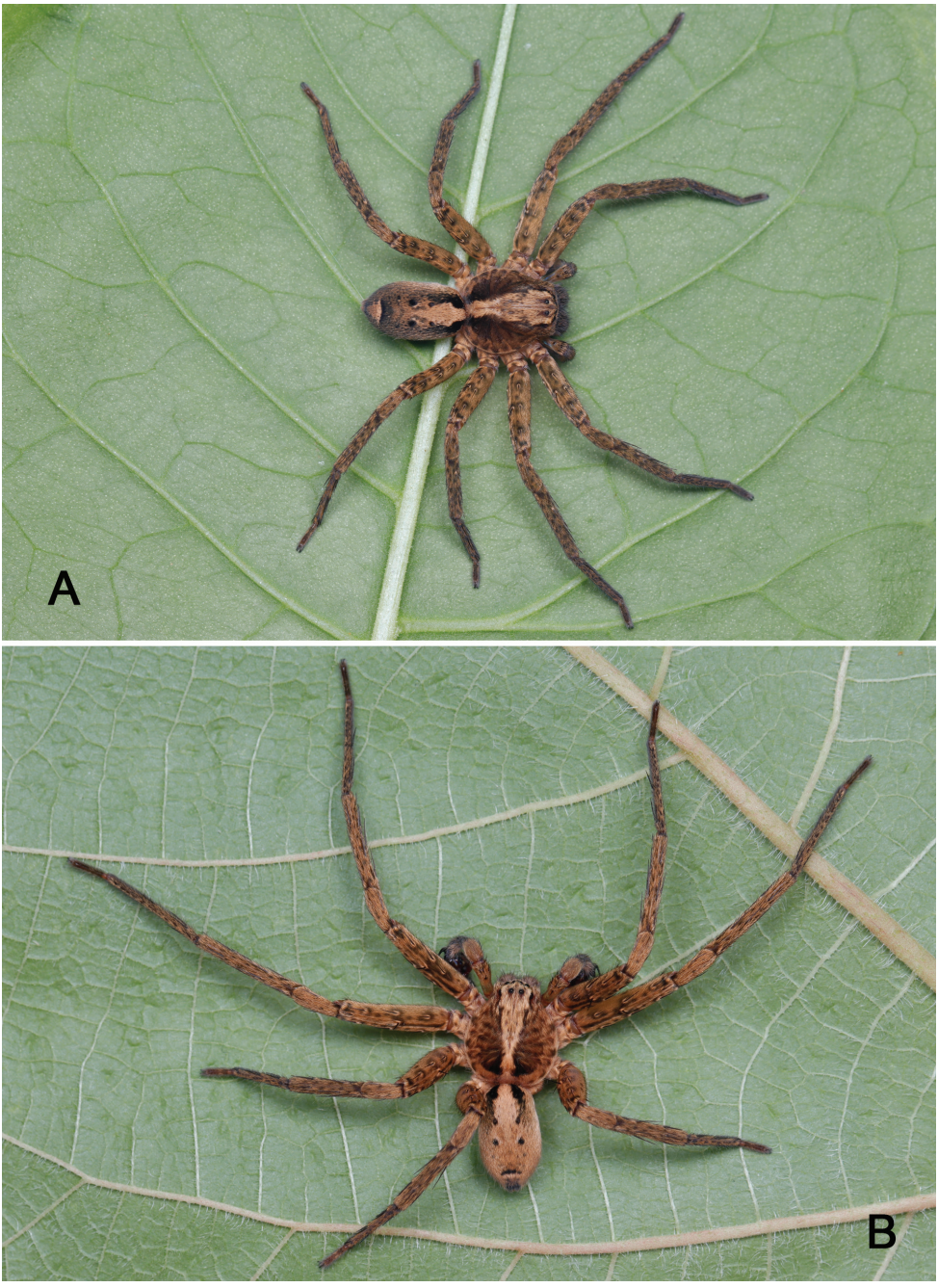

Figure 1. Photos of live *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 **A** female **B** male.

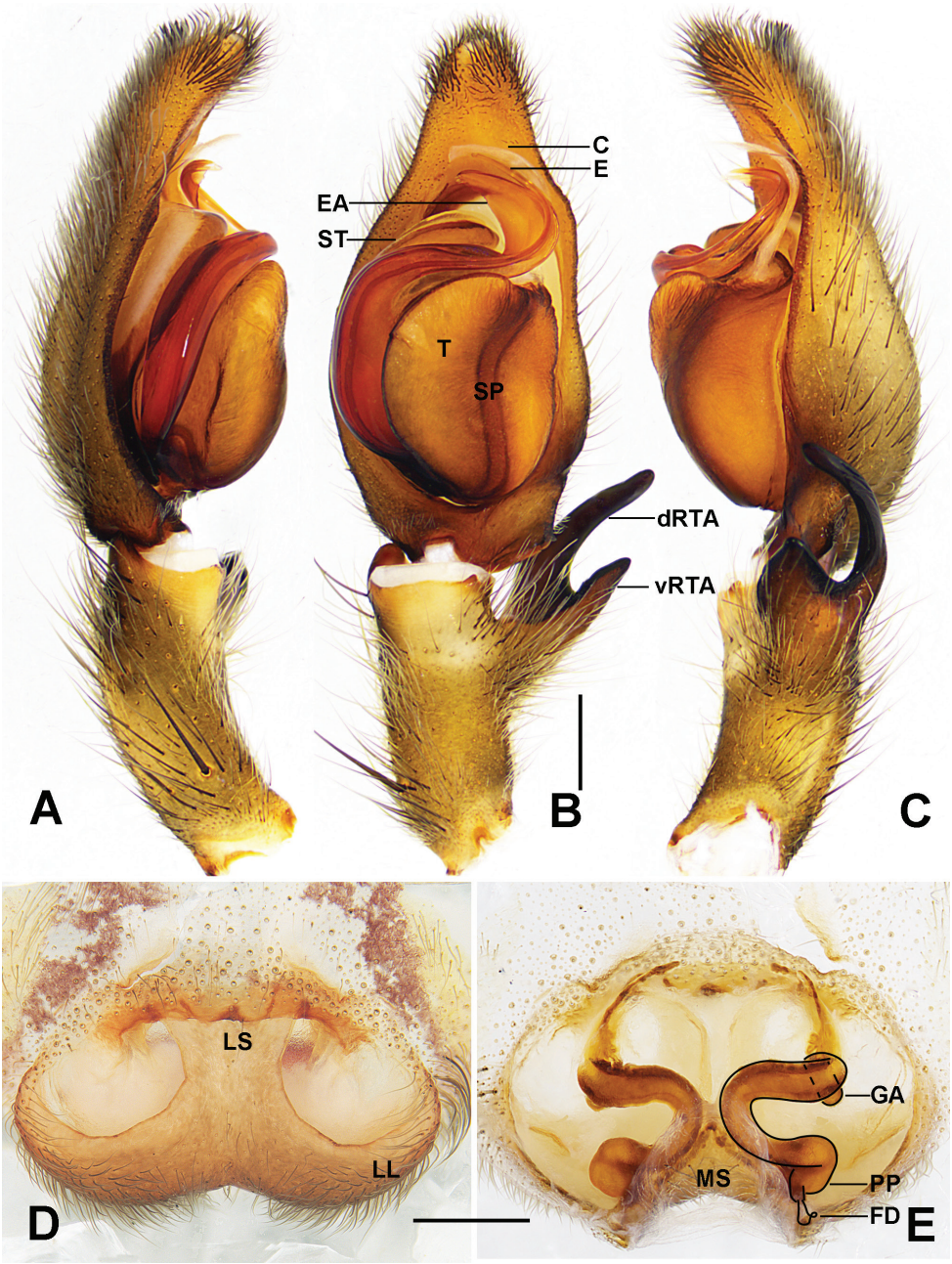

Figure 2. *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 **A–C** left male palp (**A** prolateral view **B** ventral view **C** retrolateral view) **D** epigyne **E** vulva (**D** ventral view **E** dorsal view). Abbreviations: C – conductor, dRTA – dorsal retrolateral tibial apophysis, E – embolus, EA – embolic apophysis, FD – fertilization duct, GA – glandular appendage, LL – lateral lobes, LS – lobal septum, MS – membranous sac, PP – posterior part of spermathecae, SP – spermophor, ST – subtegulum, T – tegulum, vRTA – ventral retrolateral tibial apophysis. Scale bars: 0.5 mm.

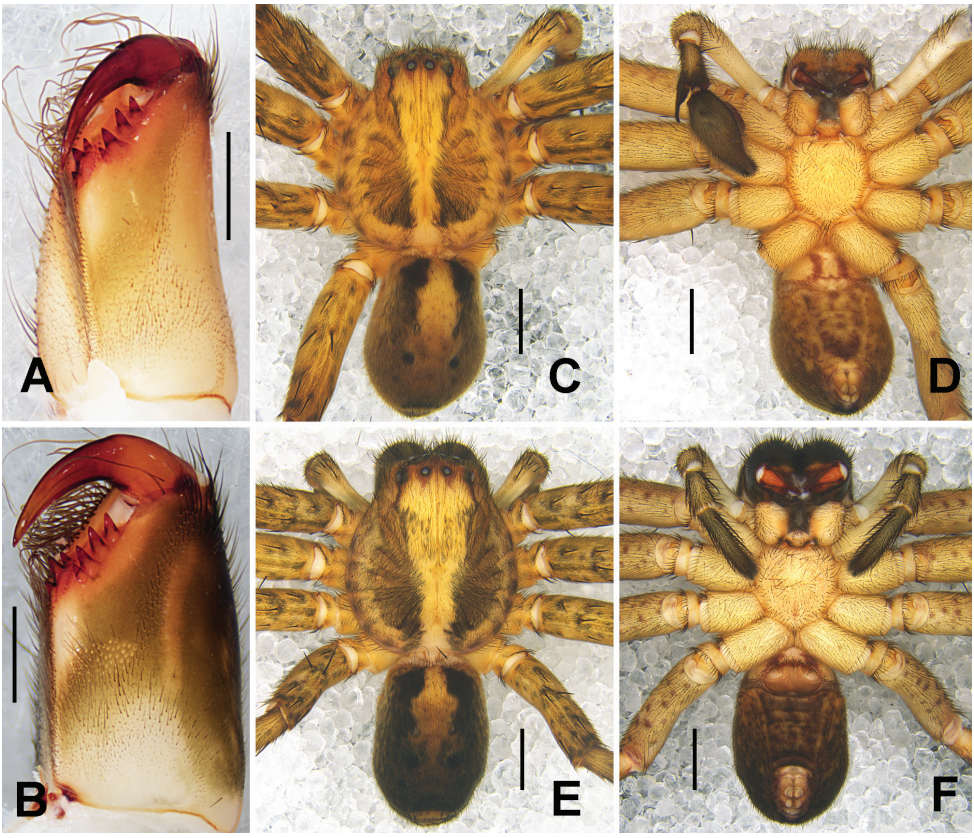

Figure 3. *Sinopoda yichangensis* Zhu, Zhong & Yang, 2020 **A, B** cheliceral dentition, ventral view (**A** male **B** female) **C, D** male habitus (**C** dorsal view **D** ventral view) **E, F** female habitus (**E** dorsal view **F** ventral view). Scale bars: 0.5 mm (**A, B**); 2 mm (**C-F**).

Variation. Male (n = 2): Total length 13.5–16.5; prosoma 6.0–7.5 long, 5.0–6.2 wide, anterior width of prosoma 2.3–3.2; opisthosoma 7.5–9.0 long, 3.5–4.5 wide. Measurements leg I: total length 34.5–36.0, Fe 8.6–9.0, Pa 3.0–3.3, Ti 9.4–9.7, Mt 10.3–10.6, Ta 3.1–3.4. Spination: legs: Mt I–II 2024. **Female (n = 2):** Total length 10.8–11.5; prosoma 5.5–6.5 long, 4.8–5.6 wide, anterior width of prosoma 3.0–3.8; opisthosoma 5.0–5.3 long, 2.8–4.0 wide. Measurements leg I: total length 15.6–18.0, Fe 4.8–5.3, Pa 2.4–2.8, Ti 4.3–4.7, Mt 3.0–3.6, Ta 1.3–1.6. Spination: legs: Ti I 2126, Mt I–II 2226.

Acknowledgements

We thank Jiangwei Zheng, Han Dong, and Mengyun Zeng for assistance in collecting specimens. The manuscript benefited greatly from comments by Drs. Facundo Martín Labarque (Universidade Federal de São Carlos São Calos, Brazil) and Cristina Rheims

(Instituto Butantan, São Paulo, Brazil). This study was financially supported by the National Natural Sciences Foundation of China (NSFC-32000303), Natural Sciences Foundation of Hubei Province (2019CFB248), a PhD grant from Hubei University Science and Technology (BK201811, BK202114).

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ZooKeys 1067: 101–157 (2021)
doi: 10.3897/zookeys.1067.72395
https://zookeys.pensoft.net

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Twelve new species of *Dipara* Walker, 1833 (Hymenoptera, Chalcidoidea, Pteromalidae, Diparinae) from Kenya, with a key to the Afrotropical species

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Academic editor: Miles Zhang | Received 30 July 2021 | Accepted 4 September 2021 | Published 29 October 2021

http://zoobank.org/893BCD8C-B8A6-49FF-B36F-637720161BFC

Citation: Braun C, Peters RS (2021) Twelve new species of *Dipara* Walker, 1833 (Hymenoptera, Chalcidoidea, Pteromalidae, Diparinae) from Kenya, with a key to the Afrotropical species. ZooKeys 1067: 101–157. https://doi.org/10.3897/zookeys.1067.72395

Abstract

Based on 261 female specimens of the genus *Dipara* Walker, 1833 from leaf litter samples of the Kakamega Forest in Kenya, we describe the following twelve new species: *Dipara andreabalzerae* **sp. nov.**, *Dipara corona* **sp. nov.**, *Dipara fastigata* **sp. nov.**, *Dipara kakamegensis* **sp. nov.**, *Dipara lux* **sp. nov.**, *Dipara nigroscutellata* **sp. nov.**, *Dipara nyani* **sp. nov.**, *Dipara reticulata* **sp. nov.**, *Dipara rodneymulleni* **sp. nov.**, *Dipara sapphirus* **sp. nov.**, *Dipara tenebra* **sp. nov.**, and *Dipara tigrina* **sp. nov.** For *Dipara albomaculata* (Hedqvist, 1963) and *Dipara nigrita* Hedqvist, 1969, we give new distribution records. We examined the available type material of all described *Dipara* species from the Afrotropical mainland, i.e., *Dipara albomaculata* (Hedqvist, 1963), *Dipara machadoi* (Hedqvist, 1971), *Dipara maculata* (Hedqvist, 1963), *Dipara nigrita* Hedqvist, 1969, *Dipara pallida* (Hedqvist, 1969), *Dipara punctulata* (Hedqvist, 1969), *Dipara saetosa* (Delucchi, 1962), *Dipara straminea* (Hedqvist, 1969), *Dipara striata* (Hedqvist, 1969), and *Dipara turneri* Hedqvist, 1969. We provide figures, descriptions, and diagnoses of the newly described species and figures and diagnoses of the ten known species as well as an identification key to all species of the Afrotropical mainland.

Keywords

Morphometry, parasitoid wasps, taxonomy

Introduction

In this study, we contribute to the taxonomic knowledge of the Afrotropical fauna of the genus *Dipara* Walker, 1833, with the first alpha-taxonomic treatment of this group and region in 50 years. We describe twelve new species and diagnose and key all new and previously described Afrotropical mainland species. *Dipara* belongs to the subfamily Diparinae within the chalcidoid family Pteromalidae (Heraty et al. 2012). The genus shows a cosmopolitan distribution (Desjardins 2007) with a total of 56 described species (Noyes 2019). The phylogenetic position of Diparinae is still unclear (Desjardins 2007; Heraty et al. 2012). Currently, it is still classified within Pteromalidae, which, however, is polyphyletic (Peters et al. 2018). Diparinae were shown to be monophyletic and can be identified by the following diagnostic characters: presence of a cercal brush and absence of a smooth convex dorsellum (Desjardins 2007). The genus *Dipara* is well characterized by a number of diagnostic characters (see below or Desjardins 2007 for a full diagnosis and a list of genera previously synonymized under *Dipara*).

The early taxonomic work on *Dipara* was confounded by the strong sexual dimorphism in this group. Males are usually macropterous and have filiform antennae. Females can range from macropterous to apterous and have clavate antennae. Additionally, males tend to be extremely similar even across different genera while females show a lot of interspecific morphological variation (Desjardins 2007). This led to the genus originally being described by Walker (1833) based on a male specimen of *Dipara petiolata* Walker, 1833 and *Dipara* females originally being described as *Tricoryphus* by Förster (1856) and as *Hispanolelaps* by Mercet (1927). The two genera were later synonymized with *Dipara* by Domenichini (1953). Because of the strong resemblance of males of different species and the morphological variation of females, most species level taxonomic work on *Dipara* (and other Diparinae) is based on female specimens (Delucchi 1962; Hedqvist 1963, 1969, 1971). For males, Desjardins (2007) provided a genus level key. Matching females and males of the same species based on morphological features is currently not possible. Mitroiu (2019) suggested to match conspecific females and males based on molecular sequence data (e.g., the DNA barcode) and this is certainly the way to go. Unfortunately, the material available for this study was not suitable for standard DNA sequencing and consistently failed in a pre-study trial (unpublished). Accordingly, our work is based solely on morphological characters of females.

A peculiar characteristic of Diparinae females is their intraspecific variation in the wing form with macropterous and brachypterous specimens being found in the same species (Bouček 1988; Desjardins 2007; Mitroiu 2019). To deal with this potentially confounding fact, we used a multivariate morphometric approach (Baur and Leuenberger 2011) in morphologically similar species with different wing forms, which has been applied successfully numerous times for taxonomic studies on parasitoid wasps (e.g., László et al. 2013; Baur et al. 2014; Baur 2015; Gebiola et al. 2017; Werner and Peters 2018). Additionally, we checked the state of the posterior notal wing process

which Desjardins (2007) suggested to be a "measure of potential wing size", i.e., a possible hint on the intraspecific wing form variation.

There is a severe lack of information about the biology of *Dipara* species. One of their main habitats is supposed to be leaf litter (Desjardins 2007). The only published information about their hosts is that of an unidentified Indian *Dipara* species which was reared from a curculionid beetle feeding on the roots of a *Cyperus* species (Bouček 1988). Additional host records from curculionids in *Lelaps* Walker, 1843 led Desjardins (2007) to suggest that the more common and typical Diparinae (like *Lelaps* and *Dipara* species) may parasitize soil-inhabiting beetles and maybe curculionids more specifically.

So far, ten species of *Dipara* have been described from the Afrotropical mainland, with a distribution ranging from the Democratic Republic of Congo to South Africa, including *Dipara albomaculata* (Hedqvist, 1963), *Dipara machadoi* (Hedqvist, 1971), *Dipara maculata* (Hedqvist, 1963), *Dipara nigrita* Hedqvist, 1969, *Dipara pallida* (Hedqvist, 1969), *Dipara punctulata* (Hedqvist, 1969), *Dipara saetosa* (Delucchi, 1962), *Dipara straminea* (Hedqvist, 1969), *Dipara striata* (Hedqvist, 1969) and *Dipara turneri* Hedqvist, 1969 (Mitroiu 2011; Noyes 2019). Larger series of *Dipara* specimens are exceedingly rare and descriptions are often based on a single or just a few specimens. Five Afrotropical *Dipara* species are known only from the holotype and nine from five specimens or less. Only *D. pallida* is known from a larger series of 13 specimens (Desjardins 2007).

We based our work on an extraordinary series of 261 female *Dipara* specimens from the Kakamega Forest in Kenya. Collection of the specimens was done in the framework of the BIOTA (BIOdiversity Monitoring Transect Analysis in Africa) East Africa project (Ross et al. 2018). The Kakamega Forest is a montane rainforest fragment in western Kenya and the easternmost remnant of the Guineo-Congolian rainforest belt (Kokwaro 1988; Clausnitzer 2005; Holstein 2015). Due to high rural population density around the Kakamega Forest it is under high threat from deforestation and habitat destruction (KIFCON 1994). Parts of its plant and animal fauna have already been studied in detail (e.g., Althof 2005; Clausnitzer 2005; Kühne 2008; Hita-Garcia et al. 2013). To preserve biodiversity, it is a most urgent and necessary task to contribute to the knowledge of highly diverse, threatened habitats, including knowledge on parasitoid wasps of these areas, by increasing visibility of species from this region and making specimens from it available.

With the description of twelve new *Dipara* species from the leaf litter of Kakamega Forest in Kenya we can show that the species diversity of the genus has not been sufficiently studied and the true diversity of Afrotropical *Dipara*, and presumably other Diparinae, has been underestimated. Since our very much geographically limited study already more than doubles the number of known species, we expect that numerous additional species of Afrotropical *Dipara* still await discovery and description. This study may serve as a starting point for future in-depth investigations, including thorough taxonomic revisions of the Afrotropical Diparinae, Chalcidoidea or, more generally, parasitoid wasp fauna.

Materials and methods

In the following, abbreviations are given of the museums where the material used in this study is stored. The abbreviations will be used throughout the text.

MDLA	Laboratório de Biologia, Dundo, Lunda, Angola
NHMUK	Natural History Museum, London, UK
NMK	National Museums of Kenya, Nairobi
RMCA	Royal Museum for Central Africa, Tervuren, Belgium
ZFMK	Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany

The terminology is based on Gibson (1997) and the Hymenoptera Anatomy Ontology portal (Yoder et al. 2010). For the terminology of the surface sculpture, we used Harris (1979).

A total of 261 female *Dipara* specimens from the Kakamega Forest in Kenya were examined. They were collected in 2007 and 2008 using Winkler extraction of a 1 m^2 leaf litter sample in multiple transects throughout the Kakamega Forest (Ross et al. 2018) and stored in 70% ethanol at room temperature at the ZFMK. All female *Dipara* specimens were isolated from the collective leaf litter samples and transferred to 99.8% ethanol. After presorting and examination, the specimens were critical point dried using a Leica EM CPD 300 AUTO and mounted on small, pointed cardboard plates with shellac-based glue. Morphological examinations were done with a Zeiss Discovery V8 stereomicroscope with a Plan S 1.0× FWD 81mm objective and PI 10×/23 eyepieces.

Digital imaging was done with a Keyence VHX-2000 digital microscope. For images of the dorsal and lateral habitus and the head the VHX-J250 objective (250–2500×) was used. The images were stacked and edited in brightness, coloration and contrast using the Keyence internal software. Further editing of figures was done with Microsoft Power Point 2010. For the images for the morphometric measurements the Keyence VH-Z20R objective (20–200×) with a magnification of 200× was used. For the body length and the gaster length magnifications of 100× or 150× were used if the character did not fit into an image with 200× magnification. After calibration, measurements were done using ImageJ 1.53a. Characters used for morphometric measurements are given and explained in Table 1.

The range of the morphometric measurements is given in the species description with the value for the holotype in parentheses. If more than five specimens were present, five specimens were used for the morphometric measurements, and their respective collection numbers are given in parentheses at the beginning of the taxonomic treatment (see below). If five or less specimens were available, all specimens were used. In a few cases the number of specimens used for a certain measurement varies from the total number of specimens used, either because the measured character was not visible in some specimens or because more specimens were used for the in-depth morphomet-

Table 1. List of morphometric characters with abbreviations and definitions (character definitions are based on Graham (1969), Gibson (1997) and Baur (2015)). Characters highlighted in bold were used for the morphometric analysis of *D. kakamegensis* sp. nov. and *D. nyani* sp. nov. (see Tables S1 and S2 for results).

Abbr.	Character	Definition
scp.l	Scape length	Length of scape exclusive of radicle, outer aspect
pdl.l	Pedicel length	Length of pedicel, outer aspect
pdl.b	Pedicel breadth	Breadth of pedicel, outer aspect
pdl.flg	Pedicel + flagellum	Combined length of pedicel plus flagellum, outer aspect
clv.l	Clava length	Length of clava, outer aspect
clv.b	Clava breadth	Breadth of clava, outer aspect
tor.d	Toruli diameter	Greatest diameter of right torulus, outer aspect
ant.d	Antennae distance	Greatest distance between outer edges of toruli
ant.eye	Distance from antennal insertion to eye	Distance between center of insertion point of antennae and level of ventral margin of the eyes measured straight down from insertion point of antennae
eye.b	Eye breadth	Greatest breadth of eye, lateral view
eye.h	Eye height	Greatest length of eye height, lateral view
mspl.l	Malar space length	Distance between the point where malar sulcus enters mouth margin and malar sulcus enters lower edge of eye, lateral view
hea.h	Head height	Distance between lower edge of clypeus and lower edge of anterior ocellus, frontal view
upf.l	Upper face length	Distance between lower edge of toruli and lower edge of anterior ocellus
hea.b	Head breadth	Greatest breadth of head, dorsal view
eye.d	Eye distance	Shortest distance between eyes, dorsal view
pol.l	POL	Shortest distance between posterior ocelli, dorsal view
ool.l	OOL	Shortest distance between posterior ocellus and eye margin, dorsal view
prn.l	Pronotum length	Length of pronotum along median line from anterior edge of pronotum collar to anterior edge of mesoscutum
prn.b	Pronotum breadth	Greatest breadth of pronotum, dorsal view
msc.b	Mesoscutum breadth	Greatest breadth of mesoscutum just in front of level of tegula, dorsal view
msc.l	Mesoscutum length	Length of mesoscutum along median line from posterior edge of pronotum to posterior edge of mesoscutum, dorsal view
mss.l	Mesosoma length	Length of mesosoma along median line from anterior edge of pronotum collar to posterior edge of nucha, dorsal view
sctl.l	Mesoscutellum length	Length of mesoscutellum along median line from posterior edge of mesoscutum to posterior edge of mesoscutellum, dorsal view
ppd.l	Propodeum length	Length of propodeum measured along median line from anterior edge to posterior edge of nucha, dorsal view
fm3.l	Metafemur length	Length of metafemur, from distal end of trochanter to tip of metafemur, measured along midline, outer aspect
fm3.b	Metafemur breadth	Greatest breadth of metafemur, outer aspect
ptl.l	Petiole length	Length of petiole measured along median line, from posterior edge of nucha to posterior edge of petiole, dorsal view
ptl.b	Petiole breadth	Greatest breadth of petiole, outer aspect, dorsal view
gst.l	Gaster length	Length of gaster along median line from posterior edge of nucha to tip of ovipositor sheath, dorsal view

ric analysis, using a subset of the characters (see below). In these cases, the collection numbers of specimens used are given in parentheses directly after the respective measurement (see Suppl. material 1: Table S1 and Suppl. material 2: Table S2). Some morphometric characters were used to calculate ratios. For these ratios different categories were defined to simplify the description of shape (Table 2). The shape ratios are given in Suppl. material 3: Table S3.

Table 2. Shape categories for morphometric measurements and ratios in the species descriptions.

Character	Categories			
Body length (in µm)	**small**	**medium**	**large**	
	< 2000	2000–3000	> 3000	
Head shape in frontal view (head breadth/head height)		**round**	**oval**	
		< 1.31	> 1.31	
Mesosoma shape in dorsal view (head breadth/mesoscutum breadth)	**robust**	**of medium breadth**	**slender**	
	< 1.20	1.20–1.50	> 1.50	
Antennae distance (antennae distance/torulus diameter)		**close**	**far apart**	
		< 1.33	> 1.33	
Distance from antennal insertion to eye (distance from antennal insertion to eye/torulus diameter)	**same level as eyes**	**short**	**long**	
	0	< 1.1	> 1.1	
Pronotum shape in dorsal view (pronotum breadth/pronotum length)	**large and elongated**	**of medium length**	**short and slim**	
	< 2.5	2.5–3.5	> 3.5	
Petiole length (petiole length/petiole breadth)	**short**	**medium**	**long**	**very long**
	< 1.5	1.5–2.0	2.0–2.5	> 2.5
Gaster length (gaster length/mesosoma length)	**short**	**medium**	**long**	
	< 1.20	1.20–2.0	> 2.0	

Morphometric analysis

Two putative species were found that clearly differed in the wing form, with one being macropterous and the other being brachypterous, but they were otherwise very similar with no obvious qualitative characters found to separate them. Since wing form might vary within species (Bouček 1988; Desjardins 2007; Mitroiu 2019), we chose to apply a quantitative approach based on multivariate morphometric analysis (Baur and Leuenberger 2011, 2020; Baur et al. 2015). For this purpose, the characters highlighted in bold in Table 1 were imaged and measured, as explained before, for 30 specimens of the first species (that later became *D. kakamegensis* sp. nov., see below) and all five specimens of the second species (that later became *D. nyani* sp. nov., see below). The measurements (given in Suppl. material 1: Table S1) were subsequently analyzed using R 4.0.2 and the R script package by Baur and Leuenberger (2020). Missing data was added using the imputation function of the mice R package.

Posterior notal wing process

As suggested by Desjardins (2007), the posterior notal wing process (pnwp) can be used as a "measure of potential wing size". The pnwp can be absent in brachypterous or apterous species, leading to the assumption that a fully developed pnwp in a brachypterous species could mean that macropterous individuals of this species exist. Desjardins (2007) lists four different character states: present and pointed, present but squarely truncate, present but truncate and rounded, and absent. We examined the state of the pnwp in each new species and imaged specimens of four different species with varying wing forms, from brachypterous to macropterous (Fig. 4), using the Keyence with the VHXJ-250 objective as described above.

Results

Morphometric analysis

The morphometric analysis of specimens of the two morphologically similar putative species showed that they can be reliably separated (Fig. 1 and 3). In the following, they will be treated as *D. kakamegensis* sp. nov. and *D. nyani* sp. nov.

Based on the results of the scree graph (not shown), only the first and second principal component (PC) were relevant for the further analysis of shape. The results of the shape PCA (Fig. 1A) of the two species show that they are separated by shape. The ratio spectrum (Fig. 1B) shows which ratios had the highest impact on the first shape PC. To confirm that these differences are based on true shape differences and not allometric size effects, the isometric size was plotted against the first shape PC (Fig. 2A). The species overlap in size but lie on different allometry axis, confirming that the separation is based on shape and not on allometry effects.

The LDA ratio extractor (Baur and Leuenberger 2020) found the best ratios to separate the two species: mss.l/sctl.l was the best ratio, clv.l/prn.l was the second best ratio (Fig. 3).

The allometry ratio spectrum (Fig. 2B) reveals the allometric variation of ratios. The characters of the best ratio (mss.l/sctl.l) lie close to each other, indicating no strong allometric effects. The characters of the second-best ratio (clv.l/prn.l) show a higher allometric effect than the first one but still not a considerable one. This confirms that the differences in these characters are based on shape and not on allometric effects.

The separating ratios were used for the diagnoses of the two species in the descriptions below.

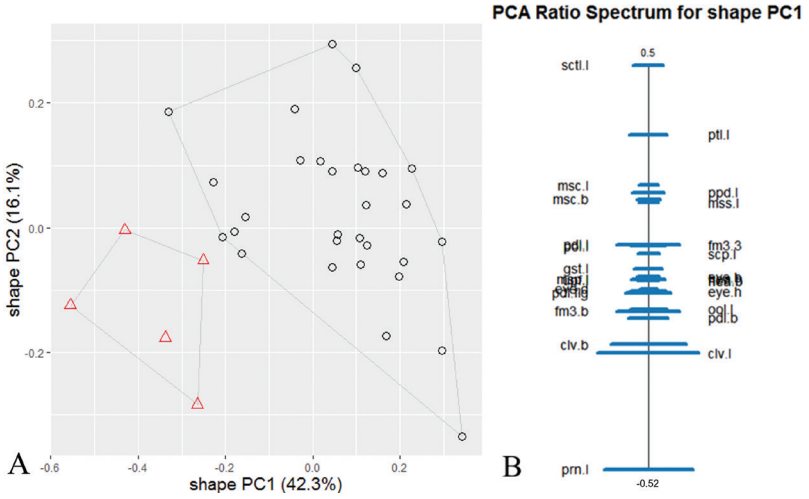

Figure 1. Shape analysis of *D. kakamegensis* sp. nov. (circles) and *D. nyani* sp. nov. (triangles) using the characters highlighted in bold in Table 1 **A** scatterplot of first against second shape PC **B** ratio spectrum of the first shape PC; horizontal bars represent 68% confidence intervals based on 1000 bootstrap replicates.

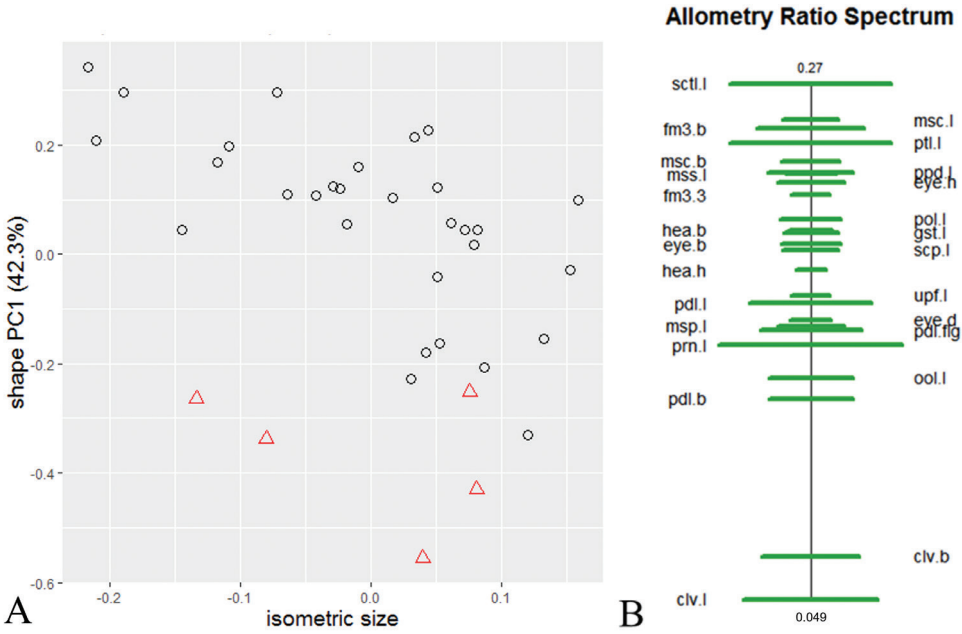

Figure 2. Allometry analysis of *D. kakamegensis* sp. nov. (circles) and *D. nyani* sp. nov. (triangles) **A** scatterplot of the isometric size against the first shape PC **B** allometry ratio spectrum; horizontal bars represent 68% confidence intervals based on 1000 bootstrap replicates.

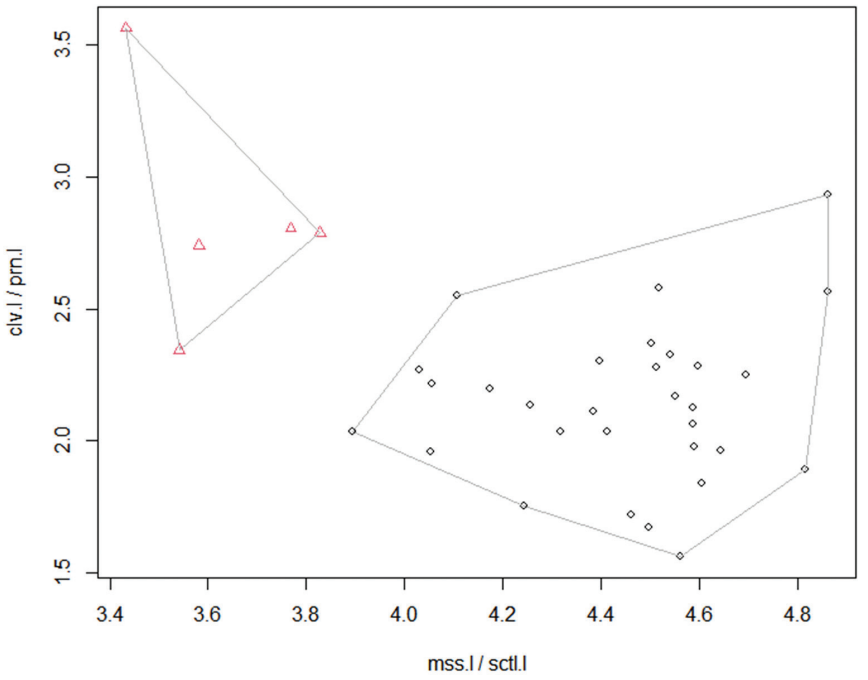

Figure 3. Scatterplot of mss.l/sctl.l against clv.l/prn.l, the ratios which separate the two species the best (based on the LDA ratio extractor); *D. kakamegensis* sp. nov. (circles) and *D. nyani* sp. nov. (triangles).

Posterior notal wing process

Examination of the posterior notal wing process (pnwp) in the newly described species showed that it was present and pointed in all cases. Figure 4 shows a selection of pnwps from species with different wing forms. The uniformity of this character can be interpreted as it either being unsuitable as a measure of potential wing size (see Desjardins 2007) or as indicating that all species, including the brachypterous ones, harbor also macropterous specimens. Accordingly, it proved little help in delimiting species, especially in the case of the very similar, but morphometrically discriminated macropterous *D. nyani* sp. nov. and brachypterous *D. kakamegensis* sp. nov. (see morphometric analysis above and taxonomic treatment below).

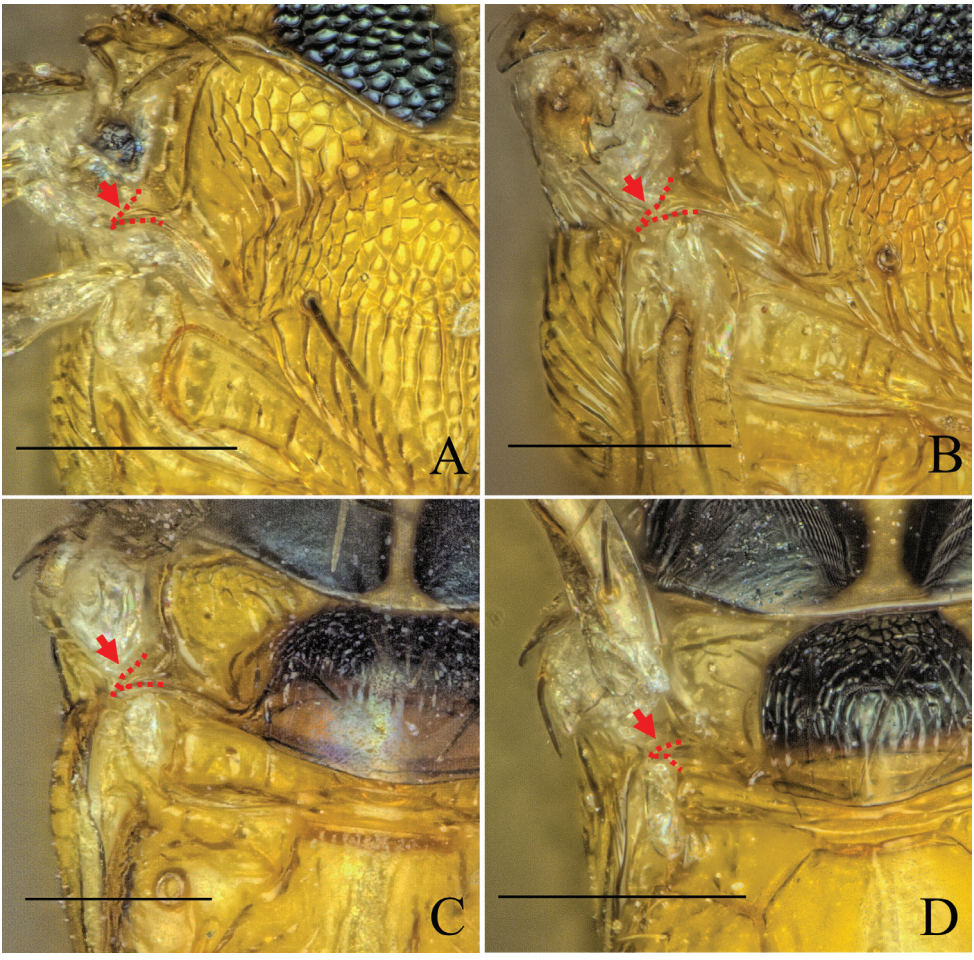

Figure 4. Dorsal view of a part of the mesosoma showing the posterior notal wing process (red) of **A** *D. nyani* sp. nov. (macropterous) **B** *D. kakamegensis* sp. nov. (brachypterous with medium sized wings), **C** *D. andreabalzerae* sp. nov. (brachypterous with medium sized wings) and **D** *D. nigroscutellata* sp. nov. (brachypterous with small wings). The former two are very similar but can be separated by morphometric analysis. Scale bar: 100 μm.

Taxonomic treatments

Dipara Walker, 1833 (modified from Desjardins 2007)

Dipara Walker 1833: 371, 373. Type species: *Dipara petiolata* Walker (by monotypy). Type locality: NHMUK.
Tricoryphus Förster 1856. Type Species: *Tricoryphus fasciatus* Thomson (by subsequent monotypy (Thomson 1876)). [Synonymized by Domenichini 1953]
Apterolelaps Ashmead 1901. Type Species: *Apterolelaps nigriceps* Ashmead (orig. desig. and by monotypy). [Synonymized by Graham 1969]
Alloterra Kieffer and Marshall 1904: 46–47. Type species: *Alloterra claviger* Kieffer and Marshall (by monotypy). [Synonymized by Desjardins 2007]
Trimicrops Kieffer 1906. Type Species: *Trimicrops claviger* Kieffer (by monotypy). [Synonymized by Desjardins 2007]
Parurios Girault 1913: 318. Type species: *Parurios australiana* Girault (by monotypy). [Synonymized by Desjardins 2007]
Epilelaps Girault 1915: 344. Type species *Epilelaps hyalinipennis* Girault (orig. desig.). [Synonymized by Bouček 1988]
Pseudipara Girault 1915: 345. Type species: *Pseudipara albiclava* Girault (orig. desig. and by monotypy). [Synonymized by Desjardins 2007]
Uriolelaps Girault 1915: 201. Type species: *Uriolelaps argenticoxae* Girault (orig. desig.). [Synonymized by Desjardins 2007]
Hispanolelaps Mercet 1927: 49–63. [Synonymized by Domenichini 1953]
Pseudiparella Girault 1927: 334–335. Type species *Pseudiparella emersoni* Girault (by monotypy). [Synonymized by Bouček 1988]
Emersonia Girault 1933: [1]. Type species: *Emersonia atriscutum* Girault (by monotypy). [Synonymized by Desjardins 2007]
Grahamisia Delucchi 1962: 379–380. Type species: *Grahamisia saetosa* Delucchi (orig. desig. and by monotypy). [Synonymized by Desjardins 2007]
Afrolelaps Hedqvist 1963: 47. Type species: *Afrolelaps maculata* Hedqvist (orig. desig.). [Synonymized by Desjardins 2007]
Pondia Hedqvist 1969: 197. Type species: *Pondia punctulata* Hedqvist (orig. desig.). [Synonymized by Desjardins 2007]
Diparomorpha Hedqvist 1971: 57–58. Type species: *Diparomorpha machadoi* Hedqvist (orig. desig. and by monotypy). [Synonymized by Desjardins 2007]

Diagnosis. Female (taken from Desjardins 2007). Absence of a median clypeal tooth; anellus broader than long; at most two pairs of mesoscutellar bristles; at least one pair of setae or bristles laterally on the petiole.

Remarks. The Diparinae genus key by Desjardins (2007) states that the petiole of females of the genus *Dipara* is usually less than 1.5× as long as wide. In the present study, seven out of twelve newly described species have a petiole length exceeding this, going up to being 2.8× as long as wide. Accordingly, the genus level key of Desjardins (2007) might be misleading. However, the diagnosis by

Desjardins (2007) uses other characters than the petiole length and can be kept unmodified (see above).

Key to the *Dipara* species from the Afrotropical mainland (females)

1 Notauli present (Figs 5–25) **2**
– Notauli absent ..... ***D. machadoi*** **(Hedqvist, 1971)**
2(1) Petiole with thicker and longer bristle anterio-laterally, reaching gt1 (Figs 20B, 21D) **3**
– Petiole with one or multiple thin and shorter setae laterally **4**
3(2) Vertex and propodeum smooth (Fig. 20) ..... ***D. pallida*** **(Hedqvist, 1969)**
– Vertex reticulate; propodeum subcarinate (Fig. 21) ..... ***D. punctulata*** **(Hedqvist, 1969)**
4(2) Head and mesosoma never completely black, usually dark brown or lighter, sometimes bright yellowish brown; if head and mesosoma partly dark brown to black, then pro- and metacoxa white (Fig. 17A) **5**
– Head and mesosoma black; coxae dark brown (Figs 18, 19) ..... ***D. nigrita*** **Hedqvist, 1969**
5(4) Face with one or two transverse dark brown to black stripes, reaching from one eye to the other, sometimes interrupted or fainter in interantennal and supraclypeal area (Figs 6B, 8B, 9B, 11B, 12B, 13B, 15B, 16B, 25B) **6**
– Face without distinct dark stripes, uniformly colored or sometimes with diffuse darker coloration (Figs 5B, 7B, 10B, 14B) **16**
6(5) Face with one transverse dark brown to black stripe, reaching from one eye to the other at the level of the ventral margin of the eyes (Figs 6B, 9B, 15B, 16B, 25B) **7**
– Face with two transverse dark brown to black stripes at the level of toruli and at the level of the ventral margin of the eyes, enclosing a stripe of brighter coloration (Figs 8B, 11B, 12B, 13B) **12**
7(6) Median and lateral area of mesoscutum with distinct transverse broad black stripe (Figs 6C, 25C) **8**
– Lateral areas of mesoscutum with two black spots (Figs 9C, 15C, 16C, 24C) **9**
8(7) Macropterous, fore wings reaching gt7; petiole distinctly longer than wide (Fig. 6C) ..... ***D. corona*** **sp. nov.**
– Brachypterous, fore wings reaching slightly beyond petiole; petiole slightly wider than long (Fig. 25C) ..... ***D. turneri*** **Hedqvist, 1969**
9(7) Petiole short, < 1.5× as long as wide (Figs 16D, 24C) **10**
– Petiole very long, > 2.5× as long as wide (Figs 9C, 15C) **11**
10(9) Propodeum medially reticulated between carinae (Fig. 16C); petiole with at least six pairs of small setae laterally (visible in dorsal view) (Fig. 16 D) ..... ***D. tigrina*** **sp. nov.**
– Propodeum without reticulation between carinae; petiole with three pairs of small setae laterally (visible in dorsal view) (Fig. 24C) ..... ***D. striata*** **(Hedqvist, 1969)**

11(9) Body brown to dark brown; vertex smooth (Fig. 15) ..... ***D. tenebra* sp. nov.**
– Body yellowish brown; vertex reticulate (Fig. 9) ..... ***D. lux* sp. nov.**
12(6) Gastral tergites smooth (Fig. 8C, 11C, 13C) **13**
– Gastral tergites reticulate (Fig. 12C) ..... ***D. reticulata* sp. nov.**
13(12) Lateral area of mesoscutum with two black spots; petiole long, < 2.1× as long as wide (Figs 8C, 11C) **14**
– Mesoscutum without distinct black coloration; petiole very long, 2.53–2.80× as long as wide (Fig. 13C) ..... ***D. rodneymulleni* sp. nov.**
14(13) Mesocoxa and petiole bright yellowish brown (Figs 8, 11) **15**
– Mesocoxa and petiole white ..... ***D. maculata* (Hedqvist, 1963)**
15(14) Brachypterous, fore wing reaching middle of gt1; mesoscutellum smaller, mesosoma length 3.90–4.86× mesoscutellum length (Fig. 8); petiole shorter, 1.15–1.72× as long as wide in dorsal view ..... ***D. kakamegensis* sp. nov.**
– Macropterous, fore wings reaching gt7; mesoscutellum larger, mesosoma length 3.43–3.83× mesoscutellum length (Fig. 11); petiole longer, 1.78–2.05× as long as wide in dorsal view ..... ***D. nyani* sp. nov.**
16(5) Mesoscutellum black (Figs 5C, 7C, 10C, 17B, 22C) **17**
– Mesoscutellum not black (14C, 23C) **21**
17(16) Propodeum medially smooth and laterally transversely carinate; gt1 without bristles (Figs 12C, 13C) **18**
– Propodeum completely smooth; gt1 with a pair of large bristles dorso-anteriorly (Figs 10C, 22C) **19**
18(17) Gaster brown to yellowish brown; anterior part of mesoscutellum and frenum forming an angle of 120–125° in lateral view (Fig. 5A) ..... ***D. andreabalzerae* sp. nov.**
– Gaster dark brown; anterior part of mesoscutellum and frenum forming an angle of 90° in lateral view (Fig. 7A) ..... ***D. fastigata* sp. nov.**
19(17) Body brown to dark brown; lateral area of mesoscutum completely black (Figs 17, 22) **20**
– Body yellowish brown to brown; lateral area of mesoscutum not completely black with small yellowish brown area on its most lateral part (Fig. 10C) ..... ***D. nigroscutellata* sp. nov.**
20(19) Vertex smooth; clava white; pro- and metacoxa white (Fig. 17) ..... ***D. albomaculata* (Hedqvist, 1963)**
– Vertex reticulate between ocelli, rest smooth; clava dark brown; pro- and metacoxa with proximal 1/3 brown and rest yellowish brown (Fig. 22) ..... ***D. saetosa* (Delucchi, 1962)**
21(16) Only slight metallic tint on black parts of the mesoscutum; lateral areas of mesoscutum with two black spots; gt1 with a pair of large bristles dorso-anteriorly (Fig. 23 C) ..... ***D. straminea* (Hedqvist, 1969)**
– Strong blue metallic tint on the following areas: vertex between ocelli, pronotum laterally, median area of mesoscutum posteriorly between notauli, lateral area of mesoscutum, mesoscutellum; lateral areas of mesoscutum without black spots; gt1 without a pair of large bristles dorso-anteriorly (Fig. 14C) ..... ***D. sapphirus* sp. nov.**

***Dipara andreabalzerae* sp. nov.**
http://zoobank.org/81FBA9DA-A6A7-4DF5-914C-64A27136D423
Fig. 5A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'22.9N, 34°51'21E; 1594 m a.s.l.; 24 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 12; ZFMK-HYM-00037130. ***Paratypes*** Kenya • 2 ♀; same data as for holotype; ZFMK-HYM-00037131 to ZFMK-HYM-00037132 • 1 ♀; Kakamega Forest, Kenya; 00°22'45N, 34°49'40.8E; 1618 m a.s.l.; 11 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 27; ZFMK-HYM-00037133 • 1 ♀; Kakamega Forest, Kenya; 00°18'13.4N, 34°48'16E; 1554 m a.s.l.; 20 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 5; ZFMK-HYM-00037134 • 1 ♀; Kakamega Forest, Kenya; 00°13'59.1N, 34°51'43.7E; 1614 m a.s.l.; 29 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 24; ZFMK-HYM-00037135 • 1 ♀; same locality as for holotype; 17 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 12; NHMUK013457232 • 1 ♀; Kakamega Forest, Kenya; 00°27'10.6N, 34°51'48.7E; 1676 m a.s.l.; 19 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 4; NHMUK013457233 • 1 ♀; Kakamega Forest, Kenya; 00°36'9.7N, 34°37'20.3E; 1513 m a.s.l.; 07 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 26; NMK: ZFMK-HYM-00037138 • 1 ♀; Kakamega Forest, Kenya; 00°33'17.9N, 34°40'55.9E; 1425 m a.s.l.; 20 Jun. 2008; Hita-Garcia, F. leg.; Winkler extraction; Transect 40; NMK: ZFMK-HYM-00037139.

Female (specimens used for morphometric measurements: ZFMK-HYM-00037130 to ZFMK-HYM-00037134).

Diagnosis. Body brown to yellowish brown (Fig. 5); mesoscutellum black, raised, anterior part of mesoscutellum and frenum forming an angle of 120–125° (122°) (specimens used for measurement: ZFMK-HYM-00037130, ZFMK-HYM-00037132 to ZFMK-HYM-00037134) in lateral view (Fig. 5A); propodeum medially smooth and laterally transversely carinate (Fig. 5C).

Description. ***Size*****:** small to medium sized, body length 1619–2183 (1809) μm.

Coloration**:** body brown to yellowish brown (Fig. 5); dorsal part of scape, pedicel, first funicular segment, and clava yellowish white, ventral part of scape white, other funicular segments uniformly brown (Fig. 5A); vertex with bluish metallic tint (Fig. 5C); pronotum laterally dark brown (Fig. 5C); lateral area of mesoscutum black (Fig. 5C); mesoscutellum black with metallic tint, frenum dark brown (Fig. 5C); coxa, trochanter and proximal quarter of femur white, rest of legs pale yellowish brown (Fig. 5A); gts lighter from gt1 to gt6 (Fig. 5C); gt7 with pale yellowish brown coloration on anterior 1/2 and brown coloration on posterior 1/2 (Fig. 5C); ovipositor sheath brown (Fig. 5A).

Head**:** head round, 1.26–1.31× (1.31) wider than high (Fig. 5B); vertex very sparsely foveolate and otherwise smooth (Fig. 5B); upper face strigate-reticulate (Fig. 5B); lower face reticulate, sparsely setose (Fig. 5B); distance of antennal insertion to eye short, 0.45–0.76× (0.45) (specimens used for measurement: ZFMK-HYM-00037130, ZFMK-HYM-00037132 to ZFMK-HYM-00037134) torulus diameter (Fig. 5B); antennae close, toruli separated by 0.84–1.07× (0.91) (specimens used for measurement:

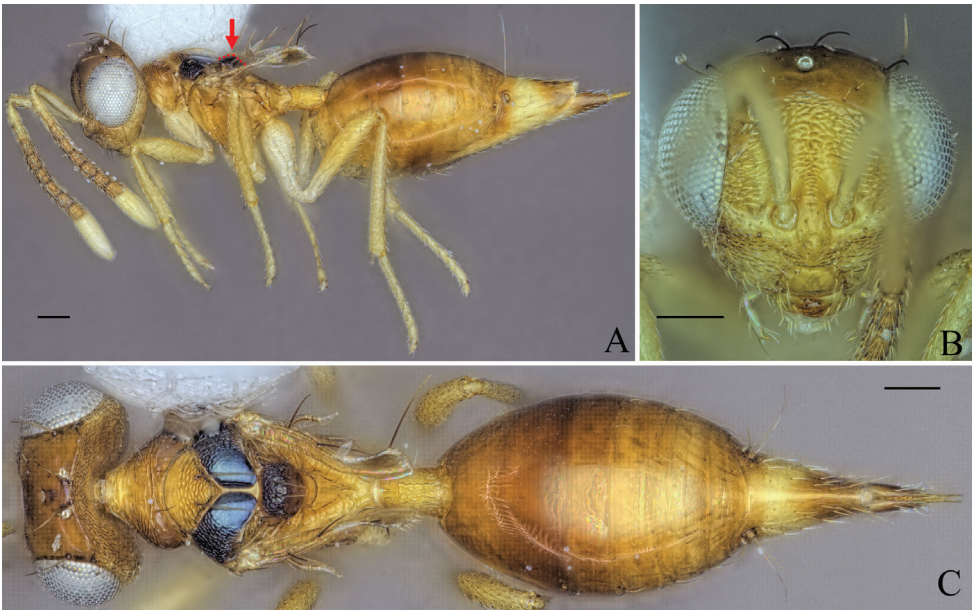

Figure 5. Holotype of *Dipara andreabalzerae* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view; red arrow: angle formed by anterior part of mesoscutellum and frenum. Scale bar: 100 μm.

ZFMK-HYM-00037130, ZFMK-HYM-00037132 to ZFMK-HYM-00037134) torulus diameter (Fig. 5B); antennal formula: 11173 (Fig. 5A); funicle segments ~ as long as wide (Fig. 5A); malar space 0.29–0.35× (0.33) eye height (Fig. 5A); POL 0.62–0.74× (0.72) OOL (Fig. 5C).

***Mesosoma*:** pronotum large and elongated, 1.99–2.14× (2.02) as wide as long, substrigate, with a pair of setae close to the posterior edge (Fig. 5C); mesosoma slender, head breadth 1.53–1.59× (1.56) mesoscutum breadth (Fig. 5C); notauli converging ca. at 1/2 the length of mesoscutum (Fig. 5C); median area of mesoscutum reticulate (Fig. 5C); lateral area medially smooth and laterally reticulate (Fig. 5C); mesoscutum with two pairs of bristles, one pair of very large bristles on median area just anterior of notauli, almost reaching the mesoscutellum, and one pair laterally on lateral area anterior of wing base (Fig. 5C); axillae reticulate (Fig. 5C); mesoscutellum reticulate-rugulose, raised, with two pairs of bristles, one pair anterio-medially and one pair laterally just anterior of frenal line, anterior part of mesoscutellum and frenum forming an angle of 120–125° (122°) (specimens used for measurement: ZFMK-HYM-00037130, ZFMK-HYM-00037132 to ZFMK-HYM-00037134) (Fig. 5A); propodeum medially smooth and laterally transversely carinate (Fig. 5C); nucha with a few longitudinal carinae (Fig. 5C); brachypterous, fore wing reaching middle of petiole, tip truncated, with two or three large brown bristles and one large black bristle at the tip, with infuscation at tip (Fig. 5A).

***Metasoma*:** petiole short, 1.25–1.44× (1.29) longer than wide in dorsal view, costate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 5C); gaster medium, 1.23–1.56× (1.56) longer than mesosoma in dorsal view (Fig. 5C); gt1 covering ~ 1/3 of gaster, gt2–4 ca. equal in size, gt5 and 6 much smaller (Fig. 5C); gt7 and ovipositor sheath sparsely setose (Fig. 5A).

Remarks. *Dipara andreabalzerae* is similar to *D. albomaculata*, *D. fastigata*, *D. nigroscutellata*, and *D. saetosa* in having a black mesoscutellum while the general body coloration is not black. *Dipara andreabalzerae* differs from *D. albomaculata*, *D. nigroscutellata* and *D. saetosa* in different propodeum sculpture. It differs from *D. fastigata* in body coloration, which is much darker in *D. fastigata* and the more obtuse angle formed by the anterior part of the mesoscutellum and the frenum in lateral view.

Male. Unknown.

Etymology. As the first author, I dedicate this species to my mother, Andrea Balzer, who sadly passed away in 2017.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara corona* sp. nov.**

http://zoobank.org/4FDFD9C7-64C0-47EA-97A6-7587DA5E1BD4

Fig. 6A–C

Material examined. *Holotype* Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 21 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; ZFMK-HYM-00040381.

Diagnosis. Female. Broad dark brown stripe across head from one eye to the other below toruli (Fig. 6B); median and lateral area of mesoscutum with distinct transverse broad black stripe (Fig. 6C); macropterous, fore wing reaching gt7 (Fig. 6A); petiole 1.20× longer than wide in dorsal view (Fig. 6C).

Description. *Size*: medium sized, body length 2346 µm.

***Coloration*:** body brown to orangish brown (Fig. 6); scape and pedicel yellowish brown, funicle segments dark brown, clava white (Fig. 6); broad dark brown stripe across head from one eye to the other below toruli (Fig. 6B); vertex between ocelli black with metallic tint (Fig. 6B); procoxa white, rest of the legs yellowish brown (Fig. 6A); median and lateral area of mesoscutum with distinct transverse broad black stripe (Fig. 6C); tip of ovipositor sheath dark brown (Fig. 6A).

***Head*:** head oval, 1.33× wider than high (Fig. 6B); upper face substrigate (Fig. 6B); lower face substrigate around dark brown stripe and smooth below, sparsely setose (Fig. 6B); antennal scrobe and interantennal area smooth (Fig. 6B); distance of antennal insertion to eye short, 0.49× torulus diameter (Fig. 6B); antennae close, toruli separated by 1.31× torulus diameter (Fig. 6B); antennal formula: 11173 (Fig. 6A); funicle

Figure 6. Holotype of *Dipara corona* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

segments getting continuously shorter: f1 longer than wide to f7 as wide as long (Fig. 6A); malar space 0.33× eye height (Fig. 6A); vertex rugose, between ocelli slightly raised (Fig. 6B); occipital margin forming sharp edge (Fig. 6A); POL 1.31× OOL (Fig. 6C).

***Mesosoma*:** pronotum of medium length, 3.01× wider than long, substrigate, with a pair of bristles medially close to the posterior edge (Fig. 6C); mesosoma robust, head breadth 1.12× mesoscutum breadth (Fig. 6C); notauli not converging (Fig. 6C); mesoscutum with median area substrigate, lateral area strigate-reticulate, with two pairs of bristles: one pair on posterior 1/3 of medium area between notauli reaching axillae, one pair laterally on lateral area anterior of wing base (Fig. 6C); axillae reticulate (Fig. 6C); mesoscutellum reticulate, frenum smooth, with two pairs of bristles: one pair anteriorly and one pair laterally on frenal line (Fig. 6C); macropterous, fore wing reaching gt7, with large bristles along submarginal vein and smaller bristles along marginal and postmarginal vein on edge, transparent, stigmal vein long, stigma thin, uncus thin and pointed (Fig. 6A); propodeum with some transverse and longitudinal carinae (Fig. 6C); nucha carinate (Fig. 6C).

***Metasoma*:** petiole short, 1.20× longer than wide in dorsal view, anterior quarter constricted and rugose, rest costate, with lateral pair of large white setae visible in dorsal view (Fig. 6C); gaster short, 1.07× longer than mesosoma in dorsal view (Fig. 6C); gt1 covering ~ 2/3 of gaster (Fig. 6C); gt7 and ovipositor sheath sparsely setose (Fig. 6C).

Remarks. *Dipara corona* is similar to *D. turneri* in having a distinct transverse broad black stripe on the median and lateral areas of the mesoscutum. In other not completely black species the black spots on the mesoscutum are restricted to the lateral area.

Dipara corona differs from *D. turneri* in the wing form and in the different petiole shape. The petiole is distinctly longer than wide in *D. corona* and slightly wider than long in *D. turneri*. Other differences include the body coloration, the shape of the mesoscutellum and the shape of the metacoxa.

Male. Unknown.

Etymology. Named after the Latin word *corona* for crown because of the raised and shiny part between the ocelli in frontal view, and additionally as a reference to the pandemic in 2020 and the following years caused by SARS-CoV-2, also known as the Corona virus.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara fastigata* sp. nov.**

http://zoobank.org/5AF8BF53-08A5-47DF-9B02-BADE13B8AC9E

Fig. 7A–C

Material examined. *Holotype* Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'6.1N, 34°52'9.2E; 1605 m a.s.l.; 28 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 23; ZFMK-HYM-00040382.

Diagnosis. Female. Body brown to dark brown (Fig. 7); mesoscutellum black, raised, anterior part of mesoscutellum and frenum forming an angle of 90° in lateral view (Fig. 7A); propodeum medially smooth and laterally transversely carinate (Fig. 7C).

Description. *Size*: small sized, body length 1946 µm.

***Coloration*:** body brown to dark brown (Fig. 7); upper face and vertex dark brown, lower face brown (Fig. 7B); scape dorsally dark brown and ventrally white, pedicel, f1, f2 and f3 yellowish brown, other funicle segments brown, clava white (Fig. 7A); fore leg with coxa white and rest yellowish brown (Fig. 7A); mid leg yellowish brown (Fig. 7A); hind leg with base of coxa, distal 1/2 of femur and distal tip of tibia yellowish brown, rest white (Fig. 7A); gt1–6 dark brown, posterior 1/2 of gt7 dorsally and ovipositor sheath brown, rest of gt7 pale yellowish white (Fig. 7A).

***Head*:** head round, 1.25× wider than high (Fig. 7B); vertex and upper 1/2 of upper face smooth, lower 1/2 laterally smooth and medially reticulate (Fig. 7B); lower face reticulate with smooth transverse stripe just below toruli from one eye to the other (Fig. 7B); upper 1/2 of upper face and lower face sparsely setose (Fig. 7B); antennal scrobe

reticulate (Fig. 7B); interantennal area smooth (Fig. 7B); distance of antennal insertion to eye long, 1.12× torulus diameter (Fig. 7B); antennae far apart, toruli separated by 1.48× torulus diameter (Fig. 7B); antennal formula: 11173 (Fig. 7A); shape of funicle segments changing: f1 longer than wide to f7 ca. as wide as long (Fig. 7A); malar space 0.33× eye height (Fig. 7A); POL 0.85× OOL (Fig. 7C).

***Mesosoma*:** pronotum large and elongated, 1.93× wider than long, with a transverse carina, anteriorly of carina substrigate and posteriorly smooth, with a pair of setae posterio-medially (Fig. 7C); mesosoma slender, head breadth 1.64× mesoscutum breadth (Fig. 7C); notauli converging ca. at 2/3 of the length of mesoscutum (Fig. 7C); mesoscutum with median area reticulate, lateral area laterally reticulate and medially smooth, with two pairs of bristles: one pair on median area, reaching mesoscutellum, one pair on lateral area anterior of wing base (Fig. 7C); axillae reticulate (Fig. 7C); mesoscutellum raised, reticulate-rugulose, with one pair of bristles medially anterior of frenal line, anterior part of mesoscutellum and frenum forming an angle of 90° in lateral view (Fig. 7A); brachypterous, fore wing reaching middle of petiole, with 4 large bristles on the edge, upper and lower 1/3 infuscate, middle part transparent, tip truncated (Fig. 7A); propodeum medially smooth and laterally transversely carinate (Fig. 7C); nucha carinate (Fig. 7C).

***Metasoma*:** petiole medium, 1.6× longer than wide in dorsal view, reticulate, with two pairs of setae laterally visible in dorsal view (Fig. 7C); gaster medium, 1.31× longer than mesosoma in dorsal view (Fig. 7C); gt1 covering ~ 1/3 of gaster, gt2 much larger than following gts; gt3–5 ca. equal in size, gt6 much smaller (Fig. 7C); gt7 and ovipositor sheath sparsely setose (Fig. 7A).

Remarks. *Dipara fastigata* is similar to *D. andreabalzerae*, *D. albomaculata*, *D. nigroscutellata* and *D. saetosa* in having a black mesoscutellum while the general body coloration is not black. *Dipara fastigata* differs from *D. albomaculata*, *D. nigroscutellata* and *D. saetosa* in different propodeum sculpture. It differs from *D. andreabalzerae* in general body coloration, which is much lighter in *D. andreabalzerae*, and the 90° angle formed by the anterior part of the mesoscutellum and the frenum in lateral view.

Male. Unknown.

Etymology. Named after the Latin adjective *fastigatus* for pointed or sharp. The name refers to the raised mesoscutellum.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara kakamegensis* sp. nov.**

http://zoobank.org/72E6846C-B5E8-424F-BDC3-0D223E05CDC1

Fig. 8A–C

Material examined. *Holotype* Kenya • 1 ♀; Kakamega Forest, Kenya; 00°21'4.9N, 34°51'41.1E; 1602 m a.s.l.; Hita-Garcia, F. leg.; Winkler extraction; Transect 1; ZFMK-HYM-00037140. ***Paratypes*** Kenya • 4 ♀; Kakamega Forest, Kenya;

Figure 7. Holotype of *Dipara fastigata* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view; red arrow: angle formed by anterior part of mesoscutellum and frenum. Scale bar: 100 μm.

00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 07 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00037141, ZFMK-HYM-00037198, ZFMK-HYM-00037199; NMK: ZFMK-HYM-00037200 • 4 ♀; Kakamega Forest, Kenya; 00°14'6.1N, 34°52'9.2E; 1605 m a.s.l.; 28 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 23; ZFMK-HYM-00037142, ZFMK-HYM-00037241 to ZFMK-HYM-00037243 • 6 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 07 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00037143, ZFMK-HYM-00037146, ZFMK-HYM-00037170, ZFMK-HYM-00037204 to ZFMK-HYM-00037206 • 1 ♀; Kakamega Forest, Kenya; 00°27'0.9N, 34°50'52.9E; 1649 m a.s.l.; 03 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 8; ZFMK-HYM-00037144 • 1 ♀; Kakamega Forest, Kenya; 00°37'24.1N, 34°51'12E; 1585 m a.s.l.; 08 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 10; ZFMK-HYM-00037145 • 8 ♀; Kakamega Forest, Kenya; 00°14'20.5N, 34°51'52.8E; 1634 m a.s.l.; 10 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 17; ZFMK-HYM-00037147, ZFMK-HYM-00037156, ZFMK-HYM-00037158, ZFMK-HYM-00037159, ZFMK-HYM-00037229 to ZFMK-HYM-00037232 • 4 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 09 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00037148, ZFMK-HYM-00037151, ZFMK-HYM-00037154, ZFMK-

HYM-00037193 • 7 ♀; Kakamega Forest, Kenya; 00°14'20.5N, 34°51'52.8E; 1634 m a.s.l.; 04 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 17; ZFMK-HYM-00037149, ZFMK-HYM-00037164, ZFMK-HYM-00037233 to ZFMK-HYM-00037237 • 7 ♀; same data as for holotype; ZFMK-HYM-00037150, ZFMK-HYM-00037212 to ZFMK-HYM-00037217 • 9 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 14 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; ZFMK-HYM-00037152, ZFMK-HYM-00037157, ZFMK-HYM-00037162, ZFMK-HYM-00037165, ZFMK-HYM-00037173 to ZFMK-HYM-00037175; NHMUK013457217, NHMUK013457218 • 1 ♀; Kakamega Forest, Kenya; 00°19'36N, 34°52'14.6E; 1570 m a.s.l.; 21 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 6; ZFMK-HYM-00037153 • 7 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 02 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00037155, ZFMK-HYM-00037167, ZFMK-HYM-00037223 to ZFMK-HYM-00037227 • 2 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 24 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; ZFMK-HYM-00037160, ZFMK-HYM-00037244 • 4 ♀; Kakamega Forest, Kenya; 00°20'52.5N, 34°51'53E; 1592 m a.s.l.; 06 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 25; ZFMK-HYM-00037161, ZFMK-HYM-00037218 to ZFMK-HYM-00037220 • 5 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00037163, ZFMK-HYM-00037166; NHMUK013457219 to NHMUK013457221 • 4 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 23 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; ZFMK-HYM-00037168, ZFMK-HYM-00037188, ZFMK-HYM-00037190; NMK: ZFMK-HYM-00037189 • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 17 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; ZFMK-HYM-00037169 • 3 ♀; Kakamega Forest, Kenya; 00°14'6.1N, 34°52'9.2E; 1605 m a.s.l.; 04 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 23; ZFMK-HYM-00037179 to ZFMK-HYM-00037181 • 4 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 21 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; ZFMK-HYM-00037182 to ZFMK-HYM-00037185 • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 07 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; ZFMK-HYM-00037186 • 1 ♀; Kakamega Forest, Kenya; 00°22'50.5N, 34°49'21.4E; 1623 m a.s.l.; 22 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 19; ZFMK-HYM-00037187 • 4 ♀; Kakamega Forest, Kenya; 00°19'36N, 34°52'14.6E; 1570 m a.s.l.; 28 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 6; ZFMK-HYM-00037194, ZFMK-HYM-00037195; NMK: ZFMK-HYM-00037196, ZFMK-HYM-00037197 • 3 ♀; Kakamega Forest, Kenya; 00°12'42.6N, 34°55'52.3E; 1615 m a.s.l.; 16 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 20; ZFMK-HYM-00037202, ZFMK-HYM-00037203; NMK: ZFMK-HYM-00037201 • 5 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 05 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction;

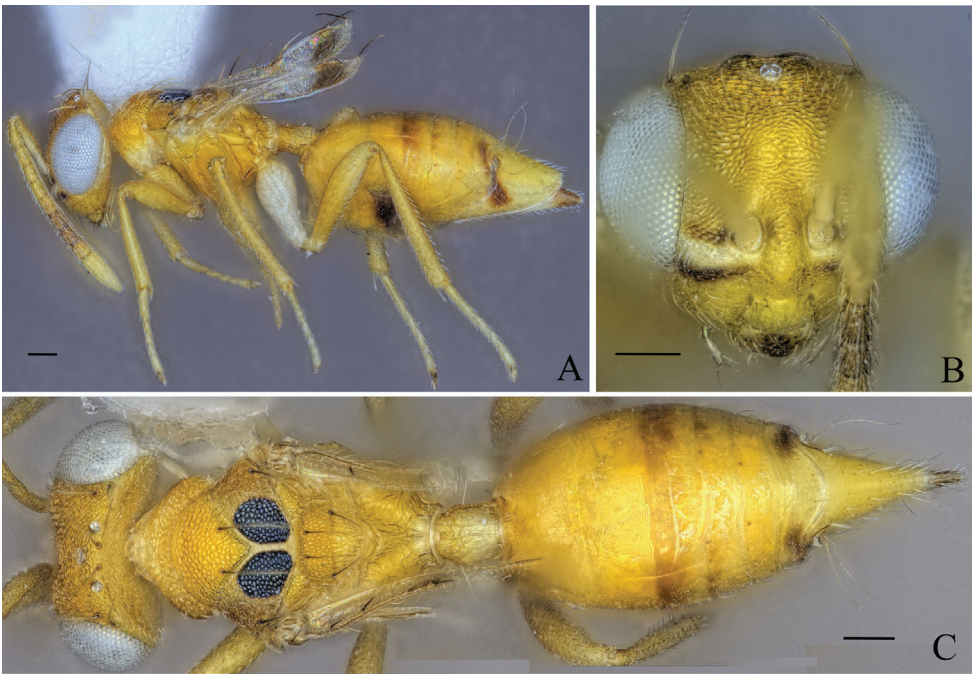

Figure 8. Holotype of *Dipara kakamegensis* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

Transect 2; ZFMK-HYM-00037207 to ZFMK-HYM-00037211 • 1 ♀; Kakamega Forest, Kenya; 00°14'22.9N, 34°51'21E; 1594 m a.s.l.; 17 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 12; ZFMK-HYM-00037221 • 1 ♀; Kakamega Forest, Kenya; 00°37'24.1N, 34°51'12E; 1585 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 10; ZFMK-HYM-00037228 • 3 ♀; Kakamega Forest, Kenya; 00°21'21.1N, 34°51'44.9E; 1632 m a.s.l.; 08 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 16; ZFMK-HYM-00037238 to ZFMK-HYM-00037240 • 3 ♀; Kakamega Forest, Kenya; 00°20'52.5N, 34°51'53E; 1592 m a.s.l.; 13 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 25; ZFMK-HYM-00037245 to ZFMK-HYM-00037247.

Female (specimens used for morphometric measurements: ZFMK-HYM-00037140 to ZFMK-HYM-00037144).

Diagnosis. Body bright yellowish brown (Fig. 8); face with two transverse stripes of very dark brown coloration just at the level of toruli and at the level of the ventral margin of the eye, interrupted in interantennal area and supraclypeal area, enclosing a stripe of pale white coloration (Fig. 8B); legs yellowish brown except for metacoxa white (Fig. 8A); brachypterous, fore wing reaching middle of gt1 (Fig. 8A); mesoscutellum small, mesosoma length 3.90–4.86× (4.86) (Fig. 8C) (specimens used for measurement: ZFMK-HYM-00037140 to ZFMK-HYM-00037170) mesoscutellum length; petiole short to medium, 1.15–1.72× (1.15) as long as wide in dorsal view.

Description. ***Size*****:** small to medium sized, body length 1483–2227 (2027) µm.

Coloration**:** body bright yellowish brown (Fig. 8); ventral part of scape and clava pale yellowish white, dorsal part of scape and last three funicle segments brown, rest of funicle segments and pedicel yellowish brown (Fig. 8A); face with two transverse dark brown stripes just at the level of toruli and at the level of the ventral margin of the eye, interrupted in interantennal area and supraclypeal area, enclosing a stripe of pale white coloration (Fig. 8B); two black spots medially on lateral areas of mesoscutum (Fig. 8C); middle part and tip of the fore wing infuscate (Fig. 8A); legs yellowish brown except for metacoxa white (Fig. 8A); nucha and posterior 2/3 of petiole pale yellowish white, rest of petiole bright yellowish brown (Fig. 8C); some darker brown stripes dorsally on gaster (Fig. 8A); brown spots on gt6 and gt7 around cerci (Fig. 8A); tip of ovipositor sheath brown (Fig. 8A).

Head**:** head round to oval, 1.25–1.63× (1.63) wider than high (Fig. 8B); vertex, upper face and interantennal area reticulate, antennal scrobe subreticulate, lower face smooth and sparsely setose (Fig. 8B); distance of antennal insertion to eye short, 0.78–0.97× (0.78) torulus diameter (Fig. 8B); antennae close, toruli separated by 1.15–1.31× (1.31) torulus diameter (Fig. 8B); antennal formula: 11173 (Fig. 8A); funicle segments slightly longer than wide (Fig. 8A); malar space 0.30–0.37× (0.30) eye height; occipital carina forming a sharp edge (Fig. 8A); POL 1.21–1.41× (1.38) OOL (Fig. 8C).

Mesosoma**:** pronotum of medium length, 2.85–3.37× (3.37) as wide as long (Fig. 8C); mesosoma of medium breadth, head breadth 1.24–1.45× (1.36) mesoscutum breadth (Fig. 8C); pronotum, mesoscutum, axillae and mesoscutellum reticulate (Fig. 8C); notauli converging ca. at 2/3 of the length of mesoscutum (Fig. 8C); mesoscutum with two pairs of bristles: one pair of very large bristles on median area just anterior of notauli, reaching posterior edge of mesoscutum and one pair laterally on lateral area anterior of wing base (Fig. 8C); mesoscutellum small, mesosoma length 3.90–4.86× (4.86) (specimens used for measurement: ZFMK-HYM-00037140 to ZFMK-HYM-00037170) mesoscutellum length, with two pairs of bristles: one pair medially close to anterior edge of mesoscutellum and one pair laterally on the frenal line (Fig. 8C); propodeum medially rugose and laterally transversely carinate-rugose, extending to nucha (Fig. 8C); brachypterous, fore wing reaching middle of gt1, with five large black bristles along the edge and one to ten bristles on the tip (Fig. 8A) (holotype: seven).

Metasoma**:** petiole short to medium, 1.15–1.72× (1.15) as long as wide in dorsal view, reticulate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 8C); gaster medium, 1.21–1.47× (1.47) longer than mesosoma in dorsal view (Fig. 8C); gt1 covering ~ 1/3 of gaster, gt2–4 ca. equal in size, gt5 and 6 much smaller (Fig. 8C); gt7 and ovipositor sheath sparsely setose (Fig. 8A).

Variations. The bristles on the forewing can vary from five to 15. This variation is found in the bristles at the tip of the wing while along the edges there are constantly five bristles. In some specimens there are just a few larger bristles at the tip and in others there can be up to ten small bristles at the tip. The number of bristles can vary between left and right wing in one specimen. The surface sculpture of the median part of the propodeum can vary from rugose to smooth.

Remarks. *Dipara kakamegensis* is very similar to *D. nyani*. It differs from *D. nyani* in the following characters: *D. kakamegensis* is brachypterous and the mesoscutellum is smaller relative to the mesosoma length, based on the morphometric analysis (Fig. 3). The stripes across the face are similar in *D. maculata*, *D. reticulata* and *D. rodneymulleni*. *Dipara kakamegensis* differs from *D. maculata* in having a yellowish brown mesocoxa and petiole. *Dipara kakamegensis* differs from *D. rodneymulleni* in many characters: *D. kakamegensis* is brachypterous, the body coloration, the length of the petiole and general body shape. *Dipara kakamegensis* differs from *D. reticulata* in having smooth gastral tergites while they are reticulated in *D. reticulata*.

Male. Unknown.

Etymology. Named after the collecting locality.

Biology. ***Habitat*:** Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara lux* sp. nov.**

http://zoobank.org/0B638A88-80E4-4462-A215-9EE691A78A37

Fig. 9A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°18'13.4N, 34°48'16E; 1554 m a.s.l.; 20 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 5; ZFMK-HYM-00040379. ***Paratype*** Kenya • 1 ♀; same data as for holotype; ZFMK-HYM-00040380.

Diagnosis. Female. Body yellowish brown (Fig. 9); face with dark brown to black stripe from one eye to the other at the level of the ventral margin of the eye (Fig. 9B); vertex reticulate (Fig. 9B); petiole very long, 2.50–2.61× (2.50) longer than wide in dorsal view (Fig. 9C).

Description. ***Size*:** medium sized, body length 2243–2772 (2772) µm.

***Coloration*:** body yellowish brown (Fig. 9); scape, pedicel and f1–3 yellowish brown, f4 yellowish brown to dark brown, f5–7 dark brown, clava yellowish brown (Fig. 9A); face with dark brown to black stripe from one eye to the other at the level of the ventral margin of the eye (Fig. 9B); mesoscutum with two black spots medially on lateral area (Fig. 9C); fore leg with distal tip of coxa brown and rest of coxa white, trochanter brown, rest yellowish brown (Fig. 9A); mid leg with coxa and trochanter white, rest yellowish brown (Fig. 9A); hind leg with anterior part of coxa white and posterior part dark brown, anterior part of femur white, rest yellowish brown (Fig. 9A); gt6 and gt7 with dark brown spots around cerci (Fig. 9A); posterior tip of gt7 dark brown (Fig. 9A); tip of ovipositor sheath dark brown, rest white (Fig. 9A).

***Head*:** head oval, 1.31–1.34× (1.34) wider than high, reticulate except for interantennal area smooth (Fig. 9B); lower face sparsely setose (Fig. 9B); distance of antennal insertion to eye short, 0.55–0.60× (0.55) torulus diameter (Fig. 9B); antennae close, toruli separated by 1.13–1.24× (1.13) torulus diameter (Fig. 9B); funicle segments

slightly longer than wide (Fig. 9A); malar space 0.34–0.38× (0.34) eye height (Fig. 9A); POL 0.92–1.00× (1.00) OOL (Fig. 9A).

***Mesosoma*:** pronotum of medium length, 3.28–3.37× (3.37) as wide as long, reticulate, with two pairs of setae close to posterior edge (Fig. 9C); mesosoma robust, head breadth 1.16–1.19× (1.16) mesoscutum breadth (Fig. 9C); notauli converging at posterior margin of mesoscutum (Fig. 9C); mesoscutum reticulate, with two pairs of bristles: one pair on median area anterior of notauli, one pair laterally on lateral area anterior of wing base (Fig. 9C); axillae reticulate (Fig. 9C); mesoscutellum anteriorly reticulate, frenum carinate, with two pairs of bristles: one pair anterio-medially and one pair laterally anterior of frenal line (Fig. 9C); macropterous, fore wing with large bristles along marginal and postmarginal vein on edge, with dense brush of setae at proximal end of marginal vein, with large area of infuscation on distal part and smaller areas of infuscation medially, stigmal vein long, stigma small and rounded, uncus short (Fig. 9A); propodeum medially smooth and laterally transversely confused carinate (Fig. 9C); nucha carinate (Fig. 9C).

***Metasoma*:** petiole very long, 2.50–2.61× (2.50) longer than wide in dorsal view, areolate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 9C); gaster medium, 1.34–1.37× (1.34) longer than mesosoma in dorsal view; gt1 covering ~ 1/3 of gaster, gt2–4 ca. equal in size, gt5–6 smaller (Fig. 9C); gt7 and ovipositor sheath sparsely setose and elongated, together ~ 1/2 as long as rest of gaster (Fig. 9C).

Remarks. *Dipara lux* is similar to *D. corona*, *D. machadoi*, *D. striata*, *D. tenebra*, *D. tigrina* and *D. turneri* in having one dark brown to black stripe across the face. *Dipara lux* is different from *D. machadoi* in having distinct notauli, which are lacking in *D. machadoi*. It differs from *D. corona*, *D. striata*, *D. turneri* and *D. tigrina* in having a very long petiole. *Dipara lux* and *D. tenebra* are very similar in body shape and differ in their body coloration which is much brighter in *D. lux* and in the surface sculpture of the head. They share the otherwise unique character of having a dense brush of setae close to the proximal end of the marginal vein on the fore wing.

Male. Unknown.

Etymology. Named after the Latin word *lux* for light, in contrast to *D. tenebra* which looks very similar but has a darker coloration.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara nigroscutellata* sp. nov.**

http://zoobank.org/8CEE0099-F1CB-4CC4-B9FC-DFC523A6B639

Fig. 10A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 07 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00037253. ***Paratypes*** Kenya • 5 ♀; Kakamega Forest, Kenya;

Figure 9. Holotype of *Dipara lux* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

00°21'21.1N, 34°51'44.9E; 1632 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 16; ZFMK-HYM-00037254; NMK: ZFMK-HYM-00040266 to ZFMK-HYM-00040269 • 4 ♀; Kakamega Forest, Kenya; 00°20'52.5N, 34°51'53E; 1592 m a.s.l.; 06 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 25; ZFMK-HYM-00037255, ZFMK-HYM-00040257, ZFMK-HYM-00040279, ZFMK-HYM-00040280 • 2 ♀; Kakamega Forest, Kenya; 00°27'10.6N, 34°51'48.7E; 1676 m a.s.l.; 19 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 4; ZFMK-HYM-00037256, ZFMK-HYM-00040309 • 1 ♀; Kakamega Forest, Kenya; 00°21'21.1N, 34°51'44.9E; 1632 m a.s.l.; 08 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 16; NHMUK013457222 • 1 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 25 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; NHMUK013457223 • 1 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 14 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; NHMUK013457224 • 1 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 23 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; NHMUK013457225 • 2 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 24 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; NHMUK013457226; ZFMK-HYM-00040263 • 1 ♀; Kakamega Forest, Kenya; 00°23'6.2N, 34°33'37.8E; 1602 m a.s.l.; 16 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 11; ZFMK-HYM-00040264 • 1 ♀; Kakamega

Forest, Kenya; 00°14'20.5N, 34°51'52.8E; 1634 m a.s.l.; 04 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 17; ZFMK-HYM-00040265 • 1 ♀; Kakamega Forest, Kenya; 00°12'42.6N, 34°55'52.3E; 1615 m a.s.l.; 10 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 20; NMK: ZFMK-HYM-00040270 • 9 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 05 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00040271 to ZFMK-HYM-00040275, ZFMK-HYM-00040301 to ZFMK-HYM-00040304 • 1 ♀; Kakamega Forest, Kenya; 00°21'4.9N, 34°51'41.1E; 1602 m a.s.l.; Hita-Garcia, F. leg.; Winkler extraction; Transect 1; ZFMK-HYM-00040276 • 2 ♀; Kakamega Forest, Kenya; 00°14'6.1N, 34°52'9.2E; 1605 m a.s.l.; 04 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 23; ZFMK-HYM-00040277, ZFMK-HYM-00040278 • 1 ♀; Kakamega Forest, Kenya; 00°27'0.9N, 34°50'52.9E; 1649 m a.s.l.; 10 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 8; ZFMK-HYM-00040281 • 3 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 02 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00040282, ZFMK-HYM-00040299, ZFMK-HYM-00040300 • 1 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 21 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; ZFMK-HYM-00040283 • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 07 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; ZFMK-HYM-00040284 • 4 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 09 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00040285 to ZFMK-HYM-00040288 • 10 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 07 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00040289 to ZFMK-HYM-00040298 • 2 ♀; Kakamega Forest, Kenya; 00°14'20.5N, 34°51'52.8E; 1634 m a.s.l.; 10 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 17; ZFMK-HYM-00040305, ZFMK-HYM-00040306 • 1 ♀; Kakamega Forest, Kenya; 00°22'45N, 34°49'40.8E; 1618 m a.s.l.; 11 Sep. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 27; ZFMK-HYM-00040307 • 1 ♀; Kakamega Forest, Kenya; 00°19'36N, 34°52'14.6E; 1570 m a.s.l.; 21 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 6; ZFMK-HYM-00040308 • 15 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 07 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00040310 to ZFMK-HYM-00040324 • 14 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00040325 to ZFMK-HYM-00040338.

Female (specimens used for morphometric measurements: ZFMK-HYM-00037253 to ZFMK-HYM-00037256, ZFMK-HYM-00040257).

Diagnosis. Body yellowish brown to brown (Fig. 10); lateral area of mesoscutum almost completely black, small area laterally yellowish brown (Fig. 10C); mesoscutellum black (Fig. 10C); gt1 with a pair of large bristles dorso-anteriorly (Fig. 10A and C).

Description. ***Size*****:** small sized, body length 1653–2015 (1815) µm.

Coloration**:** body yellowish brown to brown (Fig. 10); face yellowish brown and vertex brown (Fig. 10B); scape, pedicel and f1 yellowish brown, f2–7 brown, clava pale yellowish brown (Fig. 10A); lateral area of mesoscutum almost completely black, small area laterally yellowish brown (Fig. 10C); axillae white (Fig. 10C); fore leg with coxa

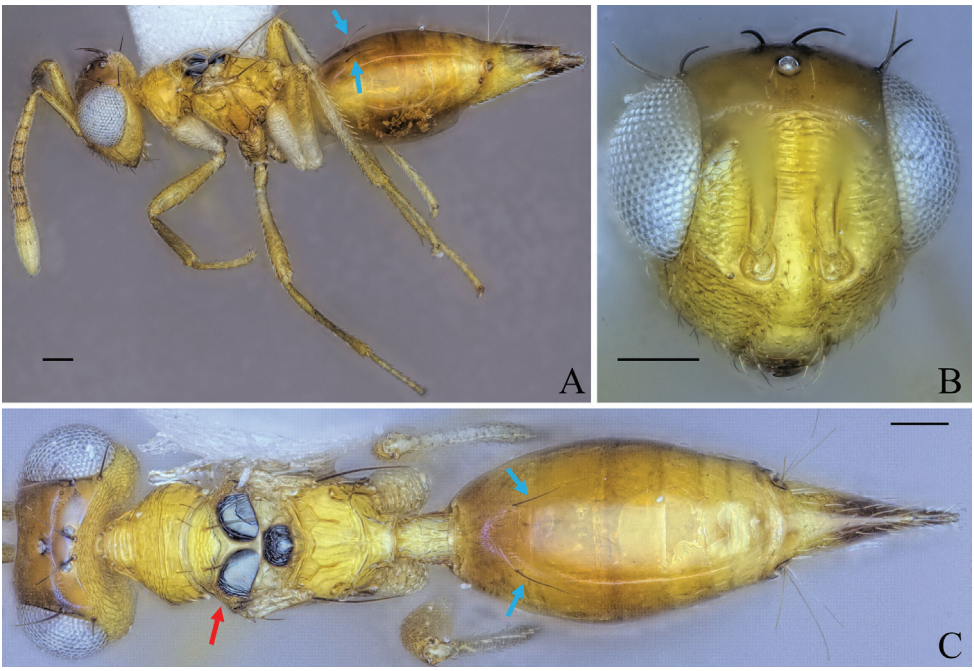

Figure 10. Holotype of *Dipara nigroscutellata* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view; red arrow: yellowish brown area on lateral area of mesoscutum; blue arrows: bristles on gt1. Scale bar: 100 μm.

white and rest yellowish brown (Fig. 10A); mid leg with proximal 1/3 of femur white, distal 1/2 of tibia brown, rest yellowish brown (Fig. 10A); hind leg with coxa, proximal 1/2 of femur and proximal 1/2 of tibia white, rest yellowish brown (Fig. 10A); color gradient on gaster, from brown (gt1) to yellowish brown (gt7) (Fig. 10C); posterior 1/2 of gt7 and tip of ovipositor sheath dark brown, rest of gt7 yellowish brown (Fig. 10A).

***Head*:** head round, 1.19–1.26× (1.21) wider than high (Fig. 10B); upper and lower face reticulate, lower face sparsely setose (Fig. 10B); vertex and interantennal area smooth (Fig. 10B); antennal scrobe strigate-reticulate (Fig. 10B); insertion point of antenna same level as ventral margin of eye (Fig. 10B); antennae close, toruli separated by 1.03–1.19× (1.04) torulus diameter (Fig. 10B); antennal formula: 11173 (Fig. 10A); funicle segments ca. as long as wide (Fig. 10A); malar space 0.37–0.40× (0.40) eye height (Fig. 10A); POL 0.60–0.94× (0.60) OOL (Fig. 10C).

***Mesosoma*:** pronotum large and elongated, 1.48–1.65× (1.48) as wide as long, strigate, with two or three pairs of setae laterally close to the posterior edge (Fig. 10C); mesosoma slender, head breadth 1.64–1.71× (1.65) mesoscutum breadth (Fig. 10C); notauli converging ca. at 1/2 the length of mesoscutum (Fig. 10C); median area of mesoscutum strigate-reticulate, black spots on lateral area mostly smooth except for lateral edges carinate-reticulate, lateral area laterally reticulate (Fig. 10C); mesoscutum with two pairs of bristles: one pair on median area, reaching posterior edge of mesoscutum, one pair laterally on lateral area anterior of wing base (Fig. 10C); axillae mostly smooth with

some confused ridges (Fig. 10C); mesoscutellum and black spots on lateral area slightly raised (Fig. 10A); mesoscutellum reticulate-rugulose with two pairs of bristles: one pair medially and one small pair posterio-laterally (Fig. 10C); brachypterous, fore wing very small, reaching propodeum, with a large black bristle at the tip (Fig. 10A); propodeum completely smooth (Fig. 10C); nucha smooth with a few longitudinal carinae (Fig. 10C).

***Metasoma*:** petiole short, 0.98–1.16× (1.06) as long as wide, costate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 10C); gt1 with a pair of large bristles dorso-anteriorly (Fig. 10A and C); gaster medium, 1.53–1.75× (1.59) longer than mesosoma in dorsal view (Fig. 10C); gt1 covering ~ 1/3 of gaster, gts smaller from gt2 to gt6 (Fig. 10C); gt7 and ovipositor sheath sparsely setose (Fig. 10A).

Variation. The bristles on the gt1 and the tip of the forewing can sometimes be missing. In this case the pit where the bristles are supposed to be is still visible.

Remarks. *Dipara nigroscutellata* is similar to *D. andreabalzerae*, *D. albomaculata*, *D. fastigata*, and *D. saetosa* in having a black mesoscutellum while the general body coloration is not black. *Dipara nigroscutellata* differs from *D. andreabalzerae* and *D. fastigata* in having a pair of large bristles dorso-anteriorly on the gt1. It differs from *D. albomaculata* and *D. saetosa* in the general body coloration, which is much brighter in *D. nigroscutellata* and in the coloration of the lateral area of the mesoscutum. In *D. nigroscutellata* the lateral area is laterally yellowish brown and in *D. albomaculata* and *D. saetosa* the lateral area is completely black.

Dipara nigroscutellata is similar to *D. straminea* in sharing the bristles on the gt1 and in propodeum sculpture. It differs from *D. straminea* in having a black mesoscutellum.

Male. Unknown.

Etymology. Named after the black mesoscutellum.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara nyani* sp. nov.**

http://zoobank.org/3290D412-E90C-4638-872F-F6CD6D8290CA

Fig. 11A–C

Material examined. *Holotype* Kenya • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 17 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; ZFMK-HYM-00037248. ***Paratypes*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°21'21.1N, 34°51'44.9E; 1632 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 16; ZFMK-HYM-00037249 • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 24 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; NHMUK013457234 • 1 ♀; Kakamega Forest, Kenya; 00°19'45.7N, 34°52'2.8E; 1573 m a.s.l.; 17 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 21; NMK: ZFMK-HYM-00037251 • 1 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 23 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; ZFMK-HYM-00037252.

Diagnosis. Female. Body bright yellowish brown (Fig. 11A); face with two transverse stripes of dark brown coloration just at the level of toruli and at the level of the ventral margin of the eye, interrupted in interantennal area and supraclypeal area enclosing a stripe of pale white coloration (Fig. 11B); legs yellowish brown except for metacoxa white (Fig. 11A); macropterous, fore wing reaching gt7 (Fig. 11A); mesoscutellum large, mesosoma length 3.43–3.83× (3.43) mesoscutellum length (Fig. 11C); petiole medium to long, 1.78–2.05× (2.02) (specimens used for measurement: ZFMK-HYM-00037248, ZFMK-HYM-00037249, ZFMK-HYM-00037252, NHMUK013457234) as long as wide in dorsal view.

Description. ***Size*****:** small to medium sized, body length 1696–2064 (2037) μm (specimens used for measurement: ZFMK-HYM-00037248, ZFMK-HYM-00037249, ZFMK-HYM-00037251, NHMUK013457234).

Coloration**:** body bright yellowish brown (Fig. 11A); scape ventrally yellowish white, dorsally brown, pedicel and f1–4 yellowish brown, f5–7 brown, clava pale yellowish white (Fig. 11A); face with two transverse stripes of dark brown coloration just at the level of toruli and at the level of the ventral margin of the eye, interrupted in interantennal area and supraclypeal area enclosing a stripe of pale white coloration (Fig. 11B); mesoscutum with pair of black spots medially on lateral area (Fig. 11C); two infuscate spots at the upper edge of the fore wing, one at 1/3 of the length and the other one in the middle (Fig. 11A); legs yellowish brown except for metacoxa white (Fig. 11A); gt6 and gt7 with brown spots around cerci (Fig. 11A); tip of ovipositor sheath brown (Fig. 11A).

Head**:** head round, 1.25–1.30× (1.30) wider than high (Fig. 11B); head except for lower face subreticulate (Fig. 11B); upper face laterally sparsely setose (Fig. 11B); lower face smooth and sparsely setose (Fig. 11B); distance of antennal insertion to eye short, 0.51–0.94× (0.94) torulus diameter (Fig. 11B); antennae close, toruli separated by 1.12–1.28× (1.28) torulus diameter (Fig. 11B); antennal formula: 11173 (Fig. 11A); shape of funicle segments changing: from f1 longer than wide to f7 ca. as long as wide (Fig. 11A); malar space 0.33–0.39× (0.33) eye height (Fig. 11A); POL 1.24–1.41× (1.38) OOL (Fig. 11C).

Mesosoma**:** pronotum short and slim, 3.84–5.79× (5.79) as wide as long, reticulate (Fig. 11C); mesosoma robust to of medium breadth, head breadth 1.16–1.33× (1.23) mesoscutum breadth (Fig. 11C); mesonotum completely reticulate (Fig. 11C); mesoscutum with two pairs of bristles: one pair on median area anterior of notauli, reaching posterior edge of mesoscutum, one pair laterally on lateral area anterior of wing base (Fig. 11C); notauli converging slightly anterior of posterior margin of mesoscutum (Fig. 11C); mesoscutellum with two pairs of bristles: one pair anterio-medially and one pair laterally on frenal line (Fig. 11C); macropterous, fore wing reaching gt7, with large bristles along submarginal vein and smaller bristles along marginal and postmarginal vein on edge, stigmal vein very short, stigma rounded, uncus short and pointed (Fig. 11A); propodeum medially smooth, laterally transversely carinate to carinate on nucha (Fig. 11C).

Metasoma**:** petiole medium to long, 1.78–2.05× (2.02) (specimens used for measurement: ZFMK-HYM-00037248, ZFMK-HYM-00037249, ZFMK-HYM-00037252, NHMUK013457234) as long as wide in dorsal view, costate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 11C); gaster medium,

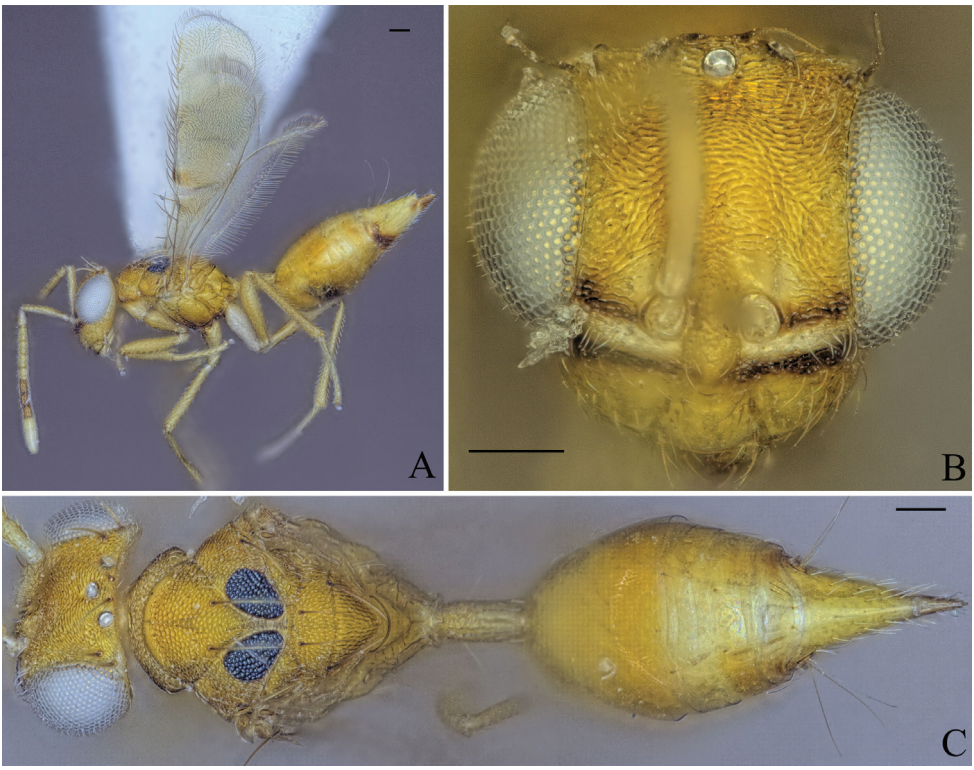

Figure 11. Holotype of *Dipara nyani* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

1.20–1.29× (1.25) longer than mesosoma in dorsal view (Fig. 11C); gt1 covering ~ 1/3 of gaster, gt2–4 ca. equal in size, gt5 and 6 much smaller (Fig. 11C); gt7 and ovipositor sheath sparsely setose (Fig. 11A).

Remarks. *Dipara nyani* is very similar to *D. kakamegensis*. It differs from it in the following characters: *D. nyani* is macropterous and the mesoscutellum is larger relative to the mesosoma length, based on the results of the morphometric analysis (Fig. 3). The stripes across the face are similar in *D. maculata*, *D. reticulata* and *D. rodneymulleni*. *Dipara nyani* differs from *D. maculata* in having a yellowish brown mesocoxa and petiole. *Dipara nyani* differs from *D. rodneymulleni* in many characters: the body coloration, the length of the petiole and the body shape. *Dipara nyani* differs from *D. reticulata* in having smooth gastral tergites while they are reticulated in *D. reticulata*.

Male. Unknown.

Etymology. Named after the word for monkey in the national language of Kenya, Swahili, because of the dorsal black dots and the mesoscutellum which resemble the face of a monkey.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara reticulata* sp. nov.**
http://zoobank.org/7ACD0DFB-0D61-437D-AA97-80FBF09E3540
Fig. 12A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'6.1N, 34°52'9.2E; 1605 m a.s.l.; 28 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 23; ZFMK-HYM-00040373. ***Paratypes*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 14 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; ZFMK-HYM-00040374 • 2 ♀; Kakamega Forest, Kenya; 00°14'52.3N, 34°52'5.3E; 1607 m a.s.l.; 21 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 18; NHMUK013457236; NMK: ZFMK-HYM-00040376.

Diagnosis. Female. Gastral tergites reticulate (Fig. 12C).

Description. ***Size*****:** medium sized, body length 2303–2927 (2303) µm.

Coloration**:** vertex and upper face brown to orangish brown, lower face yellowish brown (Fig. 12B); face with two transverse dark brown stripes just at the level of toruli and at the level of the ventral margin of the eye enclosing a stripe of white coloration, lower stripe darker than upper, upper stripe much fainter in interantennal area (Fig. 12C); scape, pedicel, first to fourth funicle segment (f1–f4) and clava yellowish brown (Fig. 12A); f5–f7 brown (Fig. 12A); pronotum and median area of mesoscutum brown to orangish brown (Fig. 12C); lateral area of mesoscutum and mesoscutellum yellowish brown (Fig. 12C); two black spots with metallic tint medially on lateral area of mesoscutum (Fig. 12C); procoxa, lower mesepisternum and anterior part of mesocoxa dark brown, rest of mesocoxa pale brown, metacoxa white with darker brown part anteriorly, rest of legs yellowish brown (Fig. 12A); mesosoma laterally, propodeum and petiole white (Fig. 12C); fore wing transparent with infuscation at tip (Fig. 12A); gaster yellowish brown (Fig. 12A); ovipositor sheath anteriorly white and posterior tip dark brown (Fig. 12A).

Head**:** head oval, 1.35–1.42× (1.35) wider than high (Fig. 12B); head except for lower face strigate-reticulate, lower face reticulate and sparsely setose (Fig. 12B); distance of antennal insertion to eye long, 1.29–1.56× (1.34) torulus diameter (Fig. 12B); antennae mostly far apart, toruli separated by 1.31–1.58× (1.31) torulus diameter (Fig. 12B); antennal formula: 11173 (Fig. 12A); funicle segments ca. as long as wide (Fig. 12A); malar space 0.26–0.29× (0.27) eye height (Fig. 12A); POL 0.93–1.12× (0.93) OOL (Fig. 12C).

Mesosoma**:** pronotum large and elongated, 1.78–2.38× (1.78) wider than long, substrigate, with two transverse rows of setae on posterior 1/2 (Fig. 12C); mesosoma mostly slender, head breadth 1.48–1.60× (1.53) mesoscutum breadth (Fig. 12C); notauli converging ca. at 1/2 the length of mesoscutum (Fig. 12C); median area of mesoscutum substrigate, black spots on lateral area strigate-reticulate, lateral area laterally reticulate (Fig. 12C); axillae, mesoscutellum, and frenum reticulate (Fig. 12C); mesoscutum with some small brown setae and two pairs of large bristles: one pair on median area just anterior of notauli, reaching posterior edge of mesoscutum, one pair laterally on lateral area anterior of wing base (Fig. 12C); axillae with some small brown setae (Fig. 12C); mesoscutellum with one pair of bristles anterio-medially and one

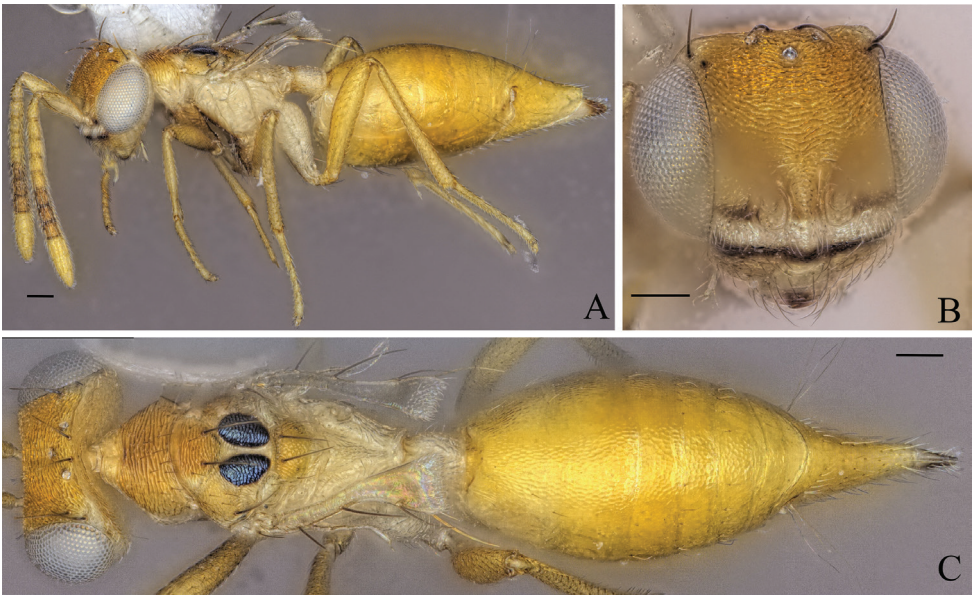

Figure 12. Holotype of *Dipara reticulata* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

pair of smaller setae laterally, anterior of frenal line, frenum much smaller than rest of mesoscutellum (Fig. 12C); brachypterous, tips truncated, fore wing reaching middle of petiole, three large black bristles along edge and one large brown bristle at the tip (Fig. 12A); propodeum medially rugulose and laterally transversely carinate transitioning to carinate on nucha (Fig. 12C).

***Metasoma*:** petiole short, 1.20–1.31× (1.24) wider than long, rugose, with four pairs small white setae laterally (Fig. 12C); gastral tergites reticulate (Fig. 12C); gaster medium, 1.47–1.56× (1.54) longer than mesosoma in dorsal view (Fig. 12C); gt1 covering ~1/3 of gaster, gt2–4 ca. equal in size, gt5–6 smaller (Fig. 12C); gt7 and ovipositor sheath sparsely setose (Fig. 12A).

Remarks. *Dipara reticulata* is similar to *D. kakamegensis*, *D. maculata*, *D. nyani*, and *D. rodneymulleni* in having transverse stripes across the face. *Dipara reticulata* is different form all other *Dipara* species in having reticulated gastral tergites. In all other species the gastral tergites are smooth.

Male. Unknown.

Etymology. Named for the reticulated gastral tergites.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara rodneymulleni* sp. nov.**
http://zoobank.org/879AFBBB-0A9B-4F26-A577-183E31E05118
Fig. 13A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°19'36N, 34°52'14.6E; 1570 m a.s.l.; 28 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 6; ZFMK-HYM-00040369. ***Paratypes*** Kenya • 2 ♀; Kakamega Forest, Kenya; 00°23'6.2N, 34°33'37.8E; 1602 m a.s.l.; 16 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 11; ZFMK-HYM-00040370; NHMUK013457235 • 1 ♀; Kakamega Forest, Kenya; 00°21'21.1N, 34°51'44.9E; 1632 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 16; NMK: ZFMK-HYM-00040372.

Diagnosis. Female. Face with two dark brown stripes at the level of the ventral margin of the eye, interrupted in supraclypeal area, and at the level of the toruli (Fig. 13B); absence of black spots on median area of mesoscutum (Fig. 13C); petiole very long, 2.53–2.80× (2.79) longer than wide (Fig. 13C).

Description. ***Size*****:** medium to large, body length 2718–3397 (3397) μm.

Coloration**:** body brown (Fig. 13); distal quarter of scape and pedicel, all funicle segments and small proximal part of the first claval segment (c1) dark brown, rest of scape white, rest of pedicel and clava yellowish brown (Fig. 13A); face with two dark brown stripes at the level of the ventral margin of the eye, interrupted in supraclypeal area, and at the level of the toruli (Fig. 13B); fore leg yellowish brown (Fig. 13A); mid leg with coxa and trochanter white, rest brown (Fig. 13A); hind leg with coxa white with dark brown coloration on posterior part, tibia dark brown, rest brown (Fig. 13A); gt7 with dark brown coloration around cerci and on posterior 1/2, rest of gt7 yellowish brown (Fig. 13A); ovipositor sheath yellowish brown on anterior 1/2 and posterior tip dark brown (Fig. 13A).

Head**:** head round, 1.22–1.29× (1.29) (specimens used for measurement: ZFMK-HYM-00040369, ZFMK-HYM-00040372, NHMUK013457235) wider than high (Fig. 13B); upper and lower face reticulate (Fig. 13B); vertex and interantennal area smooth (Fig. 13B); antennal scrobe substrigate (Fig. 13B); distance of antennal insertion to eye long, 1.49–1.76× (1.68) (specimens used for measurement: ZFMK-HYM-00040369, ZFMK-HYM-00040372, NHMUK013457235) torulus diameter (Fig. 13B); antennae close, toruli separated by 0.99–1.04× (0.99) (specimens used for measurement: ZFMK-HYM-00040369, ZFMK-HYM-00040372, NHMUK013457235) torulus diameter (Fig. 13B); antennal formula: 11173 (Fig. 13A); funicle segments longer than wide, getting shorter from f1–7 (Fig. 13A); malar space 0.30–0.32× (0.30) eye height (Fig. 13A); lower face and vertex sparsely setose (Fig. 13A); occipital margin with sharp edge (Fig. 13A); POL 1.47–1.74× (1.74) OOL (Fig. 13C).

Mesosoma**:** pronotum short and slim, 3.29–3.81× (3.74) as wide as long, strigulate-reticulate, sparsely setose (Fig. 13C); mesosoma of medium breadth, head breadth

Figure 13. Holotype of *Dipara rodneymulleni* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** and body in dorsal view. Scale bar: 100 μm.

1.25–1.28× (1.25) (specimens used for measurement: ZFMK-HYM-00040369, ZFMK-HYM-00040370, NHMUK013457235) mesoscutum breadth (Fig. 13C); notauli not converging (Fig. 13C); mesoscutum reticulate, sparsely setose, with two pairs of bristles: one pair medially on median area anterior of notauli almost reaching axillae, one pair laterally on lateral area anterior of wing base (Fig. 13C); axillae reticulate (Fig. 13C); mesoscutellum anteriorly reticulate to carinulate posteriorly and on frenum, with two pairs of bristles: one pair anterio-medially and one pair laterally on frenal line, frenum almost as large as anterior part of mesoscutellum (Fig. 13C); macropterous, fore wing with large black bristles along submarginal vein and smaller bristles along marginal and postmarginal vein, mostly infuscate with some transparent patches, stigmal vein rather short, stigma thin, uncus short and pointed (Fig. 13A); propodeum medially smooth and laterally confused carinate (Fig. 13C); nucha carinate (Fig. 13C).

***Metasoma*:** petiole very long, 2.53–2.80× (2.79) longer than wide, with anterior 2/3 rugose and rest carinate, with lateral pair of large white setae visible in dorsal view (Fig. 13C); gaster medium, 1.46–1.53× (1.53) longer than mesosoma in dorsal view (Fig. 13C); gt1 covering ~1/3 of gaster, gt2–6 ca. equal in size (Fig. 13C); gt7 and ovipositor sheath slender and elongated, together ca. as long as rest of gaster, sparsely setose (Fig. 13C).

Remarks. *Dipara rodneymulleni* shares the stripes across the face with *D. maculata*, *D. nyani*, *D. kakamegensis*, and *D. reticulata* and but other than that has a completely different morphology and coloration. The most obvious characters to distinguish *D. rodneymulleni* are the very long petiole and the absence of black spots on the lateral areas of the mesoscutum.

Male. Unknown.

Etymology. Named after professional skateboarder Rodney Mullen who revolutionized street skating like no other, reflecting the first author's lifelong passion for skateboarding.

Biology. ***Habitat*:** Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara sapphirus* sp. nov.**

http://zoobank.org/16FE1162-7E49-488A-A922-A84D432CA22B

Fig. 14A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 23 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; ZFMK-HYM-00040339. ***Paratypes*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°37'24.1N, 34°51'12E; 1585 m a.s.l.; 16 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 10; ZFMK-HYM-00040340 • 7 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 05 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00040341, ZFMK-HYM-00040353 to ZFMK-HYM-00040356; NMK: ZFMK-HYM-00040357, ZFMK-HYM-00040358 • 3 ♀; Kakamega Forest, Kenya; 00°27'0.9N, 34°50'52.9E; 1649 m a.s.l.; 10 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 8; ZFMK-HYM-00040342; NHMUK013457227, NHMUK013457228 • 7 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 09 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00040343, ZFMK-HYM-00040362, ZFMK-HYM-00040363; NMK: ZFMK-HYM-00040359 to ZFMK-HYM-00040361, ZFMK-HYM-00040366 • 1 ♀; Kakamega Forest, Kenya; 00°27'10.6N, 34°51'48.7E; 1676 m a.s.l.; 19 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 4; ZFMK-HYM-00040344 • 3 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 05 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00040345 to ZFMK-HYM-00040347 • 3 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1E; 1580 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; NHMUK013457229 to NHMUK013457231 • 1 ♀; Kakamega Forest, Kenya; 00°21'7.9N, 34°52'2.6E; 1597 m a.s.l.; 02 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 7; ZFMK-HYM-00040364 • 1 ♀; Kakamega Forest, Kenya; 00°23'6.2N, 34°33'37.8E; 1602 m a.s.l.; 23 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 11; ZFMK-HYM-00040365 • 1 ♀; Kakamega

Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 25 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; ZFMK-HYM-00040367 • 1 ♀; Kakamega Forest, Kenya; 00°13'15.5N, 34°53'24.7E; 1597 m a.s.l.; 23 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 22; ZFMK-HYM-00040368.

Female (specimens used for morphometric measurements: ZFMK-HYM-00040339 to ZFMK-HYM-00040343).

Diagnosis. Strong blue metallic tint on the following areas: vertex between ocelli, pronotum laterally, median area of mesoscutum posteriorly between notauli, lateral area of mesoscutum and mesoscutellum (Fig. 14C).

Description. ***Size*****:** small to medium sized, body length 1667–2432 (2081) μm.

Coloration**:** body dark brown (Fig. 14); scape proximally and distally dark brown, medially white, proximal 1/2 of pedicel dark brown, distal 1/2 white, funicle segments dark brown, clava pale yellowish white (Fig. 14A); strong blue metallic tint on the following areas: vertex between ocelli, pronotum laterally, median area of mesoscutum posteriorly between notauli, lateral area of mesoscutum and mesoscutellum (Fig. 14C); fore leg with coxa, trochanter and proximal 1/3 of femur white, rest yellowish brown (Fig. 14A); mid leg with proximal parts of femur and tibia yellowish white, rest yellowish brown (Fig. 14A); hind leg with distal 2/3 of femur brown, distal quarter of tibia and tarsus yellowish brown, rest white (Fig. 14A); anterior 1/2 of gt7 yellowish brown (Fig. 14A).

Head**:** head round, 1.26–1.30× (1.29) wider than high (Fig. 14B); upper face strigate-reticulate (Fig. 14B); lower face reticulate and sparsely setose (Fig. 14B); antennal scrobe substrigate with deep groove (Fig. 14B); vertex and interantennal area smooth (Fig. 14B); distance of antennal insertion to eye short, 0.85–1.08× (1.00) torulus diameter (Fig. 14B); antennae close, separated by 1.07–1.26× (1.16) torulus diameter (Fig. 14B); antennal formula: 11173 (Fig. 14A); funicle segments ca. as long as wide (Fig. 14A); malar space 0.26–0.41× (0.26) eye height (Fig. 14A); POL 0.78–0.95× (0.95) OOL (Fig. 14C).

Mesosoma**:** pronotum mostly short and slim, 3.30–3.60× (3.60) wider than long, medially and around posterior margin smooth, laterally reticulate, with some setae close to the posterior edge (Fig. 14C); mesosoma mostly robust, head breadth 1.13–1.22× (1.14) mesoscutum breadth (Fig. 14C); notauli not converging (Fig. 14C); mesoscutum with median area posteriorly between notauli smooth and rest strigate-reticulate, lateral area medially smooth and laterally reticulate, sparsely setose, with two pairs of larger bristles: one pair on median area just anterior of notauli, reaching posterior margin of mesoscutum, one pair laterally on lateral area anterior of wing base (Fig. 14C); axillae smooth and sparsely setose (Fig. 14C); mesoscutellum anteriorly reticulate to smooth posteriorly, with two pairs of bristles: one pair anterio-medially and one pair laterally on frenal line (Fig. 14C); macropterous, fore wing reaching gt7 with large bristles along submarginal vein and smaller bristles along marginal and postmarginal vein on edge, alternating infuscate and transparent, starting with infuscate at the tip, stigmal vein short, stigma round and large, uncus broad and rounded (Fig. 14A); propodeum medially smooth, laterally transversely carinate (Fig. 14C); nucha carinate (Fig. 14C).

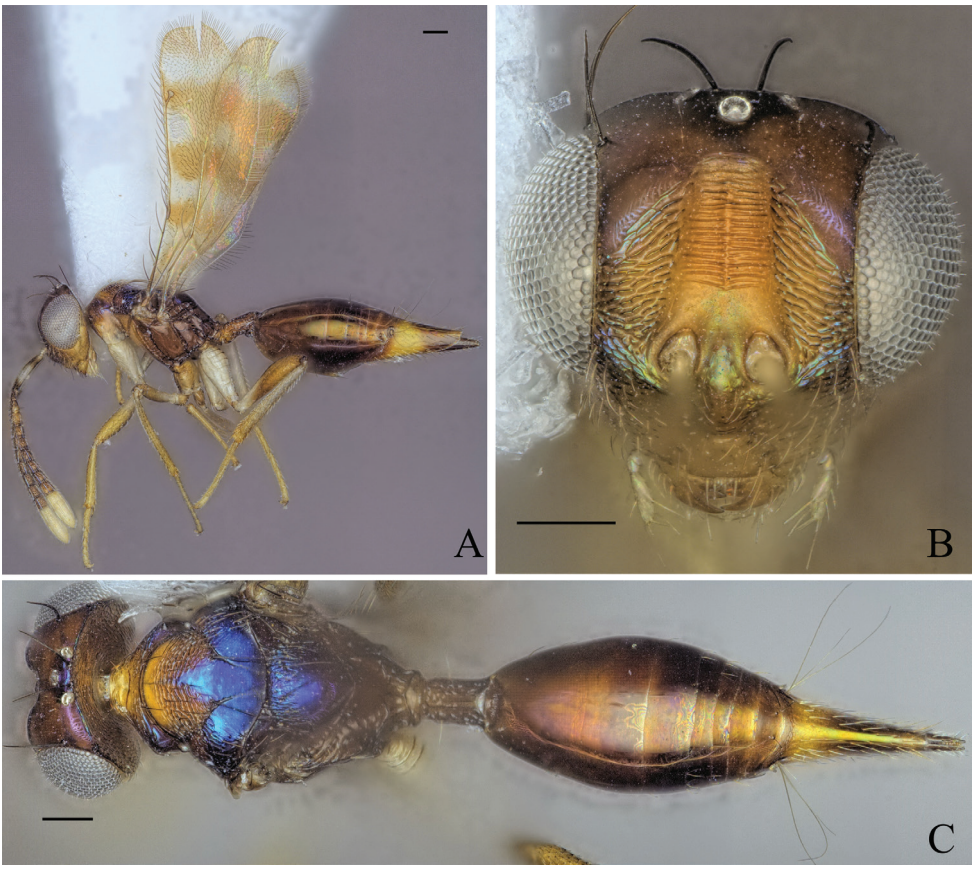

Figure 14. Holotype of *Dipara sapphirus* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

***Metasoma*:** petiole short to medium, 1.31–1.67× (1.60) longer than wide in dorsal view, costate-rugose, with lateral pair of large white setae visible in dorsal view (Fig. 14C); gaster medium 1.37–1.53× (1.47) longer than mesosoma in dorsal view (Fig. 14C); gt1 covering ~ 1/2 of gaster, gt2 larger than gt3–6, gt3–6 ca. equal in size (Fig. 14C); gt7 and ovipositor sheath elongated and sparsely setose (Fig. 14A).

Remarks. In body shape, *D. sapphirus* is similar to *D. lux* and *D. tenebra* but can be distinguished from all other *Dipara* species by having a very distinct blue metallic tint on the following body parts: vertex between ocelli, pronotum laterally, median area of mesoscutum posteriorly between notauli, lateral area of mesoscutum and mesoscutellum (Fig. 14C).

Male. Unknown.

Etymology. Named after sapphires for the blue metallic tint.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara tenebra* sp. nov.**
http://zoobank.org/90CA2ECF-B5A6-44E6-8CCF-80C6EF6A37F6
Fig. 15A–C

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°27'10.6N, 34°51'48.7E; 1676 m a.s.l.; 19 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 4; ZFMK-HYM-00040377. ***Paratype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°37'24.1N, 34°51'12E; 1585 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 10; ZFMK-HYM-00040378.

Diagnosis. Female. Body brown to dark brown (Fig. 15); face with dark brown to black stripe from one eye to the other at the level of the ventral margin of the eye, interrupted in supraclypeal area (Fig. 15B); vertex smooth (Fig. 15B); petiole very long, 2.51–2.77× (2.51) longer than wide in dorsal view (Fig. 15C).

Description. ***Size*****:** medium sized, body length 2293–2474 (2293) μm.

Coloration**:** body brown to dark brown (Fig. 15); scape and f1 yellowish brown, pedicel, f23, and f7 yellowish brown to brown, f4–6 brown, clava white (Fig. 15A); face with dark brown to black stripe from one eye to the other at the level of the ventral margin of the eye, interrupted in supraclypeal area (Fig. 15B); mesoscutum with two black spots medially on lateral area (Fig. 15C); fore leg with distal tip of coxa brown, rest of coxa white, trochanter and femur brown, tibia and tarsus yellowish brown (Fig. 15A); mid leg with coxa and trochanter white and rest yellowish brown (Fig. 15A); hind leg with anterior part of coxa, trochanter and anterior part of femur white, posterior part of coxa dark brown to black, rest of hind leg yellowish brown (Fig. 15A); gt1 brown, anterior 2/3 of gt7 yellowish brown, rest of gaster dark brown (Fig. 15A).

Head**:** head oval, 1.33–1.37× (1.33) wider than high (Fig. 15B); upper face next to toruli reticulate, rest smooth (Fig. 15B); lower face reticulate, sparsely setose (Fig. 15B); interantennal area smooth, antennal scrobe strigate-reticulate (Fig. 15B); vertex smooth (Fig. 15B); distance of antennal insertion to eye short, 0.66–0.76× (0.66) torulus diameter (Fig. 15B); antennae close, toruli separated by 1.17–1.32× (1.17) torulus diameter (Fig. 15B); antennal formula: 11173 (Fig. 15A); funicle segments getting shorter from f1 to f7, f1 much longer than wide, f7 ca. as wide as long (Fig. 15A); malar space 0.37–0.39× (0.37) eye height (Fig. 15A); POL 0.89–0.96× (0.89) OOL (Fig. 15C).

Mesosoma**:** pronotum of medium length, 3.11–3.12× (3.11) wider than long, substrigate, with row of setae close to the posterior edge (Fig. 15C); mesosoma robust, head breadth 1.15–1.18× (1.15) mesoscutum breadth (Fig. 15C); mesoscutum reticulate, with two pairs of bristles: one pair on median area anterior of notauli, one pair laterally on lateral area anterior to wing base (Fig. 15C); notauli converging at posterior margin of mesoscutum (Fig. 15C); axillae reticulate (Fig. 15C); mesoscutellum anteriorly reticulate, frenum smooth, with two pairs of bristles: one pair anteriomedially, one pair laterally anterior of frenal line (Fig. 15C); macropterous, fore wing reaching gt7, with larger bristles along marginal and postmarginal vein on edge of forewing, with dense brush of setae at proximal end of marginal vein, with large areas of infuscation, stigmal vein very short, stigma large and rounded, uncus short and

Figure 15. Holotype of *Dipara tenebra* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

pointed (Fig. 15A); propodeum medially smooth and laterally transversely carinate (Fig. 15C); nucha carinate (Fig. 15C).

***Metasoma*:** petiole very long, 2.51–2.77× (2.51) longer than wide in dorsal view, costate-rugose, with lateral pair of large setae visible in dorsal view (Fig. 15C); gaster medium, 1.20–1.24× (1.20) longer than mesosoma in dorsal view (Fig. 15C); gt1 covering ~ 1/3 of gaster (Fig. 15C); gt7 and ovipositor sheath sparsely setose (Fig. 15A).

Remarks. *Dipara tenebra* is similar to *D. corona*, *D. lux*, *D. machadoi*, *D. striata*, *D. tigrina*, *and D. turneri* and in having one dark brown to black stripe across the face. *Dipara tenebra* is different from *D. machadoi* in having distinct notauli, which are lacking in *D. machadoi*. It differs from *D. corona*, *D. striata*, *D. tigrina*, *and D. turneri* in having a very long petiole. *Dipara tenebra* and *D. lux* are very similar in body shape and differ in their body coloration which is much darker in *D. tenebra* and in the surface sculpture of the head. They share the otherwise unique character of having a dense brush of setae close to the proximal end of the marginal vein on the fore wing.

Male. Unknown.

Etymology. Named after the Latin word *tenebra* for darkness, in contrast to *D. lux* which looks very similar but is much lighter in coloration.

Biology. *Habitat*: Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

***Dipara tigrina* sp. nov.**
http://zoobank.org/E816ADB7-A279-4978-81DE-7F24CCF38422
Fig. 16A–D

Material examined. ***Holotype*** Kenya • 1 ♀; Kakamega Forest, Kenya; 00°21'4.4N, 34°51'41.1E; 1602 m a.s.l.; 05 Jun. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 2; ZFMK-HYM-00040383.

Diagnosis. Female. Propodeum laterally smooth, medially distinctly subcarinate with reticulation between carinae, carinae extending to nucha (Fig. 16C); petiole with at least six pairs of small white setae laterally (Fig. 16D).

Description. ***Size*****:** medium sized, body length 2329 μm.

Coloration**:** body yellowish brown to brown (Fig. 16); dorsal part of scape brown, ventral part of scape white, pedicel yellowish brown, funicle segments dark brown, clava white (Fig. 16A); face yellowish brown, with two brown spots at the ventral margin of the eye (Fig. 16B); vertex dark brown (Fig. 16B); mesoscutum with two large black spots medially on lateral area (Fig. 16C); fore and mid leg with coxa white, rest yellowish brown (Fig. 16A); hind leg with coxa, trochanter and proximal 1/2 of tibia white, rest yellowish brown (Fig. 16A); two broad dark brown stripes on gt1, one directly posterior to petiole and one at posterior edge (Fig. 16D); gt6 dark brown (Fig. 16D); gt7 around cerci and posterior 1/3 dark brown, rest yellowish brown (Fig. 16A); ovipositor sheath dark brown (Fig. 16A).

Head**:** head round, 1.24× wider than high, entirely reticulate (Fig. 16B); lower face sparsely setose (Fig. 16B); distance of antennal insertion to eye short, 0.66 torulus diameter (Fig. 16B); antennae close, toruli separated by 1.31× torulus diameter (Fig. 16B); antennal formula: 11173 (Fig. 16A); funicle segments getting shorter from f1 to f7, f1 slightly longer than wide and f7 as wide as long (Fig. 16A); malar space 0.34× eye height (Fig. 16A); POL 1.03× OOL (Fig. 16C).

Mesosoma**:** pronotum large and elongated, 1.95× as wide as long, reticulate, with two rows of small setae close to posterior margin (Fig. 16C); mesosoma of medium breadth, head breadth 1.46× mesoscutum breadth (Fig. 16C); notauli converging at 1/2 the length of mesoscutum (Fig. 16C); mesoscutum reticulate, with two pairs of bristles: one pair anterio-medially on median area anterior of notauli one pair laterally on lateral area anterior of wing base (Fig. 16C); axillae reticulate (Fig. 16C); mesoscutellum anteriorly reticulate, frenum porcate, with two pairs of bristles: one pair anterio-medially, one pair laterally just anterior of frenal line (Fig. 16C); brachypterous, fore wing reaching anterior edge of propodeum or shorter (Fig. 16C); propodeum laterally smooth, medially distinctly subcarinate with reticulated pattern between the carinae, carinae extending to nucha (Fig. 16C).

Metasoma**:** petiole short, 1.37× as long as wide in dorsal view, with at least six pairs of small white setae laterally visible in dorsal view, subcarinate (Fig. 16D), similar to propodeum sculpture (Fig. 16C); gaster medium, 1.51× longer than mesosoma in dorsal view (Fig. 16D); gt1 covering ~ 1/3 of gaster (Fig. 16D); gt7 and ovipositor sheath sparsely setose (Fig. 16A).

Remarks. *Dipara tigrina* is similar to *D. corona*, *D. lux*, *D. machadoi*, *D. striata*, *D. tenebra*, *and D. turneri* in having one dark brown to black stripe across the face. It

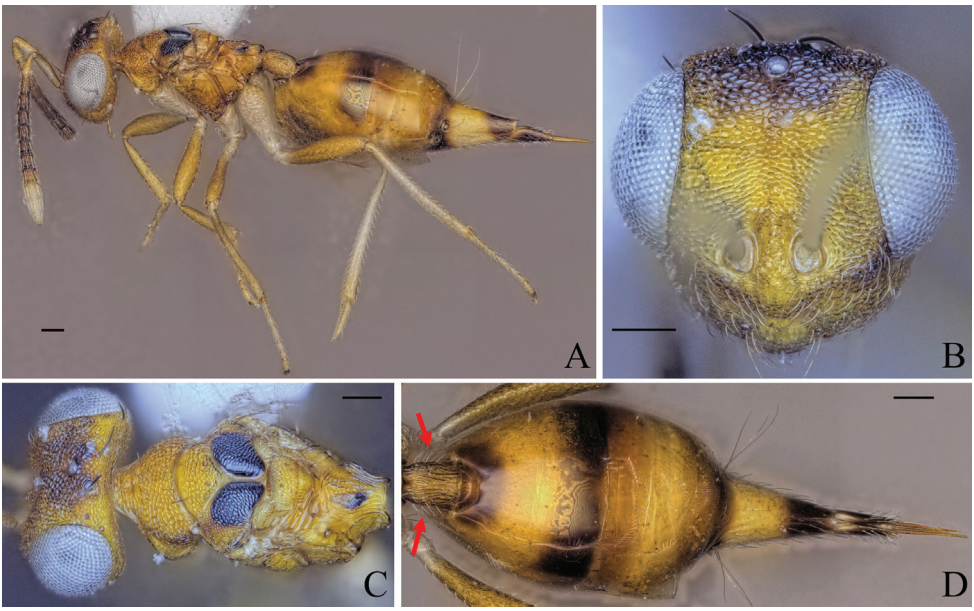

Figure 16. Holotype of *Dipara tigrina* sp. nov. **A** habitus in lateral view **B** face in frontal view **C** head and mesosoma in dorsal view **D** metasoma in dorsal view; red arrow: setae laterally on the petiole. Scale bar: 100 μm.

differs from *D. corona*, *D. lux*, *D. machadoi*, *D. tenebra*, and *D. turneri* in the propodeum sculpture. The propodeum sculpture is similar in *D. punctulata* and *D. striata*. They show a very distinct surface sculpture with a striated subcarinate pattern extending to the nucha. *Dipara tigrina* differs from *D. punctulata* and *D. striata* in having more setae laterally on the propodeum and in having a reticulated pattern medially between the carinae on the propodeum.

The only available specimen of this species has an irregular black spot on the propodeum. This spot is considered an aberration and thus is not part of the species description.

Male. Unknown.

Etymology. Named after the Latin adjective *tigrinus* for the tiger-like stripes on the gaster.

Biology. ***Habitat*:** Leaf litter.

***Host*:** Unknown.

Distribution. Kenya.

Dipara albomaculata **(Hedqvist, 1963)**

Fig. 17A, B

Afrolelaps albomaculata Hedqvist 1963: 49–50.
Grahamisia albomaculata Hedqvist 1969: 185.
Dipara albomaculata Desjardins 2007: 42, 46.

Material examined. ***Paratype*** Angola • 1 ♀; Mabete, Caungula; 20. Jul. 1962; A. de Barros Machado leg.; NHMUK013455574.

Other material. Kenya • 5 ♀; Kakamega Forest, Kenya; 00°22'43.7N, 34°41'57.3E; 1452 m a.s.l.; 25 Aug. 2008; Hita-Garcia, F. leg.; Winkler extraction; Transect 35; ZFMK-HYM-00040386 to ZFMK-HYM-00040390.

Diagnosis. Female. Body brown to dark brown (Fig. 17); vertex smooth (Fig. 17B); clava white (Fig. 17A); lateral area of mesoscutum completely black (Fig. 17B); pro- and metacoxa white (Fig. 17A); propodeum completely smooth (Fig. 17B); gt1 with a pair of large bristles dorso-anteriorly (Fig. 17B).

Remarks. The holotype of *D. albomaculata* is supposed to be stored at the MDLA but we were unable to get in contact with the museum and thus the holotype could not be located and examined. Two paratypes are stored at the BMNH and one of them was examined.

Dipara albomaculata is similar to *D. andreabalzerae*, *D. fastigata*, *D. nigroscutellata* and *D. saetosa* in having a black mesoscutellum while the general body coloration is not black. It differs from *D. andreabalzerae* and *D. fastigata* in having a pair of bristles dorso-anteriorly on the gt1. It differs from *D. nigroscutellata* in the general body coloration, which is much darker and in the coloration of the lateral area of the mesoscutum. In *D. albomaculata* the lateral area is completely black and *D. nigroscutellata* has a small yellowish brown area on its most lateral part. The differences to *D. saetosa* can be found in the smooth vertex and the white pro- and metacoxa.

Dipara albomaculata is similar to *D. straminea* in sharing the bristles on the gt1 and the propodeum sculpture. It differs from *D. straminea* in having a black mesoscutellum.

Additional specimens from this species were found in the Kakamega Forest in Kenya and the distribution is updated accordingly.

Distribution. Angola; Kenya.

Dipara machadoi (Hedqvist, 1971)

Diparomorpha machadoi Hedqvist 1971: 55–59.
Dipara machadoi Desjardins 2007: 42, 48–50.

Diagnosis. Female. Notauli absent.

Remarks. The holotype of *D. machadoi* is supposed to be stored at the MDLA but we were unable to get in contact with the museum and thus the holotype could not be located and examined. Based on the original description by Hedqvist (1971) *D. machadoi* differs from all other Afrotropical *Dipara* species in having no notauli.

Dipara maculata (Hedqvist, 1963)

Afrolelaps maculata Hedqvist 1963: 47–49.

Figure 17. Paratype of *Dipara albomaculata* (Hedqvist, 1963) **A** habitus in lateral view **B** body in dorsal view.

Grahamisia maculata Hedqvist 1969: 185.
Dipara maculata Desjardins 2007: 42, 46.

Diagnosis. Female. Face with two transverse stripes of dark brown coloration just at the level of toruli and at the level of the ventral margin of the eye, enclosing a stripe of pale yellowish white coloration; mesocoxa and petiole white.

Remarks. The holotype of *D. maculata* is supposed to be stored at the MDLA but we were unable to get in contact with the museum and thus the holotype could not be located and examined. Based on the original description by Hedqvist (1963) it is similar to *D. kakamegensis*, *D. nyani*, and *D. rodneymulleni* in having two transverse stripes on the face. It differs from *D. rodneymulleni* in having a much shorter petiole. In contrast to *D. kakamegensis* and *D. nyani*, *D. maculata* has a white petiole and mesocoxa.

***Dipara nigrita* Hedqvist, 1969**
Fig. 18A–D, 19A–C

Dipara nigrita Hedqvist, 1969: 195.

Material examined. ***Holotype*** Democratic Republic Of Congo • 1 ♀; Mount Kabobo, Terr. Albertville, Hte. Kiymbi; 1700 m a.s.l; Oct. 1958;N. Leleup leg.; "Humus en forêt"; RMCA ENT 000017982.

Other material. Kenya • 1 ♀; Kakamega Forest, Kenya; 00°14'22.9N, 34°51'21 E; 1594 m a.s.l.; 24 Jul. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 12; ZFMK-HYM-00040384 • 1 ♀; Kakamega Forest, Kenya; 00°19'49.9N, 34°52'16.1 E; 1580 m a.s.l.; 01 Aug. 2007; Hita-Garcia, F. leg.; Winkler extraction; Transect 15; ZFMK-HYM-00040385.

Diagnosis. Female. Head and mesosoma black, coxae dark brown (Figs 18, 19).

Variation. *Dipara nigrita* was originally described as brachypterous (Fig. 18) by Hedqvist (1969). In the examined material from Kenya, we found specimens that we consider to be the macropterous form of this species (Fig. 19). Differences in the wing form within Diparinae are reported from several other species (Bouček 1988; Mitroiu 2019) and the slight differences found between the macropterous forms and the brachypterous holotype were not enough to justify describing the macropterous form as a new species. Those differences were found in the color of the first claval segment. It can vary from light brown to white.

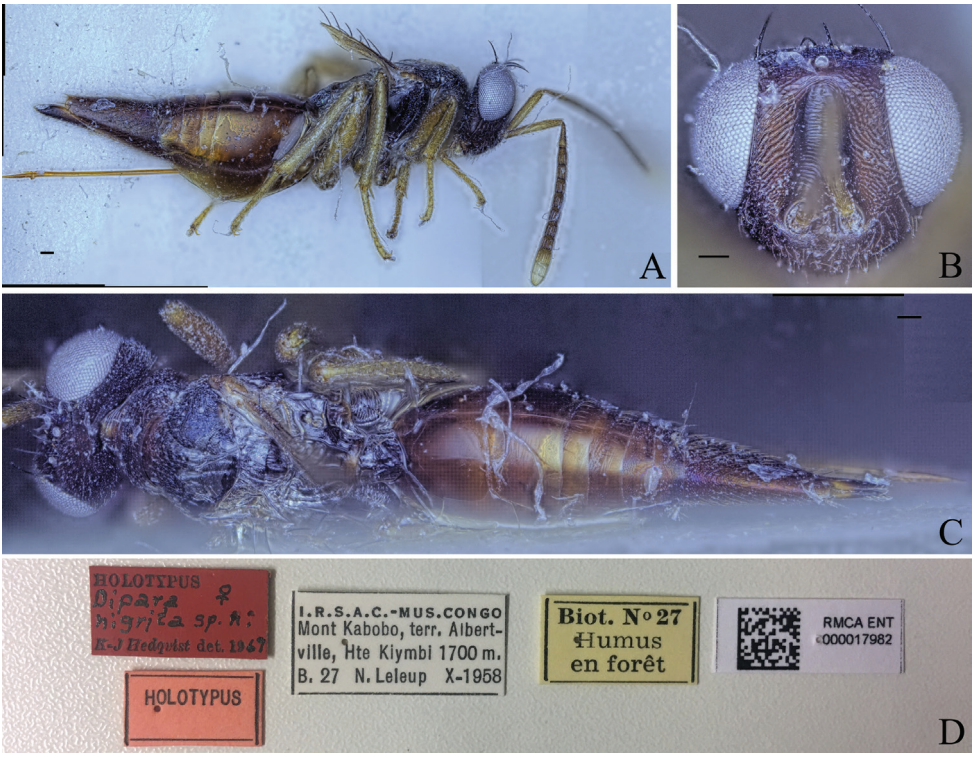

Figure 18. Holotype of *Dipara nigrita* Hedqvist, 1969 **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view **D** labels. Scale bar: 100 μm.

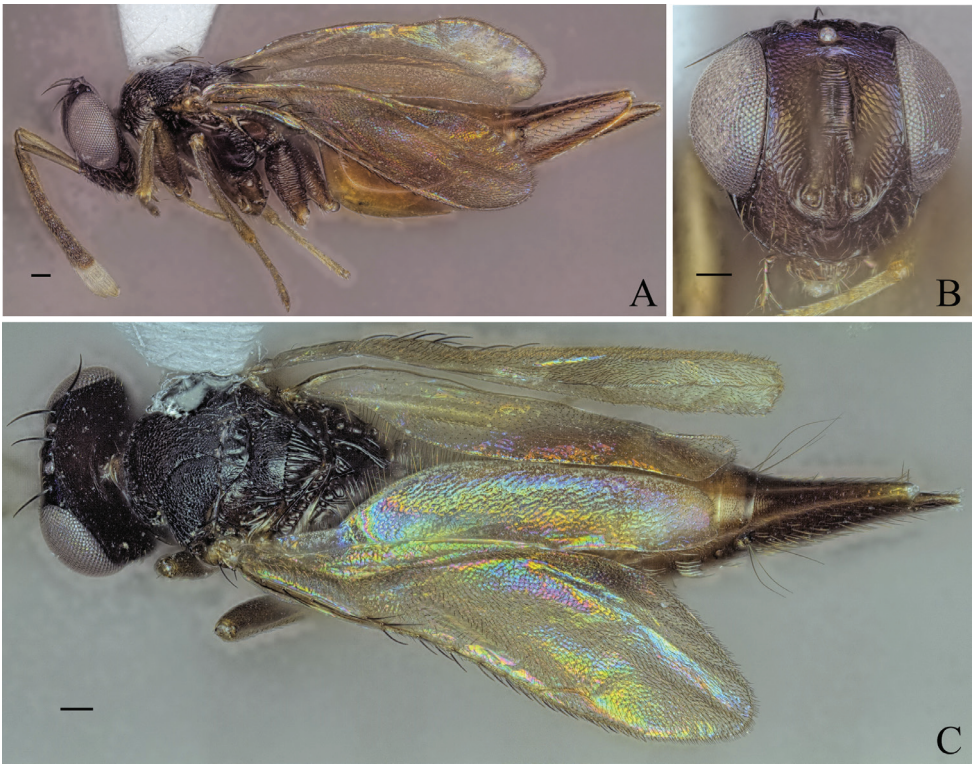

Figure 19. Macropterous specimen of *Dipara nigrita* Hedqvist, 1969 from the Kakamega Forest in Kenya **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view. Scale bar: 100 μm.

Macropterous individuals have fully developed wings with the fore wings reaching the gt7 (Fig. 19). Brachypterous individuals show much shorter wings with the fore wings reaching approximately the posterior margin of the petiole (Fig. 18).

Remarks. *Dipara nigrita* is the only species which shows a completely black coloration of the head and mesosoma. Darker specimens of *D. albomaculata* sometimes have a partly very dark brown to black head and mesosoma but never completely black. Additionally, the coxa of *D. albomaculata* are white in contrast to the dark brown coxa of *D. nigrita*.

Additional specimens from the species were found in the Kakamega Forest in Kenya and the distribution is updated accordingly.

Distribution. Democratic Republic of Congo; Kenya.

Dipara pallida **(Hedqvist, 1969)**

Fig. 20A–B

Pondia pallida Hedqvist 1969: 198–199.
Dipara pallida Desjardins 2007: 42.

Figure 20. Holotype of *Dipara pallida* (Hedqvist, 1969) **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view; red arrows: long lateral bristles on the petiole.

Material examined. ***Holotype*** South Africa • 1 ♀; Port St. John, Pondoland; Jan. 1924; R.E. Turner leg.; NHMUK013455580.

Diagnosis. Female. Vertex and propodeum smooth (Fig. 20B); petiole with long bristle anterio-laterally, reaching gt1 (Fig. 20B).

Remarks. *Dipara pallida* is similar to *D. punctulata* in having a large bristle anterio-laterally on the petiole. They differ in the surface sculpture of the vertex and the propodeum.

Dipara punctulata (Hedqvist, 1969)

Fig. 21A–D

Pondia punctulata Hedqvist 1969: 197–198.
Dipara punctulata Desjardins 2007: 42.

Material examined. ***Holotype*** South Africa • 1 ♀; Port St. John, Pondoland; Jan. 1924; R.E. Turner leg.; NHMUK013455579.

Diagnosis. Female. Vertex reticulate (Fig. 21B); propodeum subcarinate (Fig. 21C); petiole with long bristle anterio-laterally, reaching gt1 (Fig. 21D).

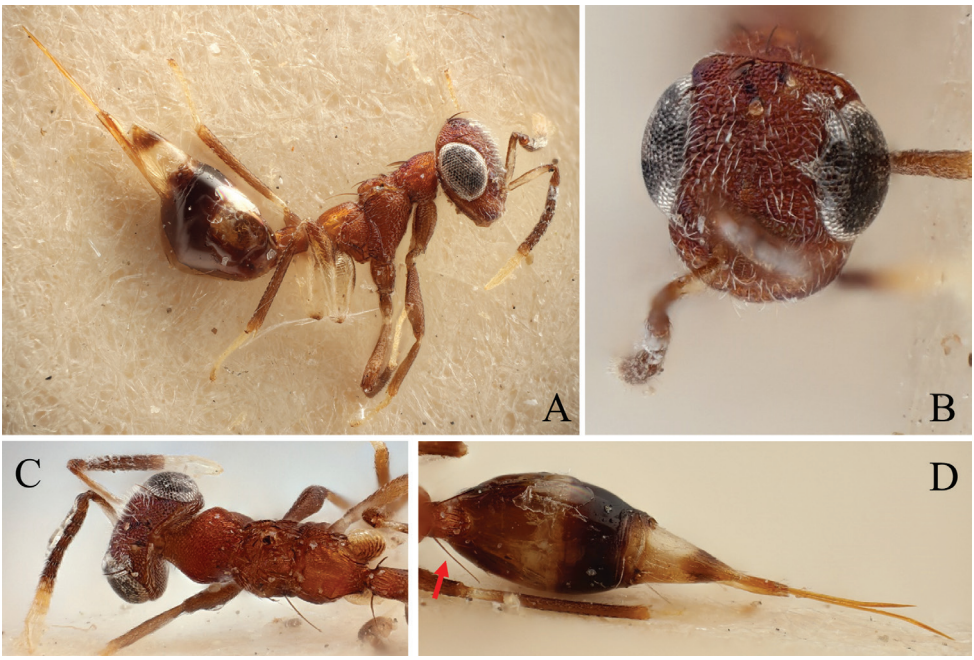

Figure 21. Holotype of *Dipara punctulata* (Hedqvist, 1969) **A** habitus in lateral view **B** face in frontal view **C** head and mesosoma in dorsal view **D** metasoma in dorsal view; red arrow: long lateral bristles on the petiole.

Remarks. *Dipara punctulata* is similar to *D. pallida* in having a large bristle anterio-laterally on the petiole. They differ in the surface sculpture of the vertex and the propodeum.

***Dipara saetosa* (Delucchi, 1962)**
Fig. 22A–D

Grahamisia saetosa Delucchi 1962: 379.
Dipara saetosa Desjardins 2007: 42, 46.

Material examined. ***Holotype*** Tanzania • 1 ♀; Tanganyika Terr., Mt. Oldeani, versant Est; 2350–2500 m a.s.l.; 6.–9. Jun. 1957; RMCA ENT 000017989.

Diagnosis. Female. Vertex reticulate between ocelli, rest smooth (Fig. 22C); clava dark brown (Fig. 22A); lateral area of mesoscutum completely black (Fig. 22C); mesoscutellum black (Fig. 22C); pro- and metacoxa with proximal 1/3 brown and rest yellowish brown (Fig. 22A); gt1 with a pair of large bristles dorso-anteriorly (Fig. 22C).

Remarks. *Dipara saetosa* is similar to *D. albomaculata*, *D. nigroscutellata*, and *D. straminea* in having a pair of large bristles dorso-anteriorly on the gt1. It differs from *D. straminea* in having a black mesoscutellum. In contrast to *D. nigroscutellata* the lateral area of the mesoscutum is completely black. Differences to *D. albomaculata*

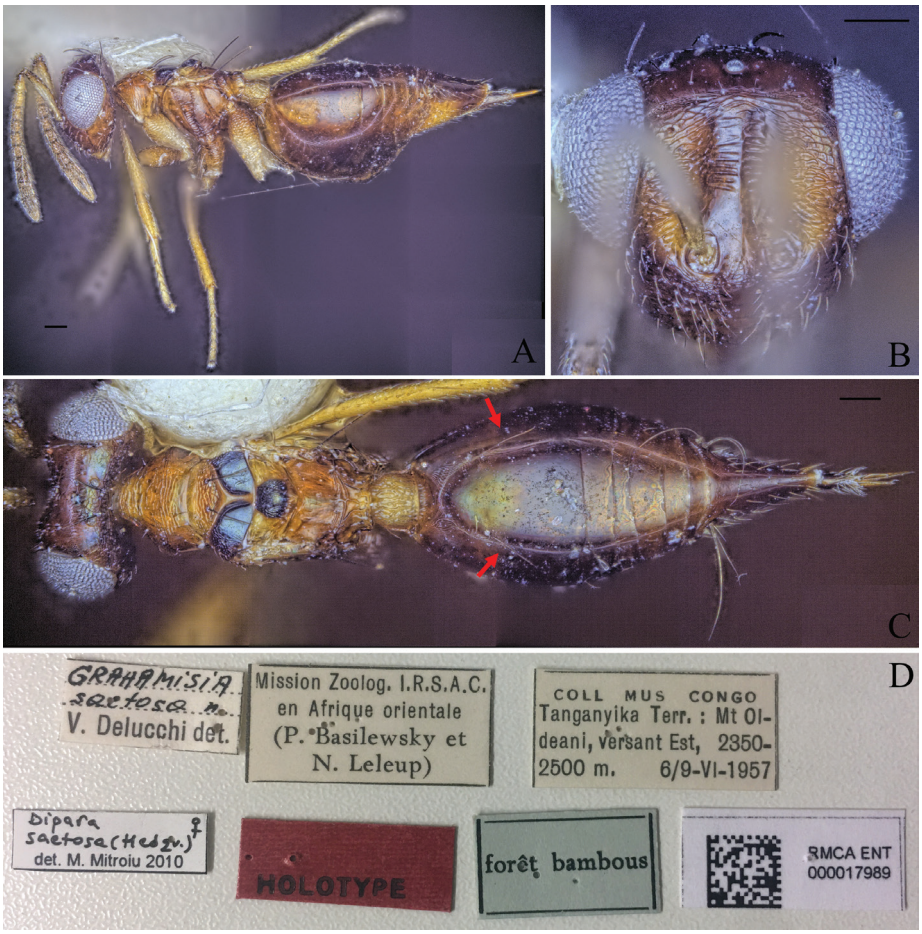

Figure 22. Holotype of *Dipara saetosa* (Delucchi, 1962) **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view **D** labels; red arrows: dorsal bristles on gt1. Scale bar: 100 µm.

can be found in the reticulation between the ocelli and the coloration of the clava and the pro- and metacoxa.

Dipara straminea (Hedqvist, 1969)

Fig. 23A–D

Grahamisia straminea Hedqvist 1969: 187–188.
Dipara straminea Desjardins 2007: 42, 46.

Material examined. ***Holotype*** Democratic Republic Of Congo • 1 ♀; Kivu, Terr. Mwenga, S.-O. Tombwe, Luiko; 2100 m a.s.l.; Jan. 1952;N. Leleup leg.; "Récolté dans l'humus"; RMCA ENT 000017981.

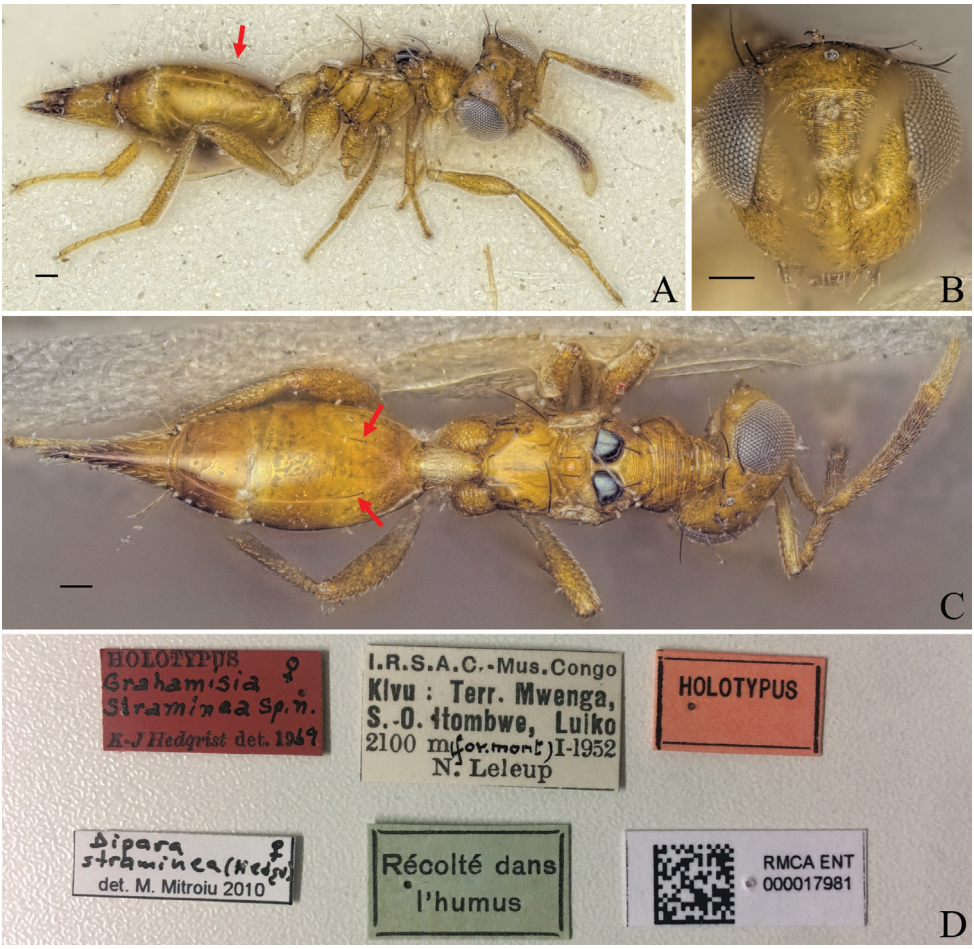

Figure 23. Holotype of *Dipara straminea* (Hedqvist, 1969) **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view **D** labels; red arrows: dorsal bristles on gt1. Scale bar: 100 μm.

Diagnosis. Female. Mesoscutellum yellowish brown (Fig. 23C); gt1 with a pair of large bristles dorso-anteriorly (Fig. 23A, C).

Remarks. *Dipara straminea* is similar to *D. albomaculata*, *D. nigroscutellata*, and *D. saetosa* in having a pair of large bristles dorso-anteriorly on the gt1. It differs from them by having a yellowish brown mesoscutellum.

***Dipara striata* (Hedqvist, 1969)**
Fig. 24A–C

Grahamisia striata Hedqvist 1969: 188.
Dipara striata Desjardins 2007: 42, 46.

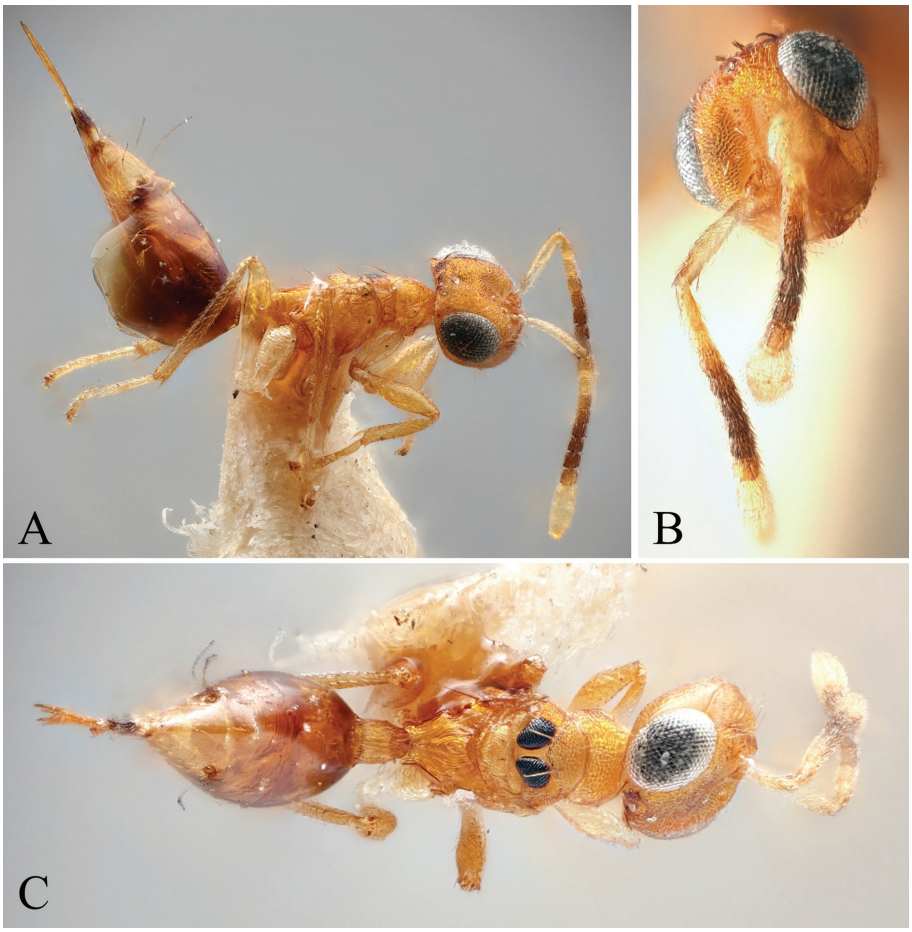

Figure 24. Holotype of *Dipara striata* (Hedqvist, 1969) **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view.

Material examined. ***Holotype*** South Africa • 1 ♀; Cape Province, Somerset East; 1.–26. Jan. 1931; R.E. Turner leg.; NHMUK013455578.

Diagnosis. Female. Propodeum laterally smooth, medially distinctly subcarinate, carinae extending to nucha (Fig. 24C); petiole with three pairs of small setae laterally (Fig. 24C).

Remarks. *Dipara striata* is similar to *D. corona*, *D. lux*, *D. machadoi*, *D. tenebra*, *D. tigrina*, and *D. turneri* in having one dark brown to black stripe across the face. It differs from *D. corona*, *D. lux*, *D. machadoi*, *D. tenebra*, and *D. turneri* in the propodeum sculpture. The propodeum sculpture is similar in *D. punctulata* and *D. tigrina*. They show a very distinct striated subcarinate pattern extending to the nucha. *Dipara striata* differs from *D. punctulata* in lacking a large bristle anterio-laterally on the petiole. *Dipara striata* differs from *D. tigrina* in having less setae laterally on the petiole and in lacking reticulation on the propodeum.

***Dipara turneri* Hedqvist, 1969**
Fig. 25A–C

Dipara turneri Hedqvist 1969: 193–194.

Material examined. ***Holotype*** South Africa • 1 ♀; Port St. John, Pondoland; 6.–25. Feb. 1924; R.E. Turner leg.; NHMUK013455576.

Diagnosis. Female. Broad dark brown stripe across head from one eye to the other below toruli (Fig. 25B); median and lateral area of mesoscutum with distinct transverse broad black stripe (Fig. 25C); brachypterous, fore wing reaching slightly beyond petiole (Fig. 25A); petiole slightly wider than long (Fig. 25C).

Remarks. *Dipara turneri* is similar to *D. corona* in having a distinct transverse broad black stripe on the median and lateral area of the mesoscutum. In other not

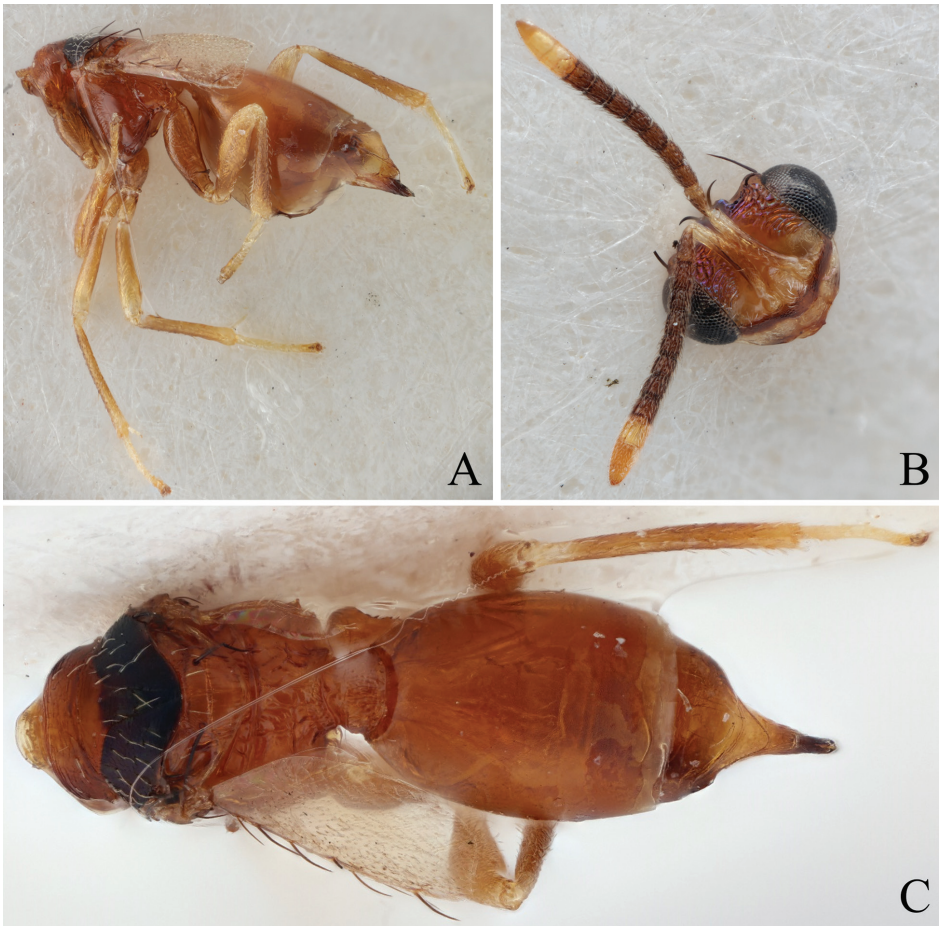

Figure 25. Holotype of *Dipara turneri* Hedqvist 1969 **A** habitus in lateral view **B** face in frontal view **C** body in dorsal view.

completely black species the black spots on the mesoscutum are restricted to the lateral area.

Dipara turneri differs from *D. corona* in the wing form and in the petiole shape. The petiole is longer than wide in *D. corona* and wider than long in *D. turneri*.

Discussion

Our results confirm that there is still a lot of undiscovered diversity within Microhymenoptera and the genus *Dipara* in particular (Desjardins 2007; Sharkey 2007; Aguiar et al. 2013; Forbes et al. 2018). Desjardins (2007) stated that there are "possibly hundreds of undescribed species" of *Dipara* left. We can support this statement based on the number of new *Dipara* species found only in the leaf litter in the small forest fragment Kakamega Forest, which more than doubled the number of known species from the Afrotropical mainland.

Some of the species descriptions in this study are based on so far unparalleled series of *Dipara* specimens. While most of the previously described *Dipara* species are known only from the holotype or just a few specimens, *D. kakamegensis*, for example, is described from 108 specimens and *D. nigroscutellata* from 86 specimens. These large series allowed for an advanced insight into intraspecific variation of *Dipara* species. The characters used for the species descriptions and diagnoses were found to be consistent among the large series, which gave us some confidence in delimiting species using the same characters in species with less specimens available. Our insights reveal that in most cases Afrotropical *Dipara* species seem to be reliably distinguishable by comparatively simple morphological characters of females like color patterns, surface sculpture or the number and position of setae or bristles. However, the intraspecific variation of the wing form of Diparinae females (Bouček 1988; Desjardins 2007; Mitroiu 2019) can pose a challenge for species delimitations, including those in this study. We decided to list wing related characters in the diagnoses and key but to always add additional non-wing characters.

While shedding more light on the species diversity of *Dipara* their biology remains largely unknown. All specimens were found in the leaf litter confirming that this might be their preferred habitat (Desjardins 2007). Reduced wings in females, which is found in 17 out of 22 Afrotropical species, can most likely be regarded as an adaptation to their ground-dwelling lifestyle and their search for hosts in the leaf litter or the soil. To gain more information about the hosts of *Dipara* more studies focusing on their biology would be needed.

Adding information on the biology, taxonomy, and distribution of species, is a crucial task. We still have only very limited knowledge on the biodiversity on this planet. We are aware, though, that we are facing presumably unprecedented biodiversity loss, especially through habitat destruction, and that this is one of the most pressing problems of our time (Steffen et al. 2015). The tropics including the Afrotropics are especially under threat because of ongoing deforestation and changes in land use, while also being biodiversity hotspots (Brooks et al. 2002). For example, the Kakamega Forest is the last large continuous forest in Kenya (Holstein 2015) and an officially protected area, but it is still under threat of habitat destruction (KIFCON 1994; Bleher et al.

2006; Lung and Schaab 2006; Müller and Mburu 2009). Studying the diversity of parasitoid wasps or other species-rich, abundant but understudied taxa can be a decisive tool for highlighting their importance for ecosystems, for conservation efforts and for understanding the evolution of the insects' megadiversification. This contribution to our knowledge on the genus *Dipara* might serve as a small but valuable addition to the overwhelming picture of the biodiversity of the Afrotropics.

Acknowledgments

Thanks to Hannes Baur for support with the morphmetric analysis and to Mircea-Dan Mitroiu for valuable information on Diparinae. We thank Natalie Dale-Skey (NHMUK) for images of type material. These images (Figs 17, 20, 21, 24, 25) are ©The Trustees of the Natural History Museum, London, and made available under Creative Commons License 4.0 (https://creativecommons.org/licenses/by/4.0/). We thank Didier Van den Spiegel (RMCA) for the loan of specimens. We thank Lars Krogmann, Mircea-Dan Mitroiu and one anonymous reviewer for valuable comments. For the presorting and labeling of the material, we thank Jennifer Werner, Gaby Nottebrock, and Dirk Rohwedder. For technical support, we thank Claudia Etzbauer and Jana Thormann. We thank Luke Schletzbaum for language editing.

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Supplementary material 1

Table S1

Authors: Christoph Braun, Ralph S. Peters

Data type: Xslx file.

Explanation note: Measurements for the morphometric analysis of *Dipara kakamegensis* sp. nov. and *Dipara nyani* sp. nov. See Table 1 for definitions of the characters.

Link: https://doi.org/10.3897/zookeys.1067.72395.suppl1

Supplementary material 2

Table S2

Authors: Christoph Braun, Ralph S. Peters

Data type: Xslx file.

Explanation note: Morphometric measurements for the descriptions of the newly described *Dipara* species. See Table 1 for definitions of the characters. N: measurement not available.

Link: https://doi.org/10.3897/zookeys.1067.72395.suppl2

Supplementary material 3

Table S3

Authors: Christoph Braun, Ralph S. Peters

Data type: Xslx file.

Explanation note: Shape ratios for the descriptions of the newly described *Dipara* species. See Table 1 for definitions of the characters and Table 1 for definitions of the characters and Table 2 for definitions of the shape categories. N: measurement not available.

Link: https://doi.org/10.3897/zookeys.1067.72395.suppl3

ZooKeys 1067: 159–208 (2021)
doi: 10.3897/zookeys.1067.72251
https://zookeys.pensoft.net

RESEARCH ARTICLE

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New species of *Labiobaetis* Novikova & Kluge from Southeast Asia and New Guinea (Ephemeroptera, Baetidae)

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Academic editor: E. Dominguez | Received 27 July 2021 | Accepted 6 September 2021 | Published 01 November 2021

http://zoobank.org/D0064766-0B19-45D7-A74D-74C8773B6094

Citation: Kaltenbach T, Gattolliat J-L (2021) New species of *Labiobaetis* Novikova & Kluge from Southeast Asia and New Guinea (Ephemeroptera, Baetidae). ZooKeys 1067: 159–208. https://doi.org/10.3897/zookeys.1067.72251

Abstract

Material collected between 2006 and 2016 in Borneo, Sulawesi, and New Guinea further increased our knowledge of *Labiobaetis* Novikova & Kluge in these regions. Five species were previously reported from Borneo, two from Sulawesi, and 33 from New Guinea. Six new species have been identified using a combination of morphology and genetic distance (COI, Kimura 2-parameter), one species from Borneo (Brunei), one from Sulawesi, and four from New Guinea. They are described and illustrated based on their larvae and keys to the species of the relevant groups are provided. Additionally, new reports, a complementary description, and the COI sequence for *L. dendrisetis* Kaltenbach & Gattolliat are presented. The distribution of *Labiobaetis* in the Wallacea region is discussed based on the new findings. The total number of *Labiobaetis* species worldwide is augmented to 153.

Keywords

Biogeography, Borneo, COI, integrated taxonomy, morphology, Sulawesi

Introduction

The family Baetidae has the highest species diversity among mayflies, comprising ca. 1,100 species in 114 genera (updated from Sartori and Brittain 2015; Jacobus et al. 2019; Cruz et al. 2020), which is approximately one third of all mayfly species

worldwide. They have a cosmopolitan distribution except New Zealand (Gattolliat and Nieto 2009). Investigations of the molecular phylogeny of the Order Ephemeroptera revealed the relatively basal position of the family in Ephemeroptera phylogeny (Ogden and Whiting 2005; Ogden et al. 2009, 2019).

The genus *Labiobaetis* Novikova & Kluge, 1987 (Novikova and Kluge 1987) is one of the richest genera of mayflies with 147 previously described species (Barber-James et al. 2013; Kaltenbach et al. 2020 and citations therein, 2021; Kaltenbach and Gattolliat 2021a, b). The distribution of *Labiobaetis* is nearly worldwide, except for the Neotropical realm, New Zealand, New Caledonia and some remote islands. The history and concept of the genus *Labiobaetis* were recently summarised in detail (Shi and Tong 2014; Kaltenbach and Gattolliat 2018). Kluge and Novikova (2016) established a new tribe Labiobaetini including the genera *Labiobaetis* and *Pseudopannota* Waltz & McCafferty, 1987, based on a unique combination of imaginal and larval characters.

Kaltenbach and Gattolliat (2018) started to create groups of species inside *Labiobaetis* based on combinations of morphological characters and later added further groups from other regions (Kaltenbach and Gattolliat 2019; Kaltenbach et al. 2020). In total, 16 groups were characterised so far. These morphological groups are primarily a working tool but could also serve as a basis for future studies on the generic delimitation and phylogeny of this genus. The inclusion of nuclear gene sequences may prove that some are natural groups.

This contribution will focus on further new species of *Labiobaetis* from Borneo, Sulawesi and New Guinea with integrative taxonomy. In the past, five species were reported from Indonesia (*L. fulmeki* (Ulmer), *L. obscurum* (Ulmer), *L. necopinatum* (Müller-Liebenau), *L. ulmeri* (Müller-Liebenau) and *L. boettgeri* (Ulmer)). All were described from adults only and no species were previously known at the larval stage (Ulmer 1913, 1924, 1939; Müller-Liebenau 1981). The generic attribution of these species is still controversial as *Labiobaetis* remains difficult to delimit in the imaginal stage. Recently, a first comprehensive study on *Labiobaetis* in Indonesia was done, including the description of 18 new species based on larvae (Kaltenbach and Gattolliat 2019). The *Labiobaetis* fauna of Borneo, including Brunei, the Malaysian part and the Indonesian part of the island was studied by Kaltenbach and Gattolliat (2020), after a first contribution by Müller-Liebenau (1984a). From the megadiverse New Guinea, the first six *Labiobaetis* species were reported by Lugo-Ortiz et al. (1999) and a subsequent larger study was published by Kaltenbach and Gattolliat (2019), including the description of 26 new species.

Indonesia is an immense archipelago of more than 18.000 islands extending over a huge area from 95°E to 141°E and from 6°N to 11°S. It is one of the most biologically rich countries in the world. The high levels of species richness and endemism are mainly attributable to a complex geological history, that brought together two different biological realms (Oriental realm and Australasian realm), separated by a transitional region (Wallacea) (Kingston 2010; Hall 2010). The main islands are Sumatra, Java, Borneo (partly, Kalimantan Province), Sulawesi, and New Guinea (partly, provinces West Papua and Papua). Borneo, Sumatra, Java, and the Malay Peninsula form the Sundaland Biodiversity Hotspot (Quek 2010), influenced by a dynamic and highly complex geophysical history including changing climates, fluctuating sea levels, volcanism, and orogenic ac-

tivity with subsequent erosion (Queck 2010). New Guinea, the second largest island after Greenland, is equally known for its megadiversity. It is a geological composite consisting of many separate terranes; the evolutionary history of the biota is linked to the accretion of these terranes to the Australian craton, and to the uplift, volcanism, and rifting that accompanied these tectonic events (Allison 2010). There is strong evidence that recent environmental change in the extremely structured central highlands of New Guinea with its ongoing formation of rich aquatic resources and remote valleys and mountain blocks has been the primary driver of diversification of aquatic insects in that area (Toussaint et al. 2013, 2014). Taking into account the extreme diversity in Southeast Asia and New Guinea, the rather poor collection activities in the past, with many still unexplored regions, and the obvious richness of *Labiobaetis* in this region, we have to expect many more species with further collections in the future.

Materials and methods

Part of the material was collected during a series of university training practicals (see also Kaltenbach et al. 2021). The specimens from Brunei were collected in 2014 and 2016 by Kate Baker (University of Exeter, UK) during ecological studies in Brunei Darussalam in collaboration with Universiti Brunei Darussalam (Baker et al. 2016a, b, 2017a, b, 2019).

All specimens were preserved in 70%–96% ethanol. The dissection of larvae was done in Cellosolve (2-Ethoxyethanol) with subsequent mounting on slides with Euparal liquid, using an Olympus SZX7 stereomicroscope.

The DNA of part of the specimens was extracted using non-destructive methods allowing subsequent morphological analysis (see Vuataz et al. 2011 for details). We amplified a 658 bp fragment of the mitochondrial gene cytochrome oxidase subunit 1 (COI) using the primers LCO 1490 and HCO 2198 (Folmer et al. 1994; see Kaltenbach and Gattolliat 2020 for details). Sequencing was done with Sanger's method (Sanger et al. 1977). The genetic variability between specimens was estimated using Kimura-2-parameter distances (K2P, Kimura 1980), calculated with the program MEGA 7 (Kumar et al. 2016, http://www.megasoftware.net).

The GenBank accession numbers are given in Table 1; the nomenclature of gene sequences follows Chakrabarty et al. (2013).

Drawings were made using an Olympus BX43 microscope. To facilitate the determination of species and the comparison of important structures, we partly used a combination of dorsal and ventral aspects in one drawing. Explanations are given in Kaltenbach et al. (2020: fig. 1).

Photographs of larvae were taken using a Canon EOS 6D camera and processed with the programs Adobe Photoshop Lightroom (http://www.adobe.com) and Helicon Focus version 5.3 (http://www.heliconsoft.com). Photographs were subsequently enhanced with Adobe Photoshop Elements 13.

The distribution maps were generated with the program SimpleMappr (https://simplemappr.net, Shorthouse 2010).

Table 1. Sequenced specimens: treated species and known species of group *claudiae*.

Species	Species group	Locality	Specimens catalog #	GenBank # (COI)	GenSeq Nomenclature
L. catadupa sp. nov.	*catadupa*	Brunei	GBIFCH00592439	MW868314	genseq-2 COI
L. toraja sp. nov.	*catadupa*	Sulawesi	GBIFCH00674627	MW868315	genseq-2 COI
			GBIFCH00674628	MW868316	genseq-2 COI
L. academicus	*claudiae*	Papua Province	GBIFCH00673069	MW041241	genseq-2 COI
			GBIFCH00673081	MW041242	genseq-2 COI
L. centralensis	*claudiae*	Papua New Guinea: Central Prov.	GBIFCH00465215	MH619495	genseq-1-COI
			GBIFCH00465216	MH619494	genseq-2 COI
L. claudiae	*claudiae*	Papua New Guinea: Madang Prov.	GBIFCH00508144	MH619479	genseq-1-COI
L. hattam sp. nov.	*claudiae*	Papua Barat	GBIFCH00763707	MW868311	genseq-2 COI
L. stagnum	*claudiae*	Papua Province	GBIFCH00465168	MH619491	genseq-2 COI
L. werneri sp. nov.	*claudiae*	Papua New Guinea: Gulf Prov.	GBIFCH00763699	MW868307	genseq-1-COI
		Papua New Guinea: Eastern Highlands	GBIFCH00763603	MW868309	genseq-2 COI
		Papua New Guinea: Morobe Prov.	GBIFCH00763700	MW868308	genseq-2 COI
L. dendrisetis	*dendrisetis*	Papua New Guinea: Central Prov.	GBIFCH00763706	MW868310	genseq-4 COI
L. arfak sp. nov.	*seramensis*	Papua Barat	GBIFCH00763714	MW868312	genseq-2 COI
			GBIFCH00763715	MW868313	genseq-2 COI

The dichotomous keys were elaborated with the support of the program DKey version 1.3.0 (http://drawwing.org/dkey, Tofilski 2018).

The terminology follows Hubbard (1995; legs orientation) and Kluge (2004; most terms, but the term gill/gills is used instead of tergalius/tergalii).

Abbreviations

MZB Museum Zoologicum Bogoriense (Indonesia);
MZL Musée de Zoologie Lausanne (Switzerland);
ZSM Zoologische Staatssammlung München (Germany).

Results

List of *Labiobaetis* species treated in this paper

catadupa group (new group)
1. *L. catadupa* sp. nov.
2. *L. toraja* sp. nov.

claudiae group
3. *L. hattam* sp. nov.
4. *L. werneri* sp. nov.

dendrisetis group

5. *L. dendrisetis* Kaltenbach & Gattolliat, 2018

seramensis group

6. *L. arfak* sp. nov.
7. *L. onim* sp. nov.

Labiobaetis catadupa group of species (new group of species)

The *catadupa* group can be recognised by the following combination of characters: A) dorsal surface of labrum with submarginal arc of feathered setae (Figs 1b, 6a, 3); B) labial palp segment II extended thumb-like, glossae much shorter than paraglossae (Figs 1i, 6h); C) claws with long subapical seta on posterior side and reduced subapical seta on anterior side (Figs 2b, 4a, b, 7d); D) hind protoptera absent; E) six pairs of gills (gill I absent).

The *L. catadupa* group is so far known from Borneo and Sulawesi, it includes the following species:

Labiobaetis catadupa sp. nov.
Labiobaetis toraja sp. nov.

***Labiobaetis catadupa* sp. nov.**

http://zoobank.org/44D4E549-FDB5-41B8-B459-8EBB70BFB2E5
Figures 1–3, 4a, 5, 17a, 21b

Type material. ***Holotype.*** Brunei • larva; Temburong District, Ulu Temburong National Park, Belalong River (near field station); 04°32'49"N, 115°09'30"E; 100 m; v. 2014; leg. K. Baker; on slide; GBIFCH00592448; MZL. ***Paratypes.*** Brunei • 17 larvae; Temburong District, Ulu Temburong National Park; 04°33'10"N, 115°09'20"E; v. 2014; leg. K. Baker; 2 on slides; GenBank MW868314; GBIFCH00592439, GBIFCH00592440; 15 in alcohol; GBIFCH00515571, GBIFCH00515573, GBIFCH00515598; MZL • 12 larvae; Temburong District, Ulu Temburong National Park; 04°32'42"N, 115°09'31"E; v. 2014; leg. K. Baker; 1 on slide; GBIFCH00592442; 11 in alcohol; GBIFCH00515597; MZL • 4 larvae; Temburong District, Ulu Temburong National Park; 04°32'23"N, 115°09'34"E; 25.–31.vii. 2016; leg. K. Baker; in alcohol; GBIFCH00515576; MZL • 9 larvae; Temburong District, Ulu Temburong National Park, Mata Ikan; 04°32'51"N, 115°09'25"E; 25.–31.vii. 2016; leg. K. Baker; 1 on slide; GBIFCH00592441; 8 in alcohol; GBIFCH00515582, GBIFCH00515583, GBIFCH00515589, GBIFCH00515590; MZL • 12 larvae; Temburong District, Ulu Temburong National Park; 04°33'39"N, 115°08'54"E; 25.–31.vii. 2016; leg. K. Baker; in alcohol; GBIFCH00515574, GBIFCH515575, GBIFCH515578; MZL • 5 larvae; Temburong District, Ulu Temburong National Park; 04°33'39"N, 115°08'51"E; 25.–31.vii. 2016; leg. K. Baker; 1 on slide;

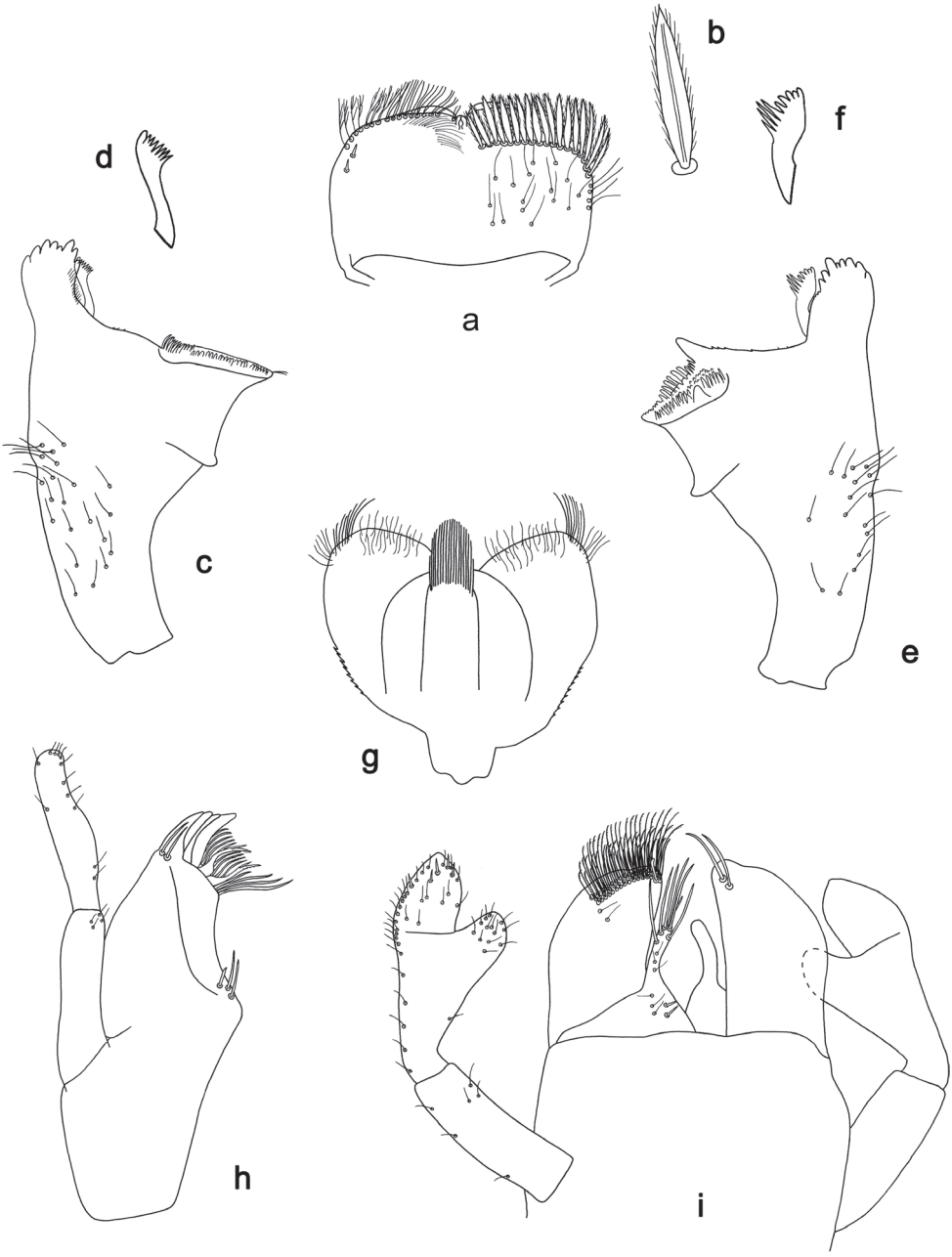

Figure 1. *Labiobaetis catadupa* sp. nov., larva morphology: **a** labrum **b** seta from arc on dorsal surface of labrum **c** right mandible **d** right prostheca **e** left mandible **f** left prostheca **g** hypopharynx and superlingua **h** maxilla **i** labium.

GBIFCH00515577; 4 in alcohol; GBIFCH00515599, GBIFCH00515572, GBIFCH00515621, GBIFCH00515600; MZL • 6 larvae; Temburong District, Ulu Temburong National Park; 04°33'10"N, 115°09'20"E; 25.–31.vii. 2016; leg. K. Baker; in

alcohol; GBIFCH00515588, GBIFCH00515593; MZL. **Other material.** Brunei • 25 larvae; Temburong District, Ulu Temburong National Park; 04°32'42"N, 115°09'31"E; 25.–31.vii. 2016; leg. K. Baker; in alcohol; GBIFCH00515584, GBIFCH00515579, GBIFCH00515587, GBIFCH00515592; MZL • 5 larvae; Temburong District, Ulu Temburong National Park; 04°32'56"N, 115°09'27"E; 25.–31.vii. 2016; leg. K. Baker; in alcohol; GBIFCH00515580, GBIFCH00515586, GBIFCH00515591; MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of 17–19 long, feathered setae with broad middle part (Figs 1a, b, 3); B) labial palp segment II with extended thumb-like distomedial protuberance, segment III slightly pentagonal; glossae much shorter than paraglossae (Fig. 1i); C) left mandible without setae at apex of mola; D) fore femur length ca. 3× maximum width, dorsal margin with 17–19 curved, spine-like setae (Fig. 2a); E) claw with long subapical seta on posterior side and reduced subapical seta on anterior side (Figs 2b, 4a); F) hind protoptera absent; G) six pairs of gills (gill I absent); H) paraproct distally expanded, with ca. 40 stout, marginal spines.

Description. Larva (Figs 1–3, 4a, 17a). Body length 2.6–6.0 mm. Cerci: ca. 2/3 of body length. Paracercus: ca. 1/5 of cerci length. Antenna: approx. twice as long as head length.

Colouration (Fig. 17a). Head, thorax and abdomen dorsally and ventrally brown. Legs light brown, caudalii light brown.

Antenna (Fig. 2f) with scape and pedicel sub cylindrical, without distolateral process at scape.

Labrum (Fig. 1a, b). Rectangular, length 0.6× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of 17–19 long, feathered setae with broad middle part. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid setae; ventral surface with ca. two short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 1c, d). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola slightly convex, with few minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 1e, f). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with minute denticles. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola absent.

Both mandibles with lateral margins slightly convex. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlingua (Fig. 1g). Lingua shorter than superlingua. Lingua approx. as long as broad; distal half laterally not expanded; medial tuft of stout setae well developed. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

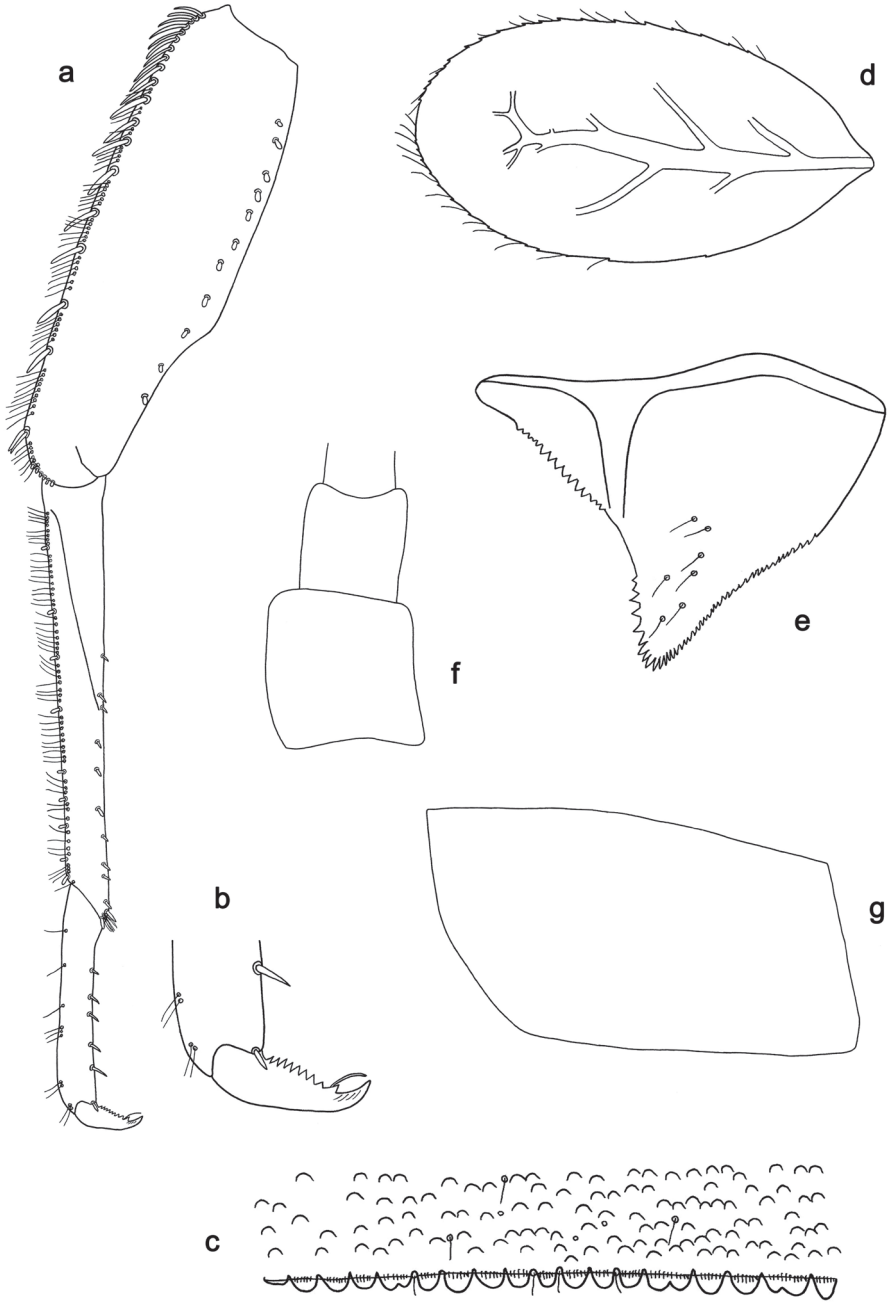

Figure 2. *Labiobaetis catadupa* sp. nov., larva morphology: **a** foreleg **b** fore claw **c** tergum IV **d** gill IV **e** paraproct **f** base of antenna **g** metanotum.

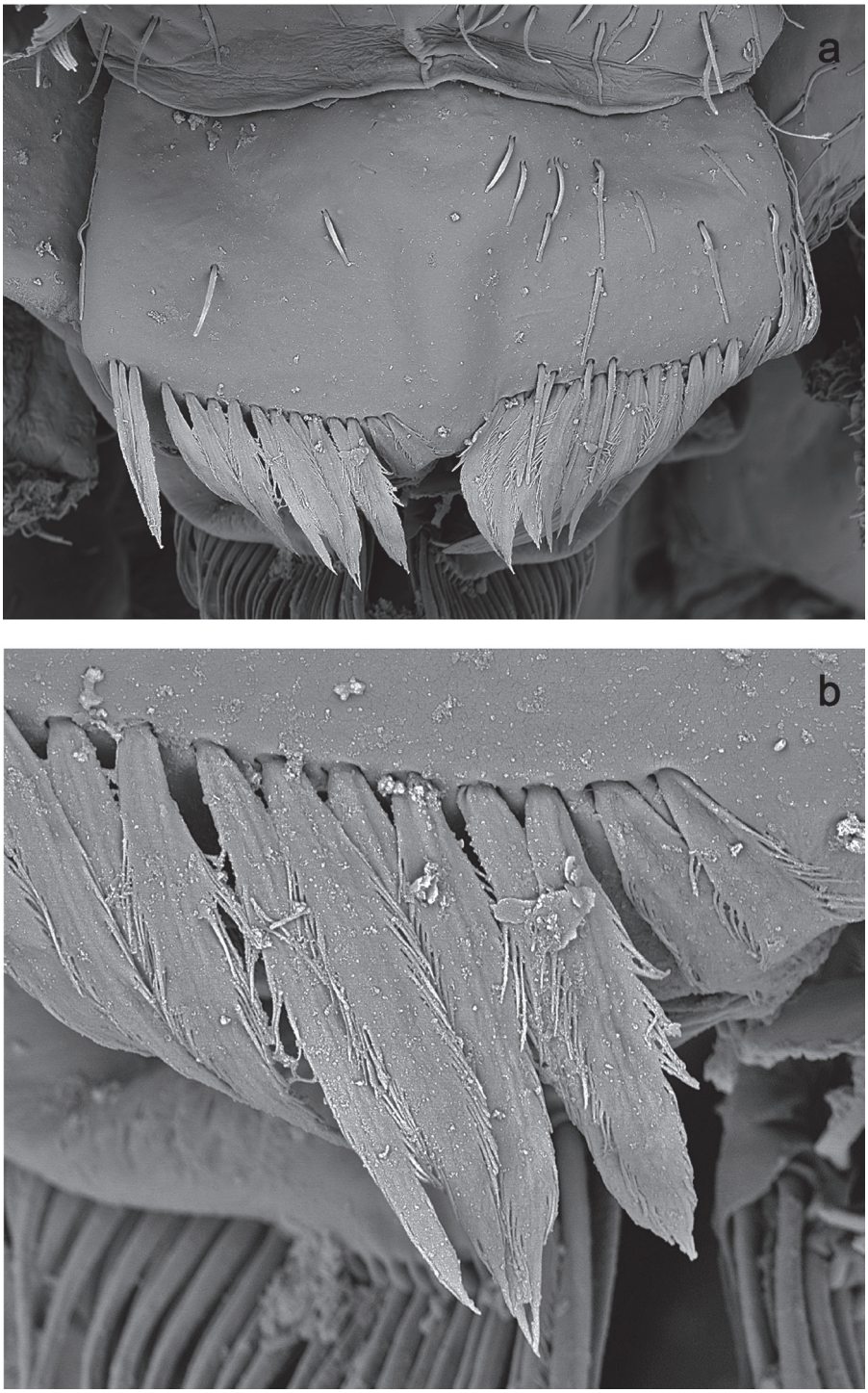

Figure 3. *Labiobaetis catadupa* sp. nov., SEM pictures: **a** labrum **b** section of labrum with setae of dorsal, submarginal arc.

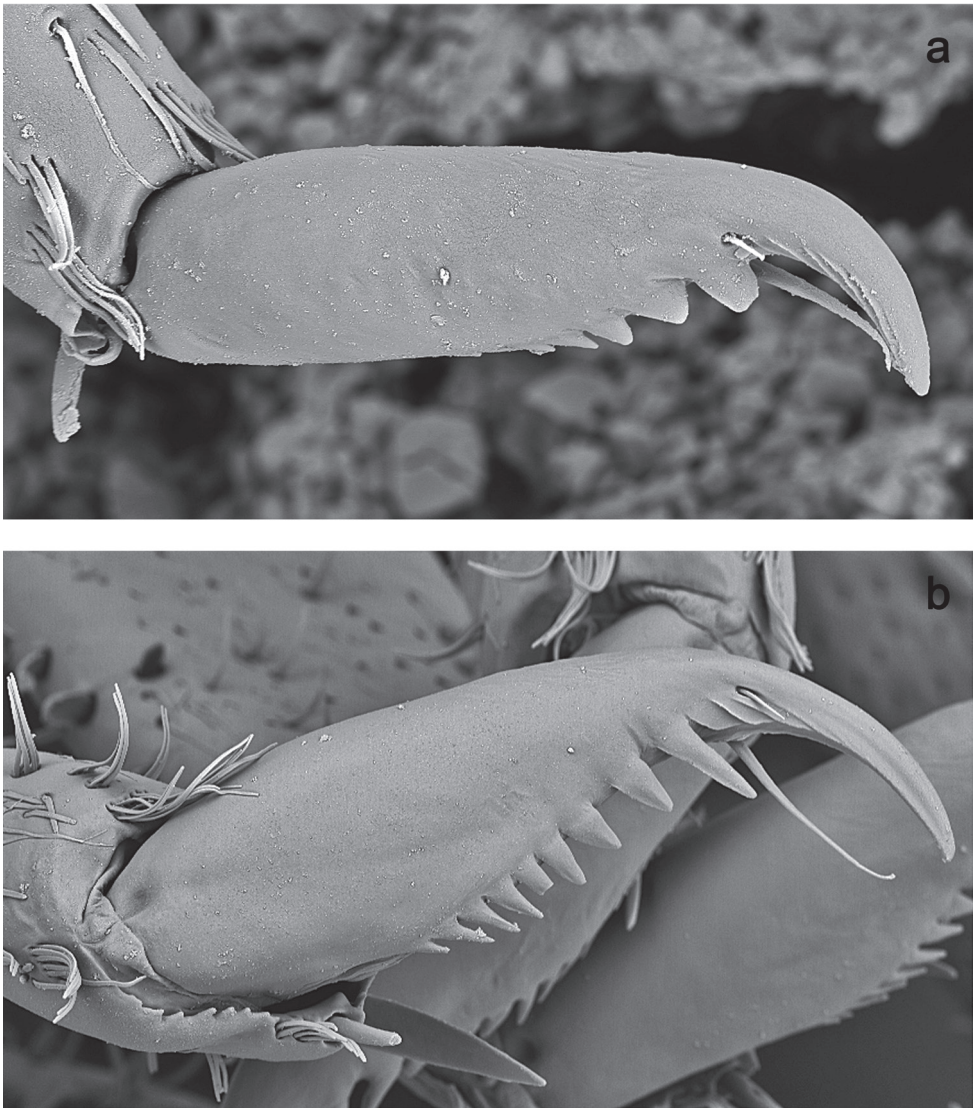

Figure 4. SEM pictures, claws: **a** *Labiobaetis catadupa* sp. nov. **b** *Labiobaetis toraja* sp. nov.

Maxilla (Fig. 1h). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and two or three medium, simple setae. Maxillary palp ca. 1.2× length of galea-lacinia; 2-segmented; palp segment II approx. as long as segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment with slight excavation at inner distolateral margin.

Labium (Fig. 1i). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with one spine-like seta; apex with two long and one medium, robust setae; outer margin with three spine-like setae; ventral surface with fine, simple,

Figure 5. *Labiobaetis catadupa* sp. nov., habitats in Brunei (photographs Kate Baker, University Exeter, UK).

scattered setae. Paraglossa sub-rectangular, slightly curved inward; apex slightly concave; with three rows of long, robust, distally pectinate setae in apical area and two or three short, simple setae in anteromedial area; dorsally with two long, spine-like setae near inner margin. Labial palp with segment I 0.7× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with extended thumb-like, distomedial protuberance, bent upwards; distomedial protuberance 0.8× width

of base of segment III; ventral surface with short, fine, simple setae; dorsally without spine-like setae near outer margin. Segment III slightly pentagonal; length 1.3× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 2g) absent.

Foreleg (Fig. 2a, b). Ratio of foreleg segments 1.2:1.0:0.5:0.2. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with a row of 17–19 curved, spine-like setae and a row of long, fine, simple setae; length of setae 0.24× maximum width of femur. Apex rounded, with a pair of spine-like setae and some short, stout setae. Stout, apically rounded setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with a row of short, spine-like setae and long, fine, simple setae. Ventral margin with a row of short, curved, spine-like setae, on apex a tuft of fine, simple setae. Patellotibial suture present on basal 1/2. ***Tarsus.*** Dorsal margin with a row of fine, simple setae. Ventral margin with a row of curved, spine-like setae. Claw with one row of eight or nine denticles; distally pointed; with ca. four stripes; with long, subapical seta on posterior side and reduced, subapical seta on anterior side.

Terga (Fig. 2c). Surface with irregular rows of U-shaped scale bases and scattered fine, simple setae. Posterior margin of tergum IV with rounded spines, wider than long.

Gills (Fig. 2d). Present on segments II–VII. Margin with small denticles intercalating fine simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and 1/3 VI combined. Gill VII as long as length of segment VIII.

Paraproct (Fig. 2e). Distally expanded, with ca. 40 stout, marginal spines. Surface scattered with fine, simple setae. Cercotractor with numerous small, marginal spines.

Etymology. Based on the Latin word *catadupa*, meaning waterfall, with reference to the habitat of the species.

Distribution. Brunei (Fig. 21b).

Biological aspects. The specimens were collected at an altitude of 150 m, mostly from waterfalls with slope angles of 16° to 50° and lengths between 5 m and 20 m (Fig. 5; Baker et al. 2017a, b). They were sampled on rock in fast flowing water and others it was a film of water with algae/moss (pers. comm. Kate Baker, University Exeter, Great Britain).

Labiobaetis toraja **sp. nov.**

http://zoobank.org/03D69309-BC3E-4BB0-975A-84F99294AEF9

Figures 4b, 6, 7, 17b, c, 21b

Type material. ***Holotype.*** Indonesia • larva; Sulawesi; Tengah, Lake Lore; 01°19'35"S, 120°18'40"E; 1600 m; 01.ix.2011; leg. Sumoked (SUL013); on slide; GBIFCH00592443; MZB. ***Paratypes.*** Indonesia • 9 larvae; same data as holotype; 2 on slides; GBIFCH00592444, GBIFCH00592446; 7 in alcohol; GenBank MW868315, MW868316; GBIFCH00674627, GBIFCH00674628, GBIFCH00515619, GBIFCH00515620, GBIFCH00515596; MZB, MZL.

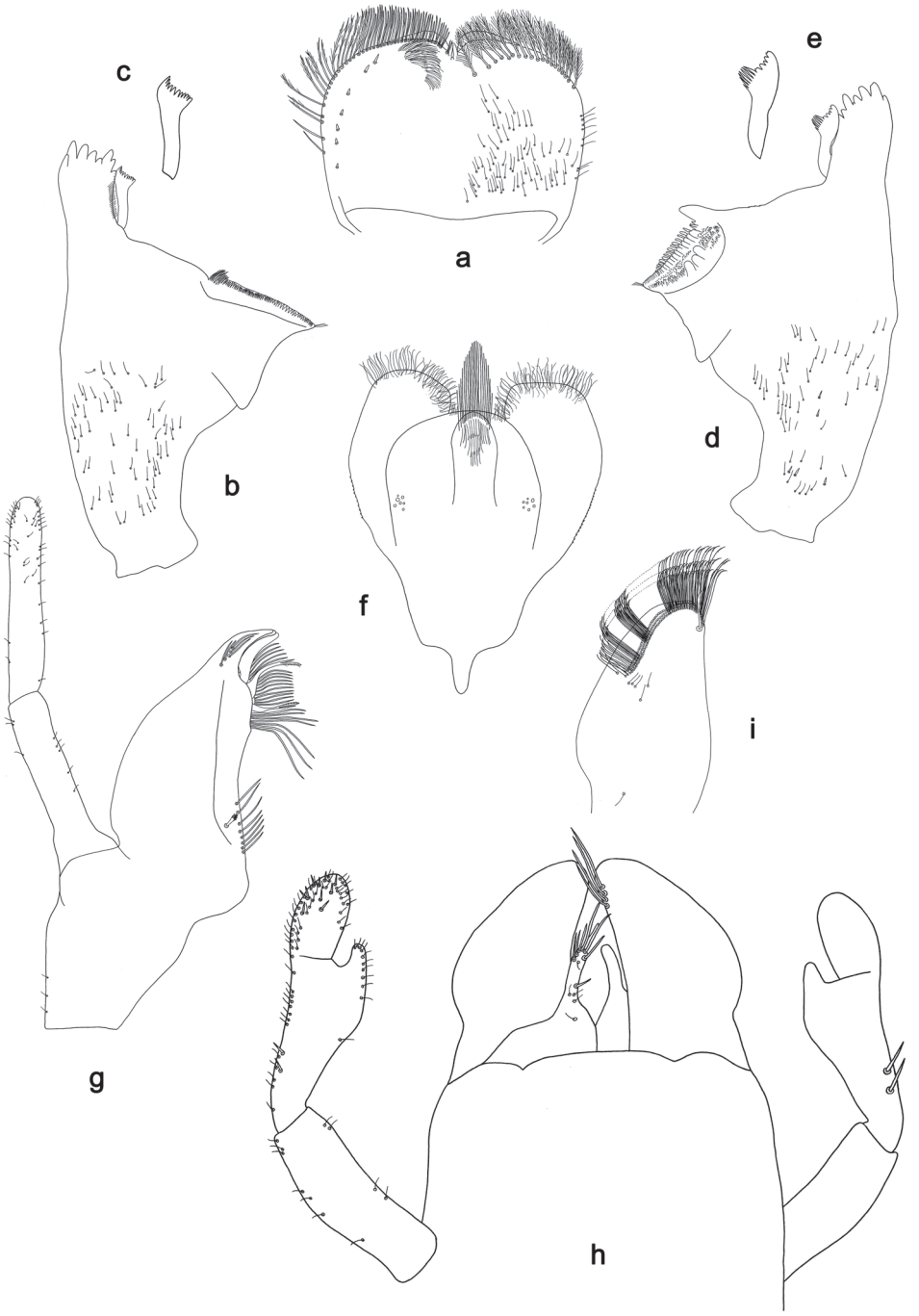

Figure 6. *Labiobaetis toraja* sp. nov., larva morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlingua **g** maxilla **h** labium **i** apex of paraglossa.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of one plus 18–21 long, feathered setae (Figs 6a, 4b); B) labial palp segment II with hook-like distomedial protuberance, segment III oblong; glossae much shorter than paraglossae (Fig. 6h); C) left mandible with setae at apex of mola; D) fore femur length ca. 3× maximum width, dorsal margin with 18–25 curved, spine-like setae (Fig. 7a); E) claw with long subapical seta on posterior side and reduced subapical seta on anterior side (Figs 4b, 7d); F) hind protoptera absent; G) six pairs of gills (gill I absent); H) paraproct distally slightly expanded, with more than 40 stout, marginal spines.

Description. Larva (Figs 4b, 6, 7, 17b, c). Body length 5.5–6.5 mm. Cerci broken. Paracercus: ca. 0.4× body length. Antenna: approx. twice as long as head length.

Colouration (Fig. 17b, c). Head, thorax and abdomen dorsally brown, with pattern as in Fig. 17b. Head, thorax and abdomen ventrally light brown, abdominal segments VII–IX laterally darker (Fig. 17c). Legs light brown; femur with dorsomedial brown streak and brown sections apically and distoventrally; tibia basally and tarsus distally darker (Fig. 17c). Caudalii ecru.

Antenna (Fig. 7h) with scape and pedicel sub cylindrical, without distolateral process at scape. Scape and pedicel with few stout setae.

Labrum (Fig. 6a). Sub-rectangular, length 0.7× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus 18–21 long, feathered setae. Ventrally with marginal row of setae composed of lateral and anterolateral long, feathered setae and medial long, bifid setae; ventral surface with ca. seven short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 6b, c). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola straight. Tuft of setae at apex of mola present.

Left mandible (Fig. 6d, e). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight, with few minute denticles. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola present.

Both mandibles with lateral margins slightly convex. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlingua (Fig. 6f). Lingua shorter than superlingua. Lingua approx. as long as broad; distal half laterally not expanded; medial tuft of stout setae well developed and long. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 6g). Galea-lacinia ventrally with five simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and 6–8 long, simple setae. Maxillary palp ca. 1.3× length of galea-

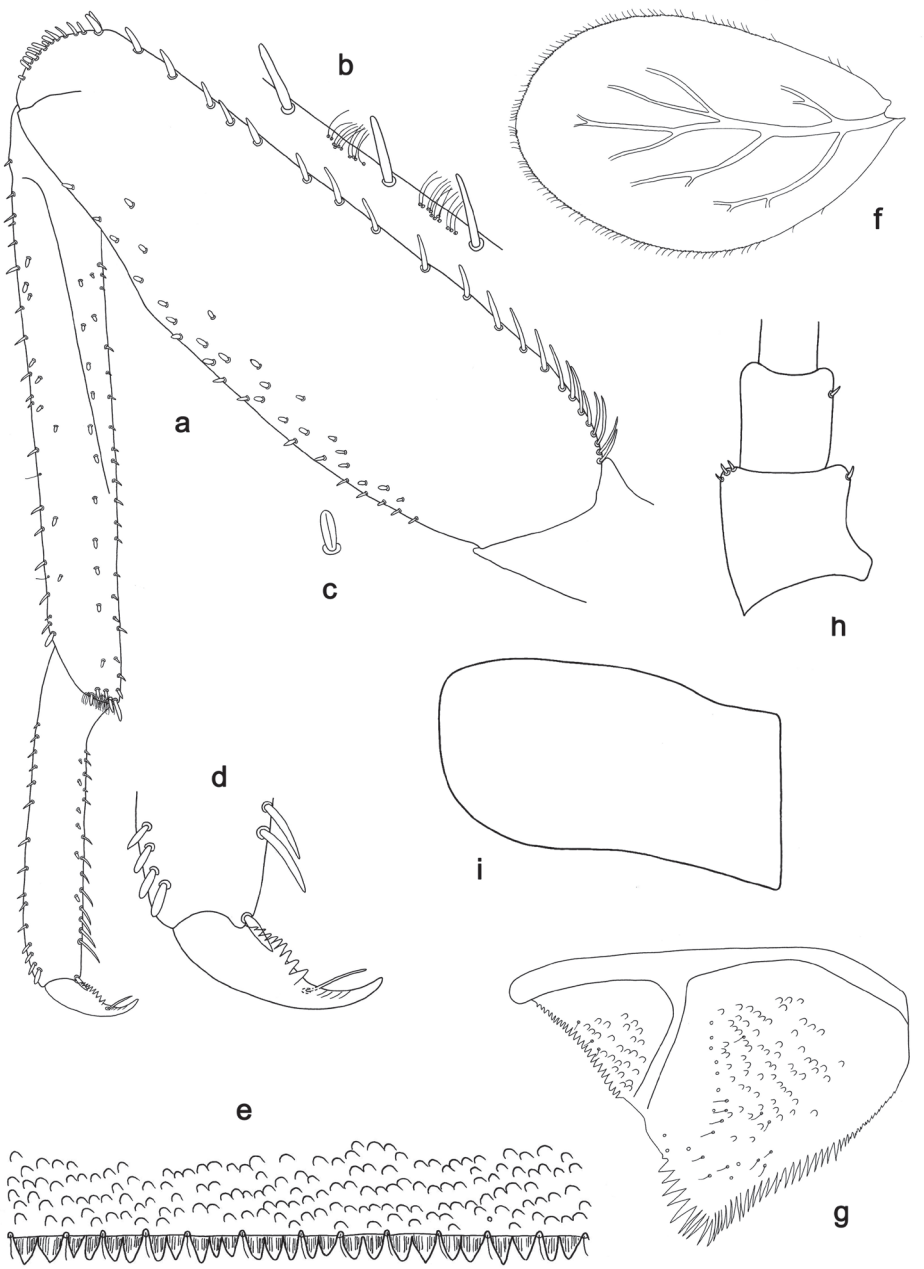

Figure 7. *Labiobaetis toraja* sp. nov., larva morphology: **a** foreleg **b** dorsal margin of femur **c** seta on ventral part of femur **d** fore claw **e** tergum IV **f** gill IV **g** paraproct **h** base of antenna **i** metanotum.

lacinia; 2-segmented; palp segment II 1.2× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without excavation at inner distolateral margin.

Labium (Fig. 6h, i). Glossa basally broad, narrowing toward apex; much shorter than paraglossa; inner margin with two spine-like setae; apex with two long and one medium, robust setae; outer margin with three spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa broad, slightly curved inward; outer margin convex; apex rounded; with three long rows of long, robust, distally pectinate setae in apical area, five or six short, simple setae in anteromedial area and one short, simple seta in posteromedial area; dorsally with a row of four long, spine-like setae near inner margin. Labial palp with segment I 0.8× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with hook-like, distomedial protuberance; distomedial protuberance 0.9× width of base of segment III; ventral surface with short, simple setae; dorsally with one or two spine-like setae near outer margin. Segment III oblong; length 1.7× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 7i) absent.

Foreleg (Fig. 7a–d). Ratio of foreleg segments 1.2:1.0:0.6:0.2. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with a row of 18–25 curved, spine-like setae and a row of long, fine, simple setae; length of setae 0.21× maximum width of femur. Apex rounded, with a pair of spine-like setae and some short, stout setae. Stout, apically rounded setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with a row of short, spine-like setae. Ventral margin with a row of short, curved, spine-like setae, on apex some longer setae and a tuft of fine, simple setae. Anterior surface scattered with stout, lanceolate setae. Patellotibial suture present on basal 2/3 area. ***Tarsus.*** Dorsal margin with a row of short, spine-like setae. Ventral margin with a row of curved, spine-like setae and a row of short, stout setae near margin. Claw with one row of nine or ten denticles; distally pointed; with ca. four stripes; with long, subapical seta on posterior side and reduced, subapical seta on anterior side.

Middle and hind legs. As foreleg, but middle leg with a reduced femoral patch and hind leg with a rather well developed femoral patch.

Terga (Fig. 7e). Surface with irregular rows of U-shaped scale bases. Posterior margin of tergum IV with triangular, apically rounded spines, slightly longer than wide, and fine simple setae.

Gills (Fig. 7f). Present on segments II–VII. Margin with small denticles intercalating fine simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and 1/2 VI combined. Gill VII as long as length of segment VIII.

Paraproct (Fig. 7g). Distally slightly expanded, with more than 40 stout, marginal spines. Surface scattered with U-shaped scale bases, fine, simple setae and micropores. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the indigenous Toraja people of Sulawesi, where the type locality is located.

Distribution. Indonesia: Sulawesi (Fig. 21b).

Biological aspects. The specimens were collected at an altitude of 1600 m in a tributary to Lake Lore.

Labiobaetis claudiae group of species (Kaltenbach and Gattolliat 2018)

The *claudiae* group is recognised by the following combination of characters: A) dorsal surface of labrum with submarginal arc of simple setae; B) labial palp segment II with rather narrow thumb-like distomedial protuberance; C) maxillary palp segment II without distolateral excavation, apex usually constricted; D) six pairs of gills (gill I absent); E) gills margin usually with both shorter and longer setae; F) hind protoptera absent; G) distolateral process at scape absent; H) femur dorsally with relatively short setae (length below 0.20× maximum width of femur); I) femur apically with stout setae on posterior side of foreleg and middle leg; J) femoral patch present on all legs.

The *L. claudiae* group is known from New Guinea only, it includes the following species:

Labiobaetis academicus Kaltenbach, Surbakti & Kluge, 2021
Labiobaetis centralensis Kaltenbach & Gattolliat, 2018 (new assignment, see discussion)
Labiobaetis claudiae Kaltenbach & Gattolliat, 2018
Labiobaetis hattam sp. nov.
Labiobaetis stagnum Kaltenbach & Gattolliat, 2018
Labiobaetis werneri sp. nov.

Key to the species of the *Labiobaetis claudiae* group (larvae)

1 Paraproct distally expanded (Fig. 9g) **2**
– Paraproct distally not expanded (Fig. 11f) **4**
2 Anal margins of gills with both longer and shorter setae (Kaltenbach et al. 2021: fig. 4c, d) ..... ***L. stagnum***
– Anal margin of gills with short setae only (Fig. 9f)..... **3**
3 Posterior margins of tergites with triangular spines, longer than wide (Fig. 9e); scape with stout setae (Fig. 9h)..... ***L. hattam* sp. nov.**
– Posterior margins of tergites with triangular spines, wider than long (Kaltenbach and Gattolliat 2018: fig. 47e); scape without stout setae.... ***L. centralensis***
4 Posterior margins of tergites with triangular spines, wider than long (Fig. 11d)..... ***L. werneri* sp. nov.**
– Posterior margins of tergites with triangular spines, longer than wide (Kaltenbach and Gattolliat 2018: fig. 9c) **5**
5 Labial palp segment II with rather broad thumb-like distomedial protuberance (Kaltenbach et al. 2021: fig. 4f) ..... ***L. claudiae***
– Labial palp segment II with narrow thumb-like distomedial protuberance (Kaltenbach et al. 2021: fig. 1h)..... ***L. academicus***

***Labiobaetis hattam* sp. nov.**
http://zoobank.org/A8E19D2A-874A-4BDC-BC26-EB900063EC91
Figures 8, 9, 18a, b, 21c

Type material. ***Holotype*.** Indonesia • larva; Papua Barat, Fumato to Kebar, forest stream; 00°52'29"S, 132°46'06"E; 492 m; 06.xi.2013; leg. UNIPA team; BH030; on slide; GBIFCH00592775; MZB. ***Paratypes*.** Indonesia • 3 larvae; same data as holotype; 2 on slides; GenBank MW868311; GBIFCH00763707, GBIFCH00592704; 1 in alcohol; GBIFCH00515652; MZB, MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of one plus six long, simple setae (Fig. 8a); B) labial palp segment II with narrow, extended, distomedial protuberance, segment III slightly pentagonal (Fig. 8h); C) fore femur rather slender, length ca. 4× maximum width, dorsal margin with 19–23 spine-like setae (Fig. 9a); D) hind protoptera absent; E) six pairs of gills (gill I absent), margin with short setae only; F) paraproct distally slightly expanded, with 38–48 stout, marginal spines (Fig. 9g); G) Scape apically with stout setae (Fig. 9h).

Description. Larva (Figs 8, 9, 18a, b). Body length 7.0–7.6 mm. Cerci and paracercus broken. Antenna: approx. 3× as long as head length.

Colouration (Fig. 18a, b). Head, thorax and abdomen dorsally dark brown, with pattern as in Fig. 18a; fore protoptera brown with bright stripes. Thorax ventrally ecru, abdomen ventrally brown, with pattern as in Fig. 18b. Legs light brown; femur with dorsomedial and apical brown spots; tibia medially and tarsus proximally brown. Caudalii brown.

Antenna (Fig. 9h) with scape and pedicel sub cylindrical, without distolateral process at scape. Scape apically with few stout setae.

Labrum (Fig. 8a). Sub-rectangular, length 0.8× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus six long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid, pectinate setae; ventral surface with ca. seven short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 8b, c). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola almost straight. Tuft of setae at apex of mola present.

Left mandible (Fig. 8d, e). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola almost straight. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

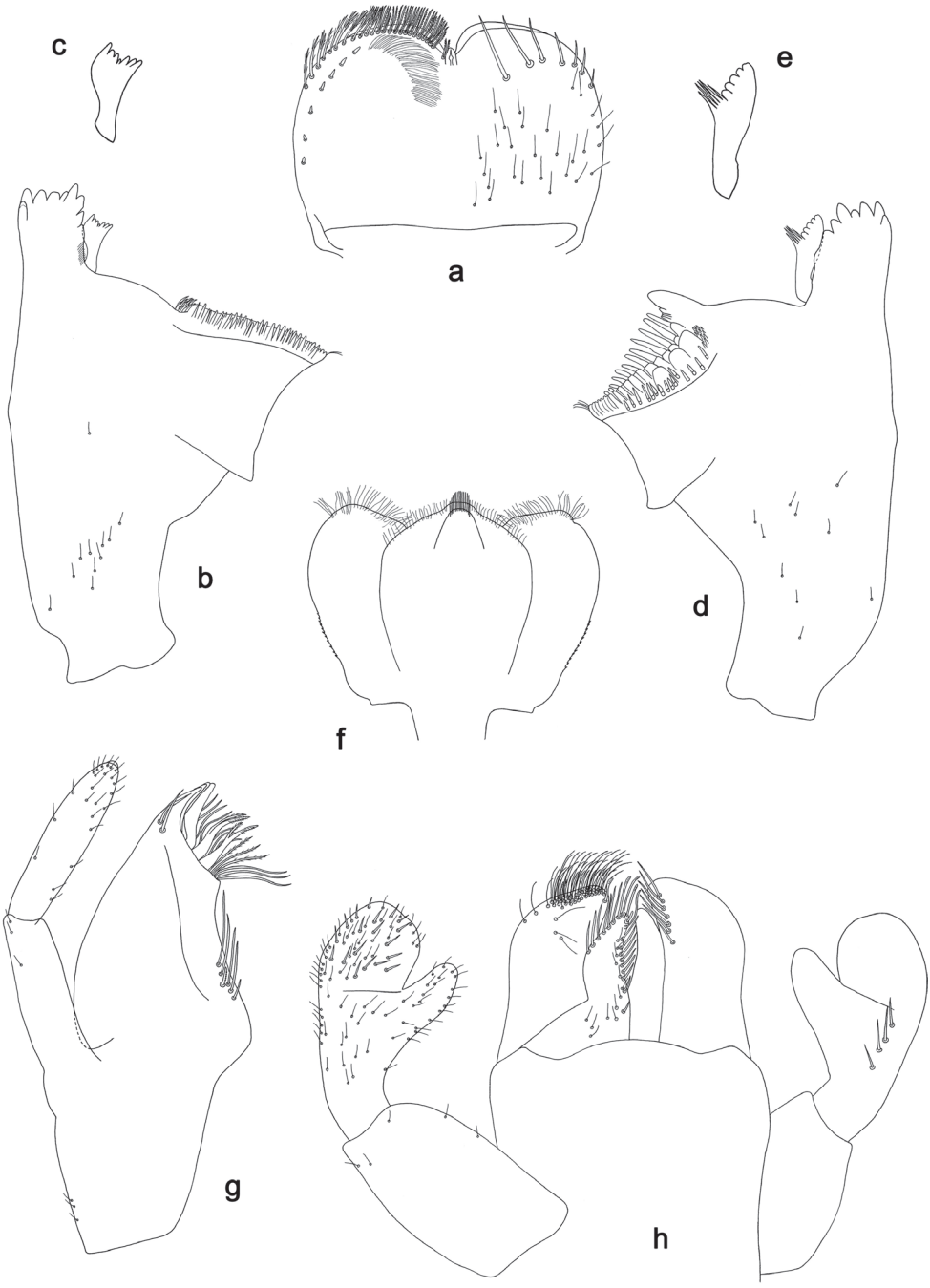

Figure 8. *Labiobaetis hattam* sp. nov., larva morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlingua **g** maxilla **h** labium.

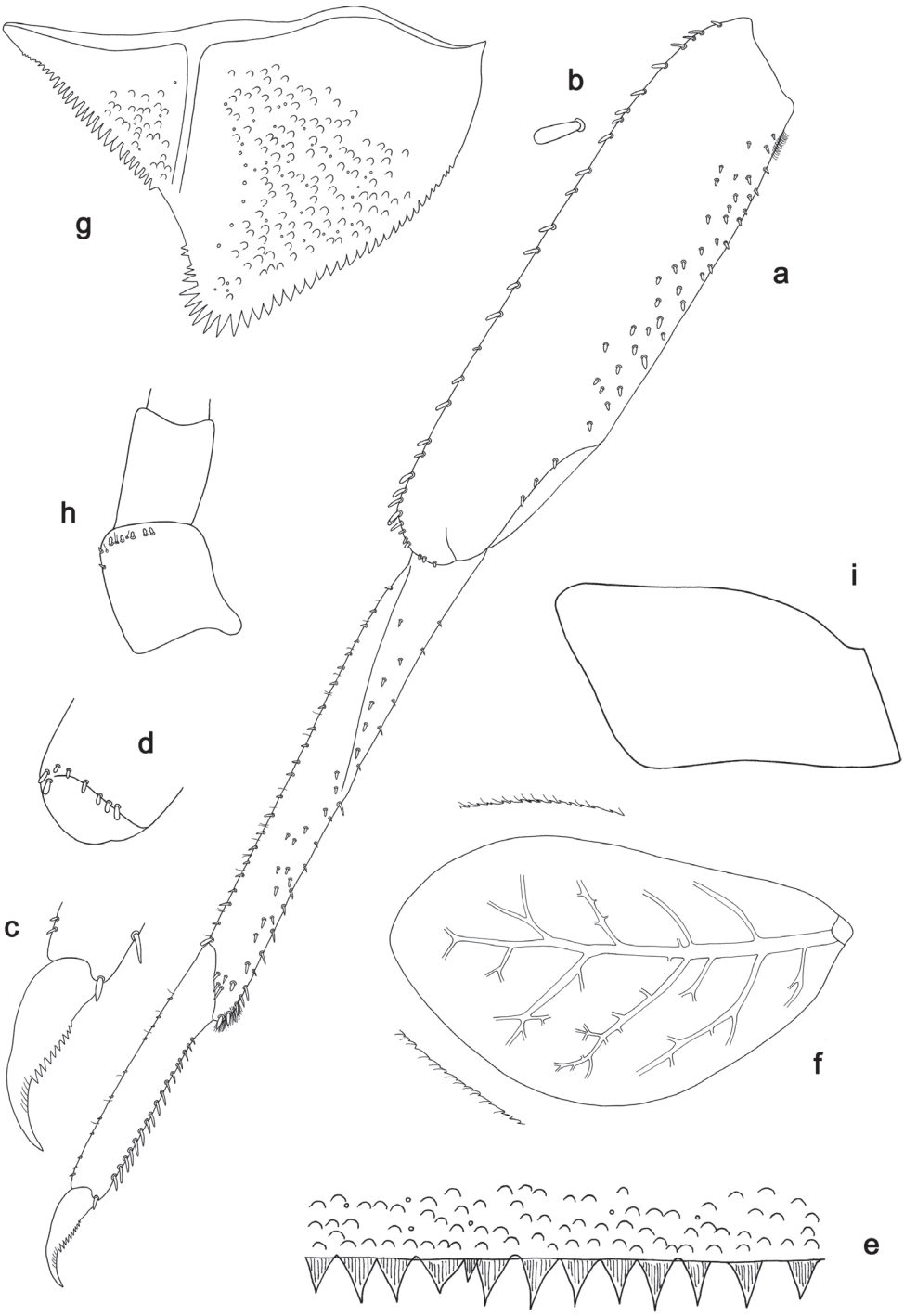

Figure 9. *Labiobaetis hattam* sp. nov., larva morphology: **a** foreleg **b** seta on dorsal margin of femur **c** fore claw **d** apex of forefemur, posterior view **e** tergum IV **f** gill IV **g** paraproct **h** base of antenna **i** Metanotum.

Hypopharynx and superlingua (Fig. 8f). Lingua approx. as long as superlingua. Lingua longer than broad; distal half laterally slightly expanded; medial tuft of stout setae well developed and short. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 8g). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and four or five long, simple setae. Maxillary palp ca. 1.1× length of galea-lacinia; 2-segmented; palp segment II 1.2× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without excavation at inner distolateral margin, apically constricted.

Labium (Fig. 8h). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with ten spine-like setae, increasing in length distally; apex with three long, robust, pectinate setae and one short, robust seta; outer margin with six or seven spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area and two or three short, simple setae in anteromedial area; dorsally with a row of six or seven long, spine-like setae near inner margin. Labial palp with segment I 0.9× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with narrow, extended, distomedial protuberance; distomedial protuberance 0.6× width of base of segment III; ventral surface with short, simple setae; dorsally with three or four spine-like setae near outer margin. Segment III slightly pentagonal; length 0.9× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 9i) absent.

Foreleg (Fig. 9a–d). Ratio of foreleg segments 1.3:1.0:0.6:0.2. ***Femur.*** Length ca. 4× maximum width. Dorsal margin with a row of 19–23 curved, spine-like, apically rounded setae; length of setae 0.1× maximum width of femur. Apex rounded, with a pair of spine-like setae and some short, stout setae. Many stout, lanceolate setae scattered along ventral margin; femoral patch present. On posterior side apically with stout setae. ***Tibia.*** Dorsal margin with a row of short, spine-like setae and fine, simple setae. Ventral margin with a row of short, curved, spine-like setae, on apex some longer setae and a tuft of fine, simple setae. Anterior surface scattered with stout, lanceolate setae. Patellotibial suture present on basal 1/2. ***Tarsus.*** Dorsal margin with a row of short, spine-like setae and fine, simple setae. Ventral margin with a row of curved, spine-like setae. Claw with one row of 10–12 denticles; distally pointed; with ca. six stripes; subapical setae absent.

Middle and hind legs (Fig. 9d). As foreleg, also with femoral patch. Stout setae on apex of posterior side present on middle leg and absent on hind leg.

Terga (Fig. 9e). Surface with irregular rows of U-shaped scale bases and scattered micropores. Posterior margin of tergum IV with triangular spines, longer than wide.

Gills (Fig. 9f). Present on segments II–VII. Margin with small denticles intercalating fine simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and VI combined. Gill VII as long as length of segments VIII and 2/3 IX combined.

Paraproct (Fig. 9g). Distally slightly expanded, with 38–48 stout, marginal spines. Surface scattered with U-shaped scale bases and micropores. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the indigenous Hattam people from West Papua.

Distribution. Indonesia: Papua Barat (Fig. 21c).

Biological aspects. The specimens were collected in a forest stream at an altitude of 500 m.

***Labiobaetis werneri* sp. nov.**

http://zoobank.org/24BA8E1B-868C-408D-9EAC-2952CA612F18

Figures 10, 11, 19a, b, 21c

Type material. ***Holotype*.** Papua New Guinea • larva; Gulf, Marawaka, Mala; 07°05'40"S, 145°44'28"E; 1400 m; 11.xi.2006; leg. Balke and Kinibel; (PNG 90); on slide; GenBank MW868307; GBIFCH00763699; ZSM. ***Paratypes*.** Papua New Guinea • 1 larva; same data as holotype; in alcohol; GBIFCH00515645; MZL • 1 larva; Eastern Highlands, Marawaka, Ande; 07°01'42"S, 145°49'48"E; 1700–1800 m; 09.xi.2006; leg. Balke and Kinibel; (PNG 87); on slide; GenBank MW868309; GBIFCH00763603; MZL • 10 larvae; Morobe, Wagau, Herzog Mts; 06°51'04"S, 146°48'04"E; 1150 m; 19.xi.2006; leg. Balke and Kinibel; (PNG 102); 1 on slide; GBIFCH00592773; MZL; 9 in alcohol; GenBank MW868308; GBIFCH00763700, GBIFCH00515644, GBIFCH00515651; MZL • 1 larva; Morobe, Garaina; 07°51'02"S, 147°07'00"E; 720 m; vi.2008; leg. Ibalim and Sosanika; (PNG216); in alcohol; GBIFCH00829895; MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of one plus six or seven long, simple setae (Fig. 10a); B) labial palp segment II with rather narrow thumb-like, distomedial protuberance, segment III sub-rectangular (Fig. 10h); C) fore femur rather broad, length 2.7× maximum width, dorsal margin with 25–33 spine-like setae plus additional setae near margin (Fig. 11a); D) hind protoptera absent; E) six pairs of gills (gill I absent), anal margin with both short and long setae (Fig. 11e); F) paraproct distally not expanded, with 18–28 stout, marginal spines (Fig. 11f).

Description. Larva (Figs 10, 11, 19a, b). Body length 5.7–6.2 mm. Cerci broken, paracercus ca. 0.4× body length. Antenna: approx. 2.5× as long as head length.

Colouration (Fig. 19a, b). Head, thorax and abdomen dorsally brown, with pattern as in Fig. 19a. Head, thorax and abdomen ventrally light brown, abdominal sternites VI–IX darker, as in Fig. 19b. Legs light brown; femur with dorsomedial and apical brown spots; tarsus distally brown. Caudalii light brown.

Antenna (Fig. 11g) with scape and pedicel sub cylindrical, without distolateral process at scape.

Labrum (Fig. 10a). Sub-rectangular, length 0.7× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus six or seven

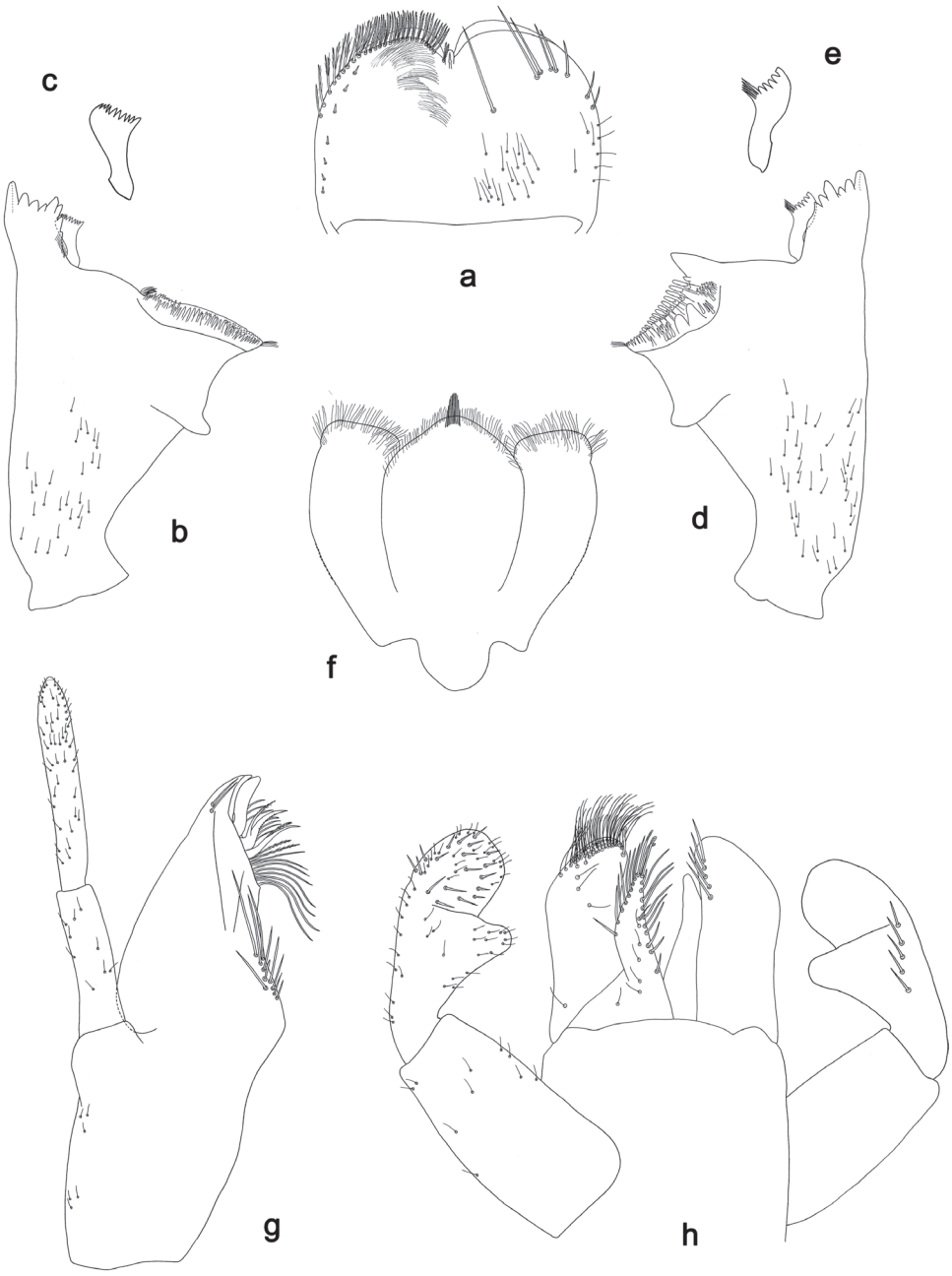

Figure 10. *Labiobaetis werneri* sp. nov., larva morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlingua **g** maxilla **h** labium.

long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid, pectinate setae; ventral surface with ca. seven short, spine-like setae near lateral and anterolateral margin.

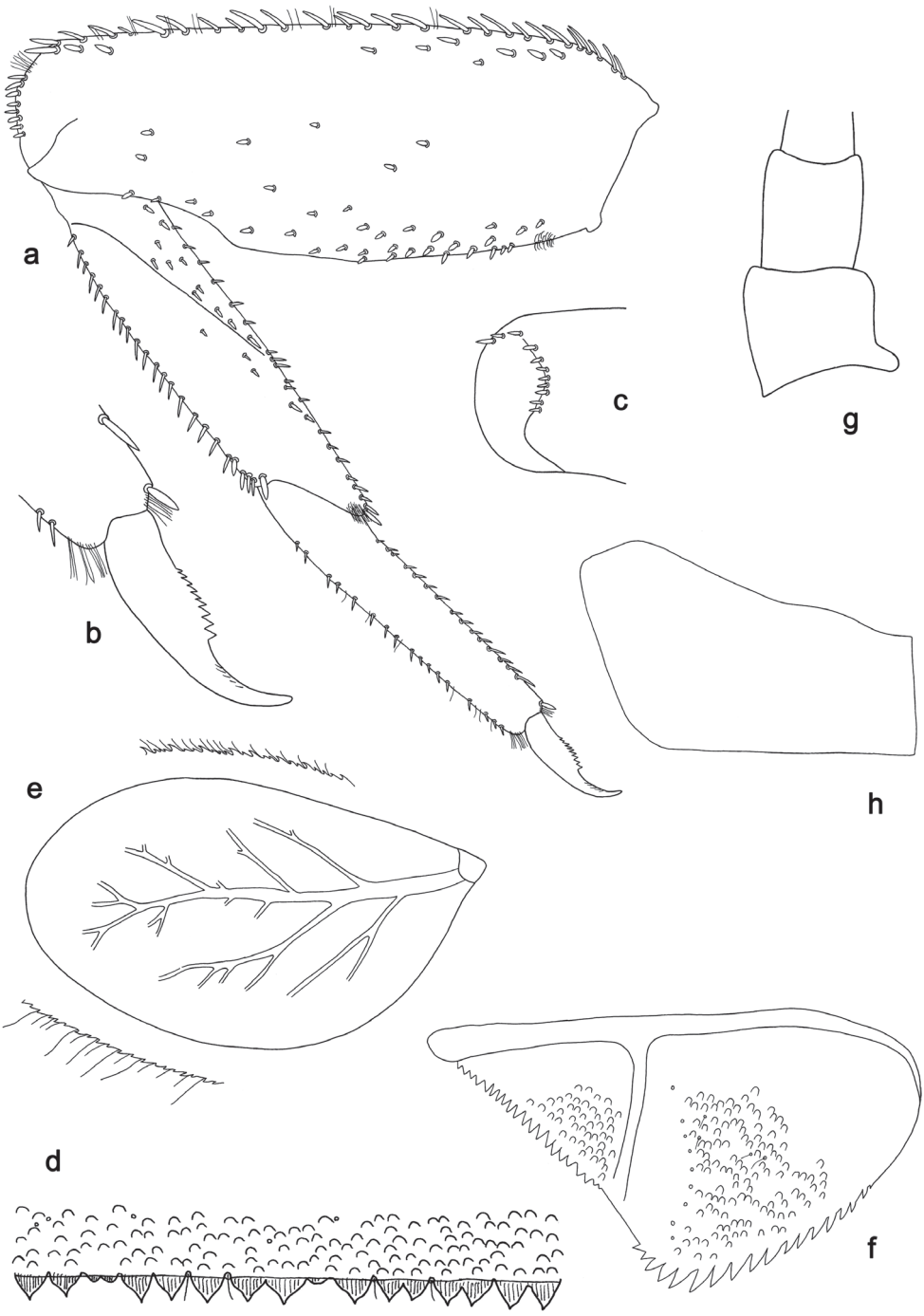

Figure 11. *Labiobaetis werneri* sp. nov., larva morphology: **a** foreleg **b** fore claw **c** apex of forefemur, posterior view **d** tergum IV **e** gill IV **f** paraproct **g** base of antenna **h** metanotum.

Right mandible (Fig. 10b, c). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola almost straight. Tuft of setae at apex of mola present.

Left mandible (Fig. 10d, e). Incisor and kinetodontium fused. Incisor with four denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola present.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlingua (Fig. 10f). Lingua approx. as long as superlingua. Lingua longer than broad; distal half laterally slightly expanded; medial tuft of stout setae well developed and short. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 10g). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and 7–9 long, simple setae. Maxillary palp ca. 1.3× length of galea-lacinia; 2-segmented; palp segment II 1.5× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without excavation at inner distolateral margin, apically constricted.

Labium (Fig. 10h). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with nine spine-like setae, increasing in length distally; apex with three long, robust, pectinate setae and one short, robust seta; outer margin with seven or eight spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa sub-rectangular, curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area, three or four short, simple setae in anteromedial area and one short, simple seta in posterolateral area; dorsally with a row of five long, spine-like setae near inner margin. Labial palp with segment I 1.1× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with narrow thumb-like, distomedial protuberance; distomedial protuberance 0.5× width of base of segment III; ventral surface with short, simple setae; dorsally with 3–5 spine-like setae near outer margin. Segment III sub-rectangular; length 1.1× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 11h) absent.

Foreleg (Fig. 11a–c). Ratio of foreleg segments 1.6:1.0:0.9:0.3. ***Femur.*** Length 2.7× maximum width. Dorsal margin with a row of 25–33 curved, spine-like setae and additional setae near margin; length of setae 0.16× maximum width of femur. Apex rounded, with a pair of spine-like setae and some short, stout setae. Many stout, lanceolate setae scattered along ventral margin and some scattered on surface; femoral patch present. On posterior side apically with stout setae. ***Tibia.*** Dorsal margin with a

row of short to medium, spine-like setae. Ventral margin with a row of short, curved, spine-like setae, on apex some longer setae and a tuft of fine, simple setae. Anterior surface scattered with stout, lanceolate setae. Patellotibial suture present on basal 1/2.
Tarsus. Dorsal margin with a row of short, spine-like setae and fine, simple setae. Ventral margin with a row of curved, spine-like setae. Claw with one row of 9–12 denticles; distally pointed; with ca. five stripes; subapical setae absent.

Middle and hind legs (Fig. 11c). As foreleg, also with femoral patch. Stout setae on apex of posterior side present on middle leg and absent on hind leg.

Terga (Fig. 11d). Surface with irregular rows of U-shaped scale bases and scattered micropores. Posterior margin of tergum IV with triangular spines, wider than long.

Gills (Fig. 11e). Present on segments II–VII. Costal margin with small denticles intercalating short, fine simple setae; anal margin with small denticles, intercalating both short and long, fine, simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and 2/3 VI combined. Gill VII as long as length of segments VIII and 1/2 IX combined.

Paraproct (Fig. 11f). Distally not expanded, with 18–28 stout, marginal spines. Surface scattered with U-shaped scale bases and fine, simple setae. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to Werner Horzel, the late stepfather of the first author.

Distribution. Papua New Guinea (Fig. 21c).

Biological aspects. The specimens were collected at altitudes from 1150 m to 1800 m.

Labiobaetis dendrisetis group of species (Kaltenbach et al. 2020)

The *dendrisetis* group can be recognised by the following combination of characters: A) dorsal surface of labrum with submarginl arc of dendritic setae; B) labial palp segment II with narrow thumb-like protuberance; C) labial palp segment III broad, rounded; D) seven pairs of gills.

The *L. dendrisetis group* is present in New Guinea and the Philippines; it includes the following species:

Labiobaetis dalisay Kaltenbach, Garces & Gattolliat, 2020
Labiobaetis dendrisetis Kaltenbach & Gattolliat, 2018

Labiobaetis dendrisetis

Figures 12, 19c, d, 21c

Kaltenbach and Gattolliat 2018: figs 48, 49.

Material examined. Papua New Guinea • 9 larvae; Central Prov., Kokoda Trek; 09°00'20"S, 147°44'15"E; 1390 m; i.2008; leg. Posman; (PNG 173); 2 on slides; GenBank MW868310; GBIFCH00763706, 592769; MZL; 7 in alcohol; GBIF-CH00515630, GBIFCH00515650; MZL • 1 larva; Central Prov., Woitape;

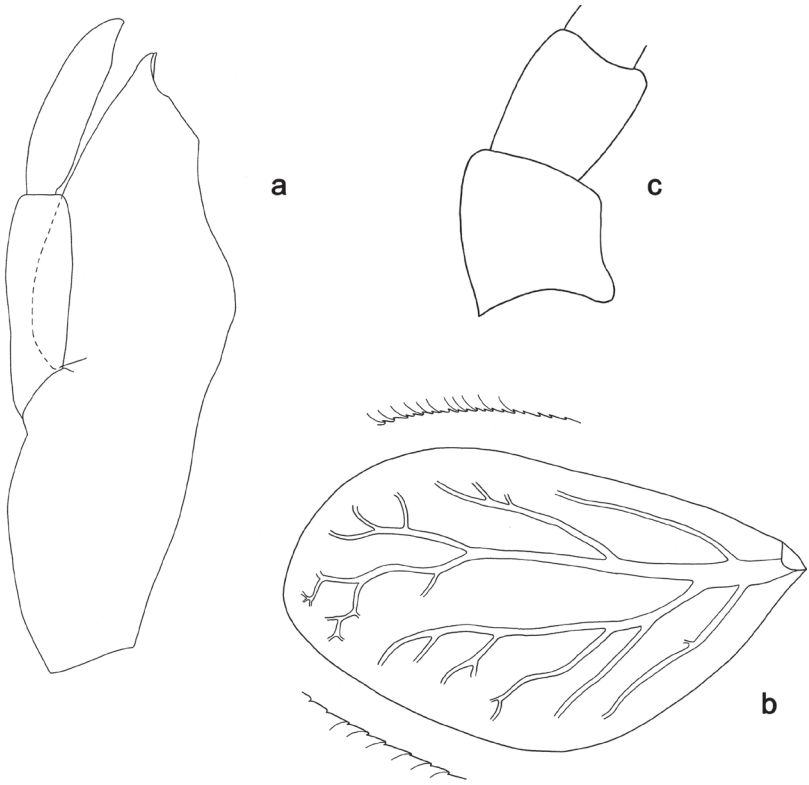

Figure 12. *Labiobaetis dendrisetis*, larva morphology: **a** maxilla **b** base of antenna **c** gill IV.

08°31'35"S, 147°14'06"E; 1600 m; i.2008; leg. Posman; (PNG 165); on slide; GBIFCH00515631; MZL • 1 larva; Central Prov., Woitape; 08°31'17"S, 147°13'41"E; 1700 m; i.2008; leg. Posman; (PNG 166); on slide; GBIFCH00592705; MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of long, dendritic setae setae (Kaltenbach and Gattolliat 2018: fig. 48a, b); B) labial palp segment II with short, narrow, thumb-like, distomedial protuberance, segment III broad, rounded (Kaltenbach and Gattolliat 2018: fig. 48k); C) mandibles with outermost incisor blade-like (Kaltenbach and Gattolliat 2018: fig. 48g); D) fore femur length ca. 3× maximum width, dorsal margin with ca. 20 curved, spine-like setae and proximally a partial second row of spine-like setae near margin (Fig. 14a); D) hind protoptera present; E) seven pairs of gills; F) scape without distolateral process (Fig. 17c).

Due to the limited material in the type series (holotype and one paratype), a few parts of the original description were missing, incomplete or have to be corrected:

Complementary description. Larva (Figs 12, 19c, d). Body length 4.1–5.3 mm. Cerci broken, paracercus ca. half body length.

Colouration (Fig. 19c, d). Head dorsally ochreous, thorax and abdomen dorsally brown, with pattern as in Fig. 19c. Head, thorax and abdomen ventrally ecru, abdominal sternites VI–VIII dark brown (Fig. 19d). Legs light brown, femur with distomedial brown streak. Caudalii light brown.

Maxillary palp (Fig. 12a) ca. 1.1× length of galea-lacinia; 2-segmented; palp segment II approx. as long as segment I; apex of last segment with slight excavation at inner distolateral margin, apically rounded.

Gills (Fig. 12b). Present on segments I–VII. Margin with small denticles intercalating fine simple setae. Tracheae extending from main trunk to inner and outer margins. Gill I as long as length of segment II. Gill IV as long as length of segments V, VI and 2/3 VII combined. Gill VII as long as length of segments VIII, IX and 1/3 X combined.

Distribution. Papua New Guinea (Fig. 21c).

Labiobaetis seramensis group of species (Kaltenbach and Gattolliat 2019)

The *seramensis* group is recognised by the following combination of characters: A) dorsal surface of labrum with submarginal arc of simple setae; B) labial palp segment II with narrow or rather narrow, thumb-like distomedial protuberance, segment III broad, rounded; C) femur dorsally with dense setation; middle and hind leg with reduced femoral patch; D) six pairs of gills (gill I absent); E) hind protoptera absent; F) distolateral process at scape absent.

The *L. seramensis* group is reported from Seram (Indonesia) and New Guinea (Indonesia: Papua Barat), it includes the following species:

Labiobaetis arfak sp. nov. (New Guinea)
Labiobaetis onim sp. nov. (New Guinea)
Labiobaetis seramensis Kaltenbach & Gattolliat, 2019 (Seram)
Labiobaetis wahai Kaltenbach & Gattolliat, 2019 (Seram)

Key to the species of the *Labiobaetis seramensis* group (larvae)

1 Dorsal margin of femur with row of more than 70 long, curved, spine-like setae (Fig. 16a); posterior margin of tergite IV with discontinued row of triangular spines (Fig. 16e) ..... ***L. onim* sp. nov.**

– Dorsal margin of femur with less than 25 curved, spine-like setae; posterior margin of tergite IV with continued row of triangular spines (Fig. 14e) **2**

2 Abdominal tergites dark brown, segments V and VI yellow brown (Fig. 20a); posterolateral margins of tergites VIII and IX with two long, pointed spines (Fig. 14f) ..... ***L. arfak* sp. nov.**

– Abdominal tergites light brown (Kaltenbach and Gattolliat 2019: figs. 50c, d); posterolateral margins of tergites VIII and IX without long spines. **3**

3 Posterior margins of tergites with triangular spines, wider than long (Kaltenbach and Gattolliat 2019: fig. 39c); paraproct distally not expanded (Kaltenbach and Gattolliat 2019: fig. 39d) ..... ***L. seramensis***

– Posterior margins of tergites with triangular spines, longer than wide (Kaltenbach and Gattolliat 2019: fig. 41c); paraproct distally expanded (Kaltenbach and Gattolliat 2019: fig. 41d) ..... ***L. wahai***

***Labiobaetis arfak* sp. nov.**
http://zoobank.org/EBC7E07E-1A03-4BD4-B98F-85F0E68CB4B6
Figures 13, 14, 20a, b, 21c

Type material. ***Holotype.*** Indonesia • larva; Papua Barat, River Je, Loc. Arfak, East of Amber village; 01°10'59"S, 133°56'51"E; 1200 m; 16.vi.2016, leg. Sumoked; on slide; GBIFCH00592770; MZB. ***Paratypes.*** Indonesia • 27 larvae; same data as holotype; 4 on slides; GenBank MW868312, MW868313; GBIFCH00763714, GBIFCH00763715, GBIFCH00592767, GBIFCH00829897; MZL; 23 in alcohol; GBIFCH00515626, GBIFCH00515648; MZB, MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of one plus two long, simple setae (Fig. 13a); B) labial palp segment II with narrow thumb-like, distomedial protuberance, segment III broad, rounded (Fig. 13h); C) fore femur rather broad, length 2.7× maximum width, dorsal margin with 17–20 spine-like setae plus a second row of spine-like setae near margin (Fig. 14a); D) hind protoptera absent; E) six pairs of gills (gill I absent); F) tergites VIII and IX posterolaterally with two long spines (Fig. 14f); G) paraproct distally not expanded, with ca. eight stout, marginal spines (Fig. 14h).

Description. Larva (Figs 13, 14, 20a, b). Body length 3.3–4.4 mm. Cerci ca. 2/3 of body length, paracercus ca. 2/3 of cerci length. Antenna: approx. 2.5× as long as head length.

Colouration (Fig. 20a, b). Head, thorax and abdomen dorsally dark brown, abdominal tergites V and VI yellow brown (Fig. 20a). Thorax ventrally ecru, abdomen ventrally brown, with pattern as in Fig. 20b. Legs light brown; femur dorsally and ventrally dark brown, basally and distomedially with dark brown areas (Fig. 20b). Caudalii light brown, basally brown.

Antenna (Fig. 14i) with scape and pedicel sub cylindrical, without distolateral process at scape.

Labrum (Fig. 13a). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus two long, simple setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid, pectinate setae; ventral surface with ca. three short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 13b, c). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola convex, with minute denticles. Tuft of setae at apex of mola present.

Left mandible (Fig. 13d, e). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola almost straight, with few minute denticles. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola absent.

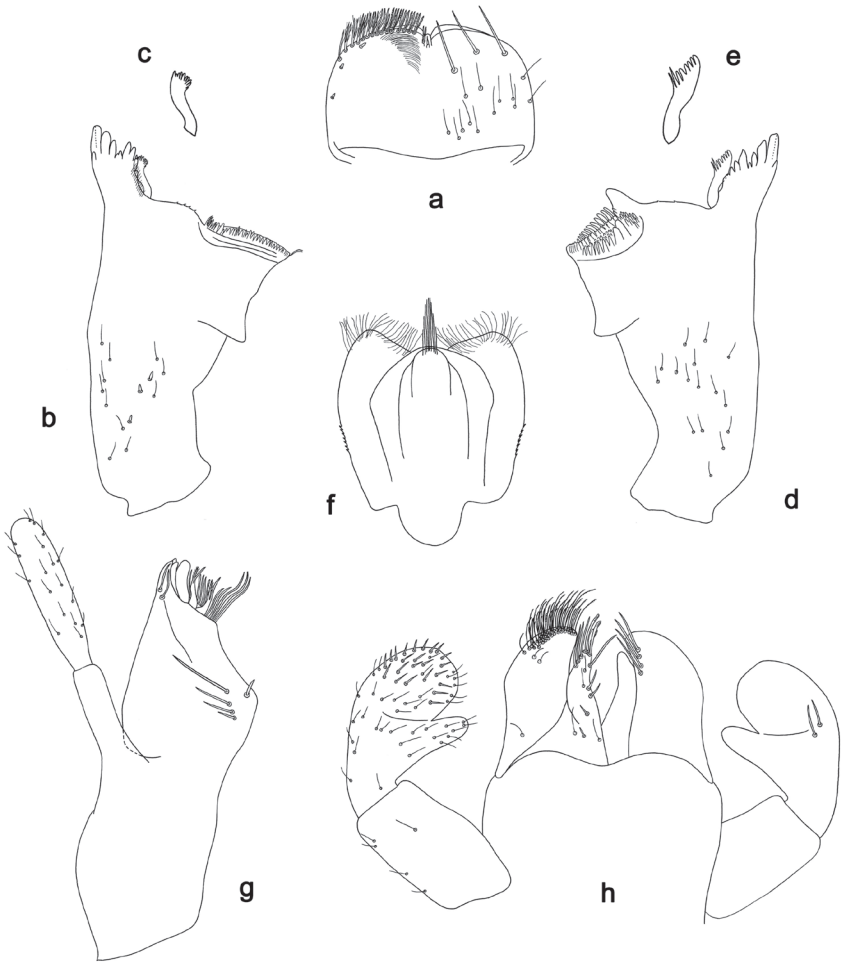

Figure 13. *Labiobaetis arfak* sp. nov., larva morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlingua **g** maxilla **h** labium.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

Hypopharynx and superlingua (Fig. 13f). Lingua shorter than superlingua. Lingua longer than broad; distal half laterally slightly expanded; medial tuft of stout setae well developed and long. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 13g). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one spine-like seta and four long, simple setae. Maxillary palp ca. 1.3× length of galea-lacinia; 2-segmented; palp segment II 1.5× length of segment I; setae on maxillary palp fine,

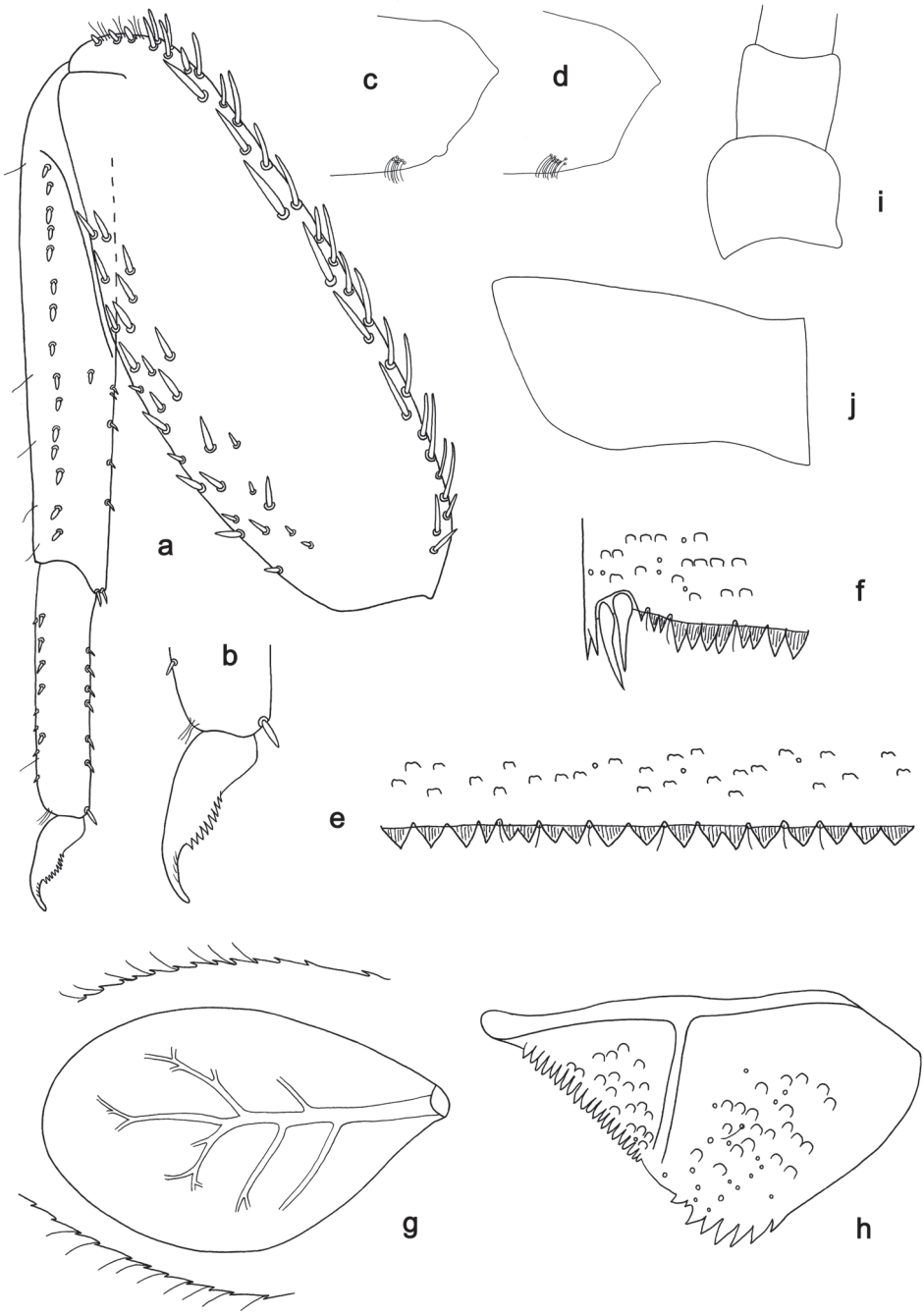

Figure 14. *Labiobaetis arfak* sp. nov., larva morphology: **a** foreleg **b** fore claw **c** base of middle femur **d** base of hind femur **e** tergum IV **f** tergum IX **g** gill IV **h** paraproct **i** base of antenna **j** metanotum.

simple, scattered over surface of segment II; apex of last segment without excavation at inner distolateral margin, apically rounded.

Labium (Fig. 13h). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with 3–5 spine-like setae, distalmost seta much longer; apex with two long and one medium robust, pectinate setae; outer margin with three or four spine-like setae; ventral surface with fine, simple, scattered setae. Paraglossa subrectangular, curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area, one or two short, simple setae in anteromedial area and one short, simple seta in posterolateral area; dorsally with a row of four long, spine-like setae near inner margin. Labial palp with segment I 0.9× length of segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with narrow thumb-like, distomedial protuberance; distomedial protuberance 0.4× width of base of segment III; ventral surface with short, simple setae; dorsally with two or three spine-like setae near outer margin. Segment III broad, rounded; length 0.9× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera (Fig. 14j) absent.

Foreleg (Fig. 14a, b). Ratio of foreleg segments 1.3:1.0:0.5:0.2. ***Femur.*** Length 2.7× maximum width. Dorsal margin with a row of 17–20 curved, spine-like setae and a second row of spine-like setae near margin; length of setae 0.25× maximum width of femur. Apex rounded, with one or two pairs of spine-like setae and some short, stout setae. Many stout, lanceolate setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with a row of short, spine-like setae and fine, simple setae. Ventral margin with a row of short, curved, spine-like setae. Anterior surface scattered with few stout, lanceolate setae. Patellotibial suture present on basal 1/2 area. ***Tarsus.*** Dorsal margin with a row of short, spine-like setae. Ventral margin with a row of curved, spine-like setae. Claw with one row of 9–11 denticles; distally pointed; with ca. five stripes; subapical setae absent.

Middle and hind legs (Fig. 14c, d). As foreleg, but with reduced femoral patch.

Terga (Fig. 14e, f). Surface with irregular rows of U-shaped scale bases and scattered micropores. Posterior margin of tergum IV with triangular spines, wider than long. Posterolateral margins of terga VIII and IX with two long, pointed spines.

Gills (Fig. 14g). Present on segments II–VII. Margin with small denticles intercalating fine simple setae. Tracheae extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and 2/3 VI combined. Gill VII as long as length of segments VIII and 2/3 IX combined.

Paraproct (Fig. 14h). Distally not expanded, with ca. eight stout, marginal spines. Surface scattered with U-shaped scale bases, micropores and fine, simple setae. Cercotractor with numerous small, marginal spines.

Etymology. Dedicated to the indigenous Arfak people of Papua Barat, where the type locality is located.

Distribution. Indonesia: Papua Barat (Fig. 21c).

Biological aspects. The specimens were collected at an altitude of 1200 m, together with *L. onim* sp. nov.

***Labiobaetis onim* sp. nov.**
http://zoobank.org/ADFC666F-D838-4FC3-AA6B-1D473939F07E
Figures 15, 16, 20c, d, 21c

Type material. ***Holotype.*** Indonesia • larva; Papua Barat, River Je, Loc. Arfak, East of Amber village; 01°10'59"S, 133°56'51"E; 1200 m; 16.vi.2016, leg. Sumoked; on slide; GBIFCH00763713; MZB. ***Paratypes.*** Indonesia • 2 larvae; same data as holotype; 2 on slides; GBIFCH00515649, GBIFCH00592706; MZB, MZL.

Diagnosis. Larva. Following combination of characters: A) dorsal surface of labrum with submarginal arc of one plus two long, simple setae (Fig. 15a); B) labial palp segment II with short thumb-like (atypical for the group), distomedial protuberance, segment III broad, rounded (Fig. 15h); C) fore femur rather broad, length ca. 3× maximum width, dorsal margin with more than 70 long, curved spine-like setae plus some additional spine-like setae near margin (Fig. 16a); D) hind protoptera absent; E) six pairs of gills (gill I absent); F) paraproct distally not expanded, with 8–12 stout, marginal spines (Fig. 16g).

Description. Larva (Figs 15, 16, 20c, d). Body length 5.6–5.9 mm. Cerci ca. 1/2 of body length, paracercus ca. 2/3 of cerci length. Antenna: approx. twice as long as head length.

Colouration (Fig. 20c, d). Head dorsally light brown, thorax and abdomen dorsally dark brown, with light brown pattern on thorax as in Fig. 20c, abdominal segment I light brown and abdominal segments V–VII orange. Head, thorax, and abdomen ventrally light brown, with pattern as in fig. 20d, abdominal segments V–VII light orange and abdominal segments VIII–X dark brown. Legs ecru, caudalii ecru.

Antenna (Fig. 16h) with scape and pedicel sub cylindrical, without distolateral process at scape.

Labrum (Fig. 15a). Sub-rectangular, length 0.6× maximum width. Distal margin with medial emargination and a small process. Dorsally with medium, fine, simple setae scattered over surface; submarginal arc of setae composed of one plus two long, simple setae; large distance between both arc setae. Ventrally with marginal row of setae composed of anterolateral long, feathered setae and medial long, bifid, pectinate setae; ventral surface with ca. five short, spine-like setae near lateral and anterolateral margin.

Right mandible (Fig. 15b, c). Incisor and kinetodontium fused. Incisor with six denticles; kinetodontium with three denticles, inner margin of innermost denticle with a row of thin setae. Prostheca robust, apically denticulate. Margin between prostheca and mola slightly convex. Tuft of setae at apex of mola present.

Left mandible (Fig. 15d, e). Incisor and kinetodontium fused. Incisor with five denticles; kinetodontium with three denticles. Prostheca robust, apically with small denticles and comb-shaped structure. Margin between prostheca and mola straight. Subtriangular process long and slender, above level of area between prostheca and mola. Denticles of mola apically constricted. Tuft of setae at apex of mola absent.

Both mandibles with lateral margins almost straight. Basal half with fine, simple setae scattered over dorsal surface.

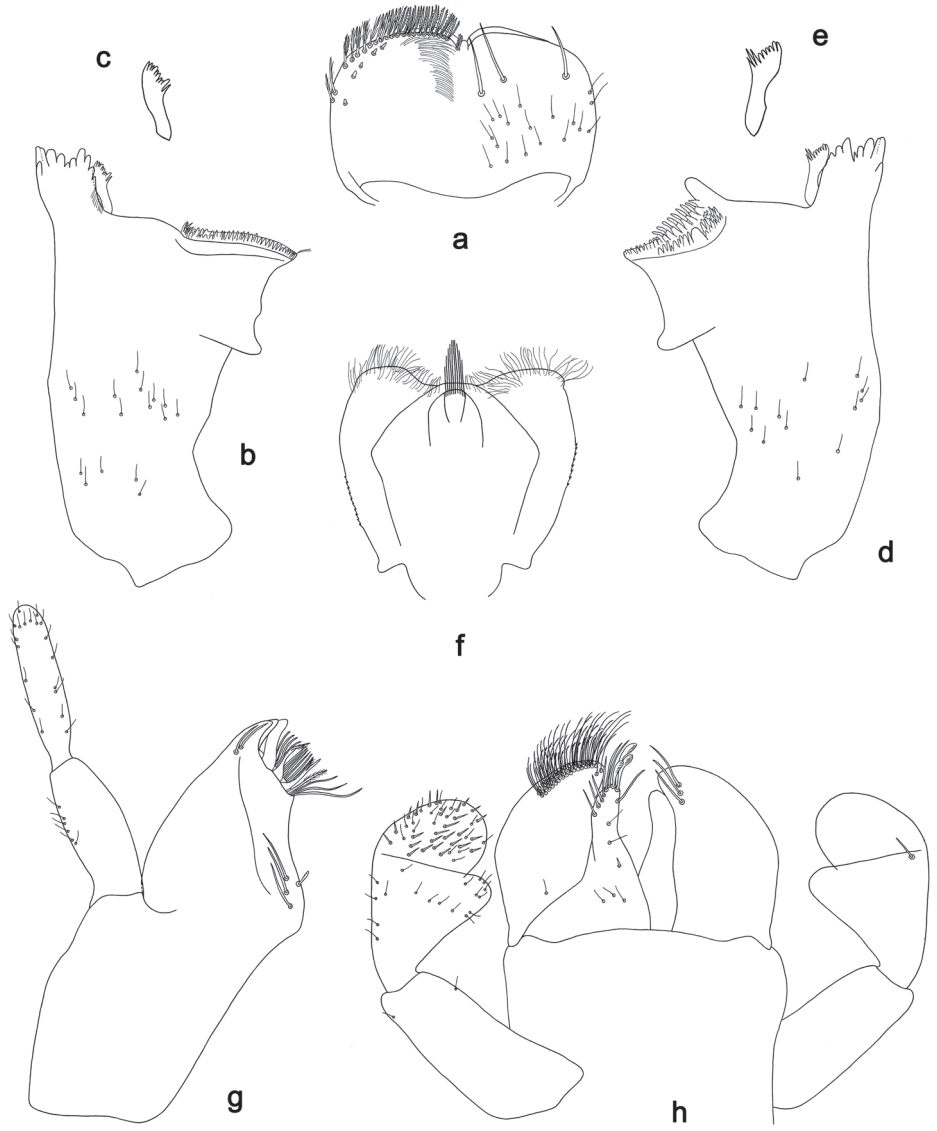

Figure 15. *Labiobaetis onim* sp. nov., larva morphology: **a** labrum **b** right mandible **c** right prostheca **d** left mandible **e** left prostheca **f** hypopharynx and superlingua **g** maxilla **h** labium.

Hypopharynx and superlingua (Fig. 15f). Lingua shorter than superlingua. Lingua longer than broad; distal half laterally slightly expanded; medial tuft of stout setae well developed and long. Superlingua distally rounded; lateral margins rounded; fine, long, simple setae along distal margin.

Maxilla (Fig. 15g). Galea-lacinia ventrally with two simple, apical setae under canines. Inner dorsal row of setae with three denti-setae, distal denti-seta tooth-like, middle and proximal denti-setae slender, bifid and pectinate. Medially with one pectinate, spine-like seta and three long, simple setae. Maxillary palp ca. 1.3× length of

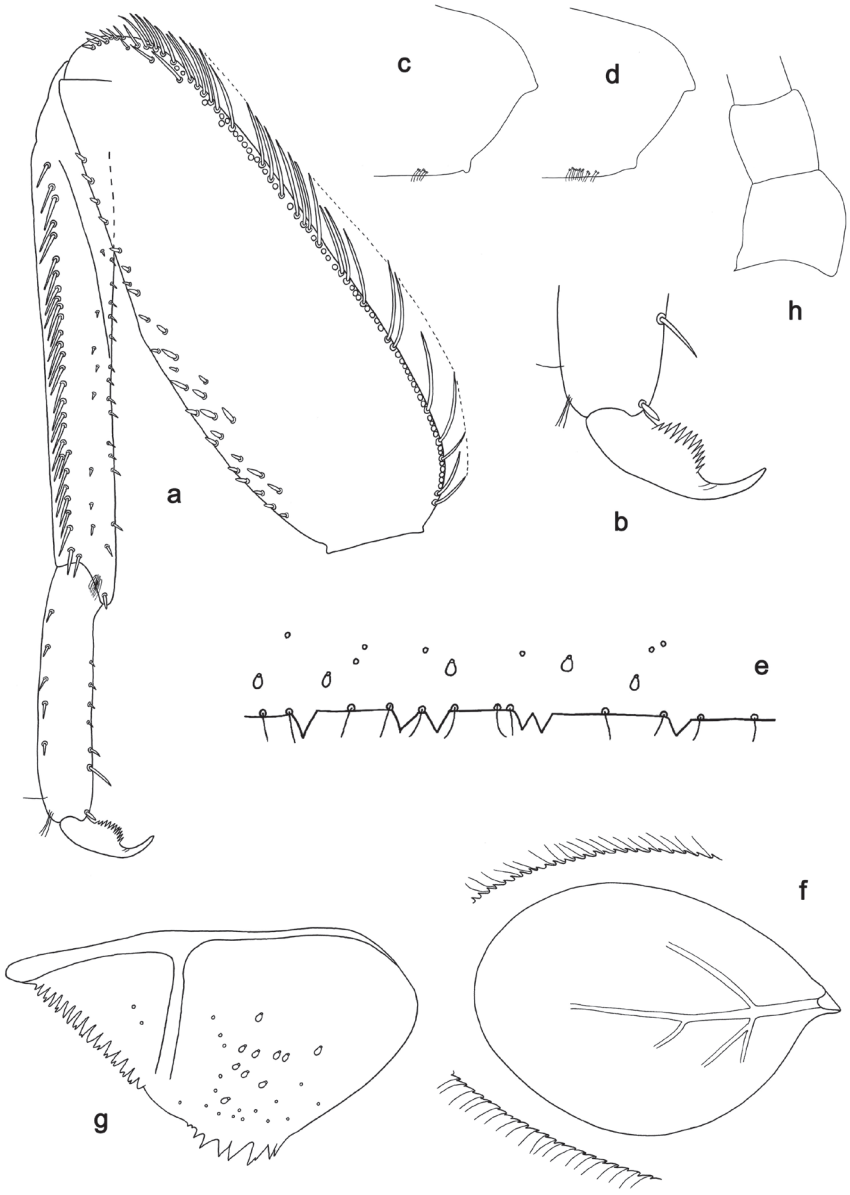

Figure 16. *Labiobaetis onim* sp. nov., larva morphology: **a** Foreleg **b** Fore claw **c** Base of middle femur **d** Base of hind femur **e** Tergum IV **f** Gill IV **g** Paraproct **h** Base of antenna.

galea-lacinia; 2-segmented; palp segment II 1.1× length of segment I; setae on maxillary palp fine, simple, scattered over surface of segments I and II; apex of last segment without excavation at inner distolateral margin, apically rounded.

Labium (Fig. 15h). Glossa basally broad, narrowing toward apex; shorter than paraglossa; inner margin with one long, spine-like seta; apex with two long and one medium robust, pectinate setae; outer margin with five or six spine-like setae; ventral

Figure 17. Habitus, larvae: **a** *Labiobaetis catadupa* sp. nov., dorsal view **b** *Labiobaetis toraja* sp. nov., dorsal view **c** *Labiobaetis toraja* sp. nov., ventral view.

surface with fine, simple, scattered setae. Paraglossa sub-rectangular, curved inward; apex rounded; with three rows of long, robust, distally pectinate setae in apical area, sometimes one short, simple seta in anteromedial area, and one short, simple seta in posteromedial area; dorsally with a row of three long, spine-like setae near inner margin. Labial palp with segment I approx. as long as segments II and III combined. Segment I ventrally with short, fine, simple setae. Segment II with short thumb-like, distomedial protuberance; distomedial protuberance 0.3× width of base of segment III; ventral surface with short, simple setae; dorsally with one spine-like seta near outer margin. Segment III broad, rounded; length 0.7× width; ventrally covered with short, spine-like, simple setae and short, fine, simple setae.

Hind protoptera absent.

Figure 18. Habitus, larvae: **a** *Labiobaetis hattam* sp. nov., dorsal view **b** *Labiobaetis hattam* sp. nov., ventral view.

Foreleg (Fig. 16a, b). Ratio of foreleg segments 1.2:1.0:0.5:0.2. ***Femur.*** Length ca. 3× maximum width. Dorsal margin with a dense row of more than 70 long, curved, spine-like setae and distally some additional long, spine-like setae near margin; length of setae 0.40× maximum width of femur. Apex rounded, with some short, stout setae. Many stout, lanceolate setae scattered along ventral margin; femoral patch absent. ***Tibia.*** Dorsal margin with a dense row of long, spine-like setae. Ventral margin with a row of short, curved, spine-like setae. Anterior surface scattered with short, stout, lanceolate setae. Patellotibial suture present on basal 1/2 area. ***Tarsus.*** Dorsal margin with a row of short, spine-like setae. Ventral margin with a row of short, curved, spine-like setae, distalmost seta much longer. Claw with one row of ten or eleven denticles; distally pointed; with two or three stripes; subapical setae absent.

Middle and hind legs (Fig. 16c, d). As foreleg, but with reduced femoral patch.

Terga (Fig. 16e). Surface with scattered scales and micropores. Posterior margin of tergum IV with discontinuous row of triangular spines, spines wider than long. Triangular spines present on segments IV–VII, absent on segments I–III.

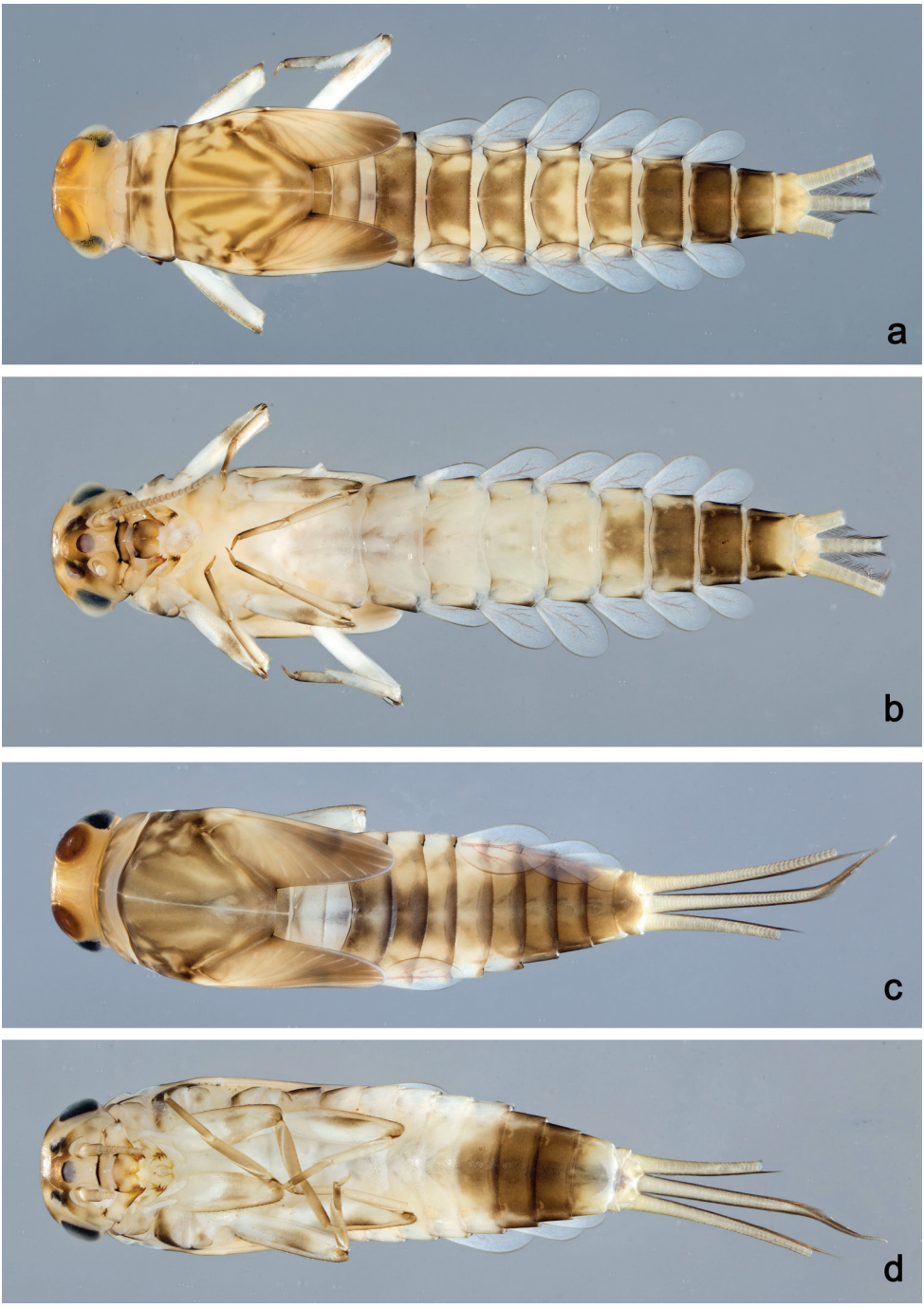

Figure 19. Habitus, larvae: **a** *Labiobaetis werneri* sp. nov., dorsal view **b** *Labiobaetis werneri* sp. nov., ventral view **c** *Labiobaetis dendrisetis*, dorsal view **d** *Labiobaetis dendrisetis*, ventral view.

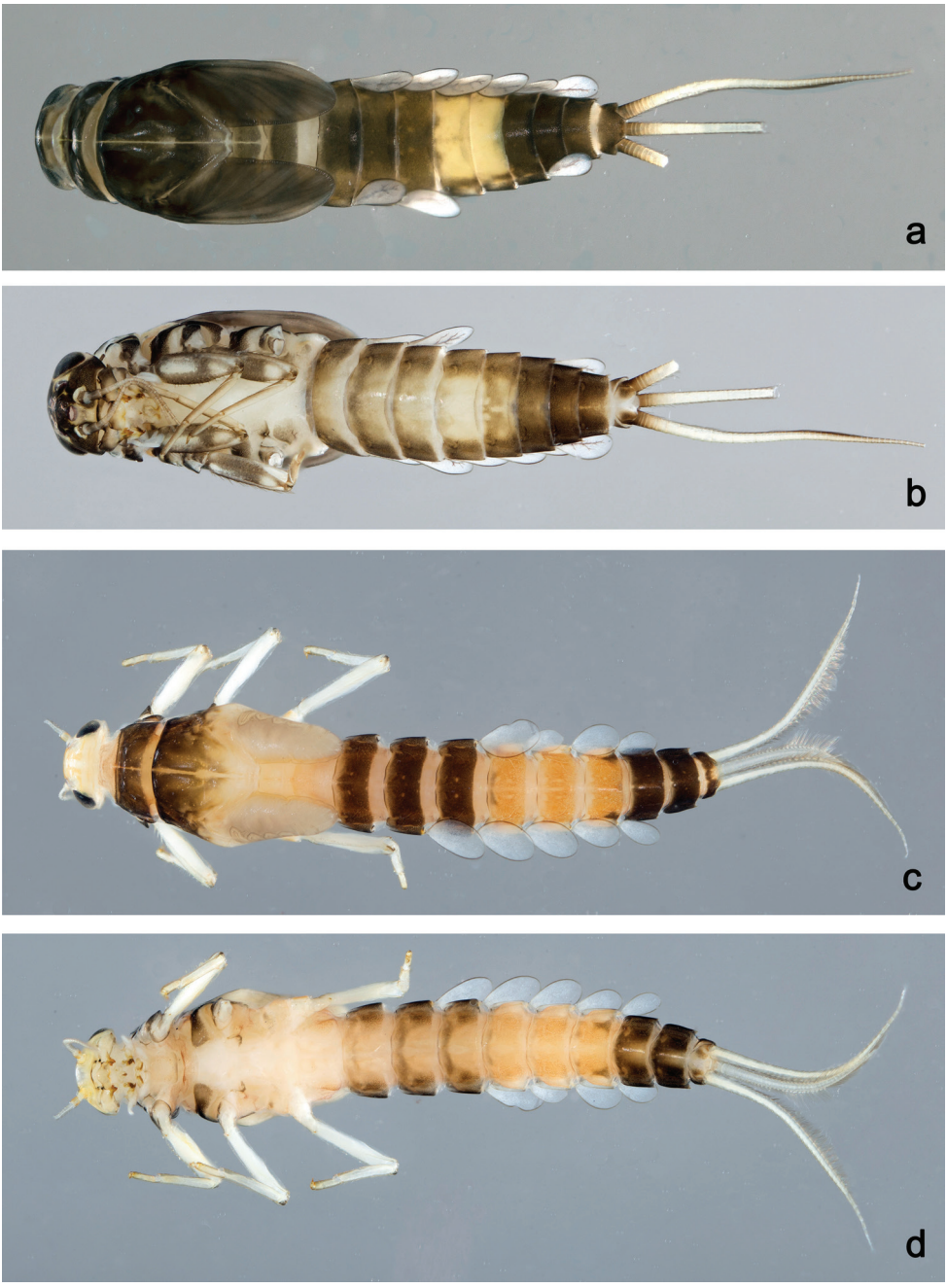

Figure 20. Habitus, larvae: **a** *Labiobaetis arfak* sp. nov., dorsal view **b** *Labiobaetis arfak* sp. nov., ventral view **c** *Labiobaetis onim* sp. nov., dorsal view **d** *Labiobaetis onim* sp. nov., ventral view.

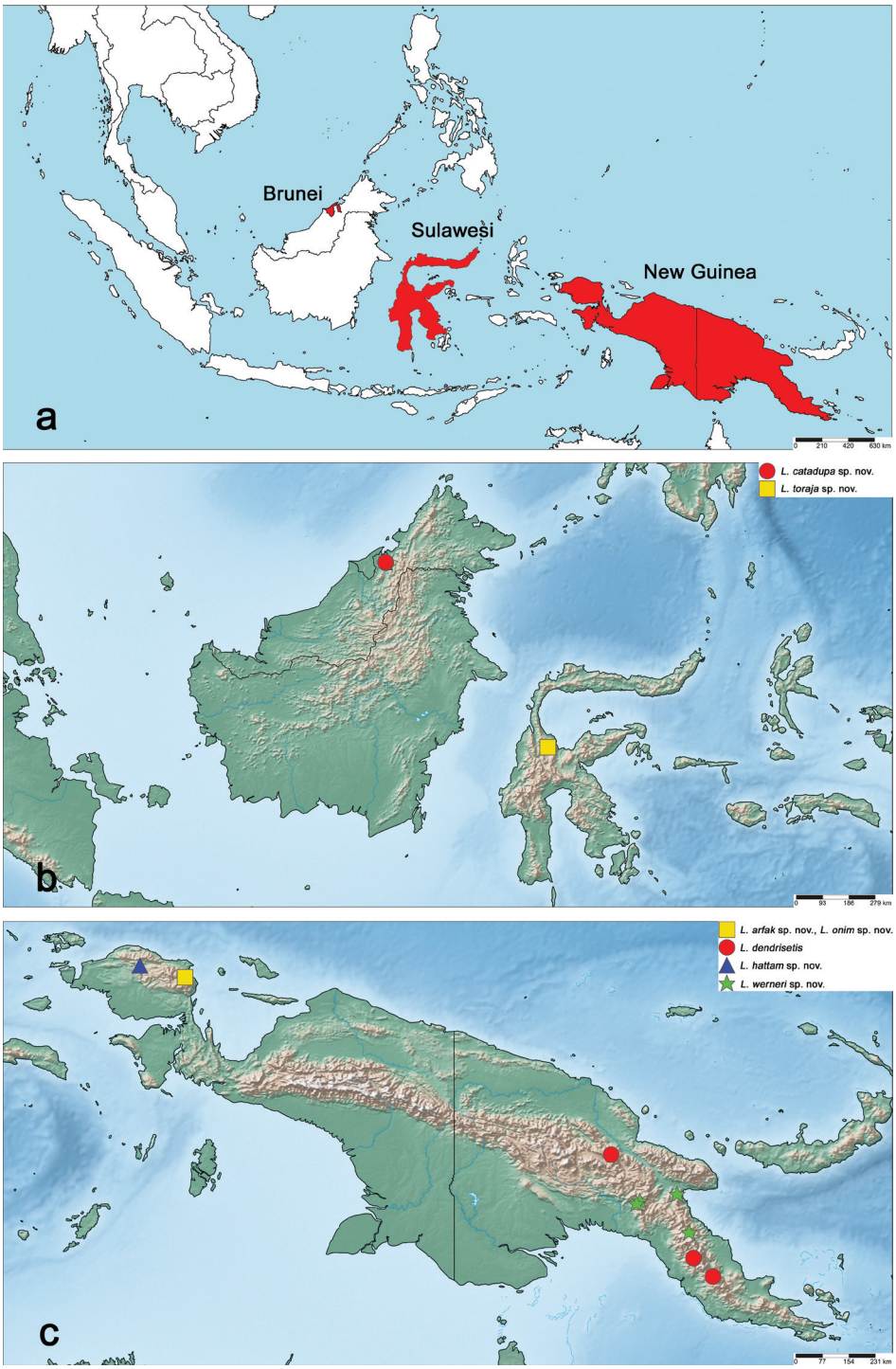

Figure 21. Maps: **a** overview of the region treated in this study (marked in red) **b** distribution of the new *Labiobaetis* species in Borneo and Sulawesi **c** distribution of the treated *Labiobaetis* species in New Guinea.

Table 2. GPS coordinates of locations of examined specimens.

Species	Locality	GPS coordinates
L. catadupa sp. nov.	Brunei: Temburong National Park	04°32'49"N, 115°09'30"E
		04°33'10"N, 115°09'20"E
		04°32'42"N, 115°09'31"E
		04°32'23"N, 115°09'34"E
		04°32'51"N, 115°09'25"E
		04°32'56"N, 115°09'27"E
		04°33'39"N, 115°08'51"E
		04°33'39"N, 115°08'54"E
L. toraja sp. nov.	Sulawesi	01°19'35"S, 120°18'40"E
L. hattam sp. nov.	Papua Barat	00°52'29"S, 132°46'06"E
L. werneri sp. nov.	Papua New Guinea	07°01'42"S, 145°49'48"E
	Papua New Guinea	07°05'40"S, 145°44'28"E
	Papua New Guinea	06°51'04"S, 146°48'04"E
	Papua New Guinea	07°51'02"S, 147°07'00"E
L. dendrisetis	Papua New Guinea: Simbu Prov.	05°49' 00"S, 145°04'30"E
	Papua New Guinea: Central Prov.	08°31'35"S, 147°14'06"E
	Papua New Guinea: Central Prov.	08°31'17"S, 147°13'41"E
	Papua New Guinea: Central Prov.	09°00'20"S, 147°44'15"E
L. arfak sp. nov.	Papua Barat	01°10'59"S, 133°56'51"E
L. onim sp. nov.	Papua Barat	01°10'59"S, 133°56'51"E

Gills (Fig. 16f). Present on segments II–VII. Margin with small denticles intercalating fine simple setae. Tracheae partly extending from main trunk to inner and outer margins. Gill IV as long as length of segments V and 1/2 VI combined. Gill VII slightly longer than length of segment VIII.

Paraproct (Fig. 16g). Distally not expanded, with 8–12 stout, marginal spines, partly with split tips. Surface scattered with scales and micropores. Cercotractor with numerous small, marginal spines, partly with split tips.

Etymology. Dedicated to the indigenous Onim people of Papua Barat, where the type locality is located.

Distribution. Indonesia: Papua Barat (Fig. 21c).

Biological aspects. The specimens were collected at an altitude of 1200 m, together with *L. arfak* sp. nov.

Discussion

Assignment to *Labiobaetis*

For the assignment of the new species to *Labiobaetis* we refer to Kluge and Novikova (2014), Müller-Liebenau (1984b), and McCafferty and Waltz (1995). *Labiobaetis* is characterised by a number of characters, some of which are not found in other taxa (Kluge and Novikova 2014): antennal scape sometimes with a distolateral process (Kaltenbach et al. 2020: fig. 2h); maxillary palp two segmented with excavation at inner distolateral margin of segment II, excavation may be poorly developed or absent

(Fig. 1h; Kaltenbach et al. 2020: fig. 2n–p); labium with paraglossae widened and glossae diminished; labial palp segment II with distomedial protuberance (Figs 1i, 6h, 8h, 10h, 13h, 15h). All these characters vary and may be secondarily lost (Kluge and Novikova 2014). The concept of *Labiobaetis* is also based on additional characters, summarised and discussed in Kaltenbach and Gattolliat (2018, 2019).

Labiobaetis catadupa sp. nov. group

This group is formed for two new species sharing distally very slender glossae, much shorter than paraglossae; an extended thumb-like, hooked protuberance of labial palp segment II; the presence of a long subapical seta on the claw and opposite a rudimentary subapical seta; and the absence of the first pair of gills, hind protoptera and a distolateral process at scape (Figs 1i, 2f, g, 4, 6h, 7h, i). Also, both have a submarginal arc of setae dorsally on the labrum composed of feathered setae. However, the type of these setae of *L. toraja* sp. nov. (Fig. 6a) is common in *Labiobaetis*, present in all species of the groups *operosus* and *difficilis* from Southeast Asia and in almost all species of the Afrotropical realm (Lugo-Ortiz and McCafferty 1997; Gattolliat 2001; Gattolliat et al. 2018; Kaltenbach and Gattolliat 2021a, b). On the contrary, the type of *L. catadupa* sp. nov. with a broadened middle part (Figs 1a, b, 3a, b) is unusual and only known from *L. elouardi* (Gillies, 1993) in West Africa (Kaltenbach and Gattolliat 2021b: fig. 8h–j). Many other characters are very different in *L. elouardi* and *L. catadupa* sp. nov. (see Figs 1, 2; Kaltenbach and Gattolliat 2021b: fig. 8), we therefore assume that these setae evolved independently in both species. The presence of subapical setae on the claw is a first report for *Labiobaetis*. However, one single, long subapical seta is known from other Baetidae (e.g., *Baetodes* Needham & Murphy, 1924; *Gratia* Thomas, 1992, *Indobaetis* Müller-Liebenau & Morihara, 1982) and one on each side was described from e.g., *Baetis* Leach, 1815; *Madaechinopus* Gattolliat & Jacobus, 2010; *Offadens* Lugo-Ortiz & McCafferty, 1998; *Liebebiella* Waltz & McCafferty, 1987, and *Monocentroptilum* Kluge, 2018 (Müller-Liebenau and Morihara 1982; Thomas 1992; Lugo-Ortiz and McCafferty 1999; Gattolliat 2002; Dominguez et al. 2006; Kluge 2018; Yanai et al. 2018).

The genetic distance (COI, Kimura 2-parameter) between *L. catadupa* sp. nov. and *L. toraja* sp. nov. is 23% and thus well in line with distances found between different species of *Labiobaetis* in Southeast Asia (15%–27% in the Philippines, Kaltenbach et al. 2020; 11%–24% in Indonesia, Kaltenbach and Gattolliat 2019; 19%–25% in Borneo, Kaltenbach and Gattolliat 2020).

Labiobaetis claudiae group

Based on the discovery of two further species of this group, *L. hattam* sp. nov. and *L. werneri* sp. nov., we adapted the diagnosis of the group (see in the results section) and added another species, *L. centralensis*, already described earlier (Kaltenbach and Gattolliat 2018): *L. hattam* sp. nov. and *L. centralensis* have only short setae at the gills margin and not alternately shorter and longer setae, as it is the case in the other species. However, all other diagnostic characters of the *claudiae* group are present in both spe-

cies as well and especially the presence of a femoral patch on all legs, which is rare in *Labiobaetis* in this region, is considered to be a strong character. Therefore, we include these two species in this group as well.

The interspecific genetic distances between the species of the *claudiae* group are rather high, between 18% and 27% (Table 3), which is in line with the values reported for other *Labiobaetis* species in New Guinea (13%–28%; Kaltenbach and Gattolliat 2018).

Ball et al. (2005) reported a mean interspecific, congeneric distance of 18% for mayflies from the United States and Canada. The intraspecific distances are very low in most cases as expected, ranging from 0% to 3% (K2P). This result is certainly biased as it is based on a limited number of sequenced specimens per species, which were partly from a single population. The exception is *L. werneri* sp. nov., where one of the three sequenced specimen has a distance of 5% and 6% respectively to the two other sequenced specimens. Here, the larger genetic distance may be explained by a possible isolation of some locations in the central mountain chain of New Guinea, where the species occurs (Fig. 21c). Intraspecific distances of 4%–6% were also reported in some cases for other *Labiobaetis* species in New Guinea, Indonesia, Borneo, and the Philippines (Kaltenbach and Gattolliat 2018, 2019, 2020; Kaltenbach et al. 2020), as well as in aquatic beetles in the Philippines (Komarek and Freitag 2020). Ball et al. (2005) also reported a case with 6% intraspecific distance in a mayfly in North America and intraspecific K2P distances of more than 3.5% are not uncommon within Plecoptera as well (Gill et al. 2015; Gattolliat et al. 2016).

Labiobaetis seramensis group

Due to the discovery of two new species of the *L. seramensis* group in New Guinea, *L. arfak* sp. nov. and *L. onim* sp. nov., and the re-examination of the types of *L. seramensis* and *L. wahai* from Seram (Indonesia), we could complement the diagnosis of this group (see in section results). The presence of a reduced femoral patch on middle and hind legs and its absence on forelegs is identified as an additional character of the group. As femoral patches are generally rare in *Labiobaetis* in Southeast Asia and New Guinea, it is considered to be a strong character.

Labiobaetis onim sp. nov. has three remarkable characters, which are atypical for *Labiobaetis*: the femur has a very dense and long setation with more than 70 setae at the dorsal margin, the tibia also has a dense and rather long setation along its dorsal margin and the posterior margins of the tergites have a discontinuous row of triangular spines, similar as in *Baetis noa* Yanai & Gattolliat, 2018 from Israel (Yanai et al. 2018: fig. 13C). However, most characters of the *L. seramensis* group are present in *L. onim* sp. nov. and the mouthparts are generally very similar to *L. arfak* sp. nov. On the other hand, a femoral patch is absent on the foreleg, contrary to what should be expected for *Baetis* and the labial palp has the characteristics of *Labiobaetis*. We could not investigate the folding of the protogonostyli developing under the larval cuticle of last instar male larvae. We are convinced that the remarkable posterior margins of the tergites are a convergent development and that the species belongs to the *seramensis* group of *Labiobaetis*.

Table 3. Intraspecific (bold) and interspecific genetic distances of the species of the *L. claudiae* group (COI; Kimura 2-parameter).

		1	2	3	4	5	6	7	8	9
1	*L. academicus*									
2	*L. academicus*	**0.00**								
3	*L. centralensis*	0.22	0.22							
4	*L. centralensis*	0.23	0.23	**0.01**						
5	*L. claudiae*	0.21	0.21	0.24	0.24					
6	*L. hattam* sp. nov.	0.23	0.23	0.23	0.23	0.23				
7	*L. stagnum*	0.20	0.20	0.26	0.27	0.23	0.23			
8	*L. werneri* sp. nov.	0.19	0.19	0.25	0.25	0.20	0.21	0.23		
9	*L. werneri* sp. nov.	0.18	0.18	0.25	0.25	0.20	0.21	0.22	**0.03**	
10	*L. werneri* sp. nov.	0.19	0.19	0.25	0.25	0.20	0.21	0.22	0.05	**0.06**

Distribution of *Labiobaetis* in the Wallacea region

The *L. seramensis* group is present with two species on the island Seram (Indonesia, Moluccas) and with two others in New Guinea. Moreover, *L. arfak* sp. nov. from New Guinea is morphologically very similar to *L. seramensis* from Seram (Kaltenbach and Gattolliat 2018: figs. 38, 39). Differences are the dorsal setation of tibia and tarsus and two posterolateral spines on tergites VIII and IX in *L. arfak* sp. nov. (Fig. 14f), absent in *L. seramensis*. Kaltenbach and Gattolliat (2018) already discussed the general morphological affinities of *L. seramensis* and *L. wahai* with species from New Guinea rather than with species from the Oriental realm. *Labiobaetis* from New Guinea (and Australia) are characterised by the absence of an antennal scape process, all but one species have only six pairs of gills, hind protoptera are absent in all species, and most species have simple setae forming the submarginal arc of setae on the dorsal surface of the labrum. The number of setae at the dorsal margin of the femur is mostly above 20, sometimes even above 40, and only in one case less than 12 (Kaltenbach and Gattolliat 2018). In the Oriental realm as well as in other regions, these character states are more evenly distributed and there are at least several species with or without antennal scape process, with six or seven pairs of gills, and with or without hind protoptera. The proportion of the different types of dorsal labrum arc setae (simple, feathered, clavate) is more equalised. The latter is especially true in the Oriental realm, whereas only the feathered type is present in the Afrotropical region (Lugo-Ortiz and McCafferty 1997; Gattolliat 2001; Kaltenbach and Gattolliat 2019, 2020, 2021a, b; Kaltenbach et al. 2020). Additionally, the number of setae at the dorsal margin of the femur in the Oriental realm is usually below 20 and often below 12.

The Wallace Line is marking the eastern boundary of the Oriental fauna, and Lydekker's Line is considered to be the western boundary of the strictly Australian fauna. The mixed zone in between is referred to as Wallacea by many biogeographers (Cox et al. 2016: fig. 11.9). It encompasses Sulawesi, Halmahera, the Moluccas, the Lesser Sunda Islands (e.g., Lombok, Sumbawa, Sumba, Flores, Timor) and many smaller islands. For *Labiobaetis*, the two reported species of Seram are clearly faunal

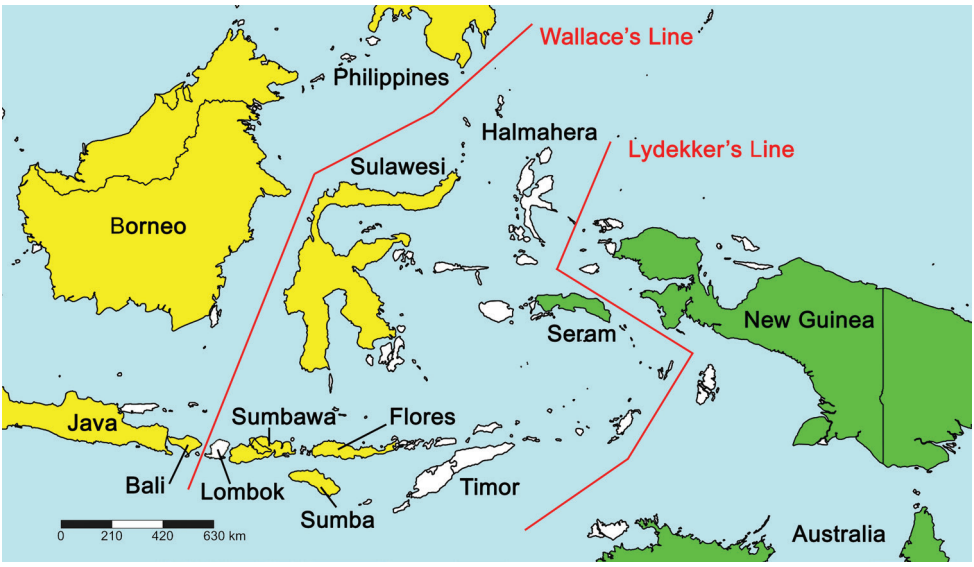

Figure 22. Distribution of *Labiobaetis* in the Wallacea, with indication of morphological affinities to species of the Oriental realm (yellow) or New Guinea (green). White: Islands without reported species. Wallace's Line and Lydekker's Line adapted after Cox et al. 2016: fig. 11.9.

elements of New Guinea, but all other known species of the Wallacea have strong morphological affinities to the Oriental realm (Fig. 22): *L. pilosus* Kaltenbach & Gattolliat, 2019 (Sulawesi) is part of the *numeratus* group, which is widely distributed in the Oriental realm, but absent in New Guinea; *L. itineris* Kaltenbach & Gattolliat, 2019 (Bali, Sumbawa) is part of the *sumigarensis* group, which is widely distributed in the Oriental realm, but absent in New Guinea; *L. weifangae* Kaltenbach & Gattolliat, 2019 (Sumbawa, Sumba), *L.* cf. *weifangae* (unpublished, Flores) and *L. jonasi* Kaltenbach & Gattolliat, 2019 (Sumba) are part of or very close (for *L. jonasi*) to the *difficilis* group, distributed in Southeast Asia, but absent in New Guinea; *L. sulawesiensis* Kaltenbach & Gattolliat, 2019 (Sulawesi) and *L. sumbensis* Kaltenbach & Gattolliat, 2019 (Sumba) belong to the *batakorum* group, additionally present in Sumatra and absent in New Guinea.

Independent from the situation in the Wallacea, there could have been a limited stepping stone exchange between the Philippines and New Guinea, as we found members of the groups *vallus* and *dendrisetis* in both these archipelagos (Kaltenbach and Gattolliat 2018; Kaltenbach et al. 2020) and both groups are unknown from other areas.

Taking into account the extreme diversity in Southeast Asia and New Guinea, the rather poor collection activities in the past, with many still unexplored regions, and the obvious richness of *Labiobaetis* in this region, we have to expect many more species with further collections in the future.

Acknowledgements

We sincerely thank Kate Baker (University of Exeter, UK) for the collection of this precious material and to make it available to the Museum of Zoology Lausanne (MZL). It was collected during ecological studies in Brunei Darussalam, funded by Natural Environment Research Council (NERC), and in collaboration with Universiti Brunei Darussalam. We are also deeply thankful to Lars Hendrich (SNSB-Zoologische Staatssammlung München, ZSM, Germany) and Janice Peters (Florida A&M University, Tallahassee, USA) for the loan of *Labiobaetis* type material from Southeast Asia and Sri Lanka. Further, we are also grateful to Michel Sartori (MZL) for his constant interest and support for our projects, to Antonio Mucciolo (University Lausanne, UNIL) for the SEM pictures, and to Marion Podolak (MZL) for her support with lab work and preparation of the COI barcodes. Finally, we are thankful to the reviewers, Carolina Nieto, Frederico Salles, and Will Flowers for their valuable comments and corrections.

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