

A new millipede of the family Ammodesmidae found in central Africa (Diplopoda, Polydesmida)

Didier VandenSpiegel¹, Sergei I. Golovatch²

1 Royal Museum for Central Africa, B-3480 Tervuren, Belgium **2** Institute for Problems of Ecology and Evolution, Russian Academy of Sciences, Leninsky prospekt 33, Moscow 119071 Russia

Corresponding author: *Didier VandenSpiegel* (dvdspiegel@africamuseum.be)

Academic editor: *Pavel Stoev* | Received 16 December 2014 | Accepted 4 February 2015 | Published 19 February 2015

<http://zoobank.org/37110396-0D48-4666-85F0-D2FFDAAE38D6>

Citation: VandenSpiegel D, Golovatch SI (2015) A new millipede of the family Ammodesmidae found in central Africa (Diplopoda, Polydesmida). ZooKeys 483: 1–7. doi: 10.3897/zookeys.483.9150

Abstract

The first species of the small Afrotropical family Ammodesmidae discovered in central Africa (Democratic Republic of the Congo) belongs to the genus *Ammodesmus* Cook, 1896, which was hitherto known only from two species in western Africa. A key is given to incorporate *A. congoensis* sp. n., a species also showing an evident sex dimorphism: ♂ densely hirsute, ♀ with much longer and sparser tergal setae.

Keywords

Ammodesmus, taxonomy, new species, key, sex dimorphism, Democratic Republic of the Congo

Introduction

The Afrotropical millipede family Ammodesmidae has hitherto been known by only two genera: *Ammodesmus* Cook, 1896, with two species from western Africa (Guinea, Liberia and Ivory Coast), and *Elassystremma* Hoffman & Howell, 1981, with four species from eastern Africa (Kenya, Tanzania and Malawi) (VandenSpiegel and Golovatch 2012). The huge geographical gap between these genera has long remained enigmatic as to which ammodesmids could possibly occur there (e.g. Hoffman and Howell 1981, Hoffman 1993).

At the moment, *Ammodesmus* contains *A. granum* Cook, 1896, the type species, from several places in Guinea, Liberia and Ivory Coast, including Mt. Nimba, as well as *A. nimba* VandenSpiegel & Golovatch, 2012, from a single forest patch on Mt. Nimba, at the border between these three countries. This genus is easily distinguished by the particularly small size of its species (adults < 3.0 mm in length) and, especially, the strongly modified last legs in both sexes, in which the tibia is supplied with a long flagellum distodorsally (VandenSpiegel and Golovatch 2012).

Examination of some old material from the Democratic Republic of the Congo (formerly, first Belgian Congo, then Zaire) revealed the first ammodesmid samples. These represent a new species of *Ammodesmus* which is described here. This discovery shows a far vaster distribution of *Ammodesmus* in western and central Africa than previously known. In addition, a key is provided to all three known species of the genus.

Material and methods

The material examined belongs to the collection of the Royal Museum for Central Africa (MRAC), Tervuren, Belgium, with only a few duplicates shared with the collection of the Zoological Museum, State University of Moscow (ZMUM), Russia, as indicated hereafter. All samples are stored in 70% ethanol. Specimens for scanning electron microscopy (SEM) were air-dried, mounted on aluminium stubs, coated with gold and studied using a JEOL JSM-6480LV scanning electron microscope.

Description

Ammodesmus congoensis sp. n.

<http://zoobank.org/FD3B5F5E-37B0-433B-BDB9-32DF3A4426AC>

Figs 1–3

Type material. Holotype ♂ (MRAC 20150), Democratic Republic of the Congo, Parque National Albert, secteur Sud, Berlese extraction, 1956, leg. R.P. Celis. Paratypes: 3 ♂ (MRAC 20150), same data, together with holotype; 5 ♀ (MRAC 20151), same data; 1 ♂, 1 ♀ (ZMUM p2441), same data; 2 ♀ (MRAC 20171), same data; 4 ♂, 2 ♀ (MRAC 20149), same data; 1 ♂, 1 subadult ♀ (MRAC 20274), same data; 1 ♂ (MRAC 20201), same data; 5 ♂, 16 subadult & earlier instar ♂, 1 ♀ (MRAC 20294), same data.

Name. To emphasize the provenance of the new species from Congo.

Diagnosis. Minute polydesmidans (length 1.5–2.1 mm, width 0.6–0.8 mm) with 18 or 19 body segments in both sexes, missing ozopores, simple biramous gonopods, and evident sexual dimorphism in tergal structure: metaterga in ♂ very densely pilose all over, with only few longer setae, devoid of a median transverse gutter, whereas ♀ metaterga with a deep transverse gutter in anterior third supporting a single row of ca 10–18 long setae positioned at gutter's bottom.

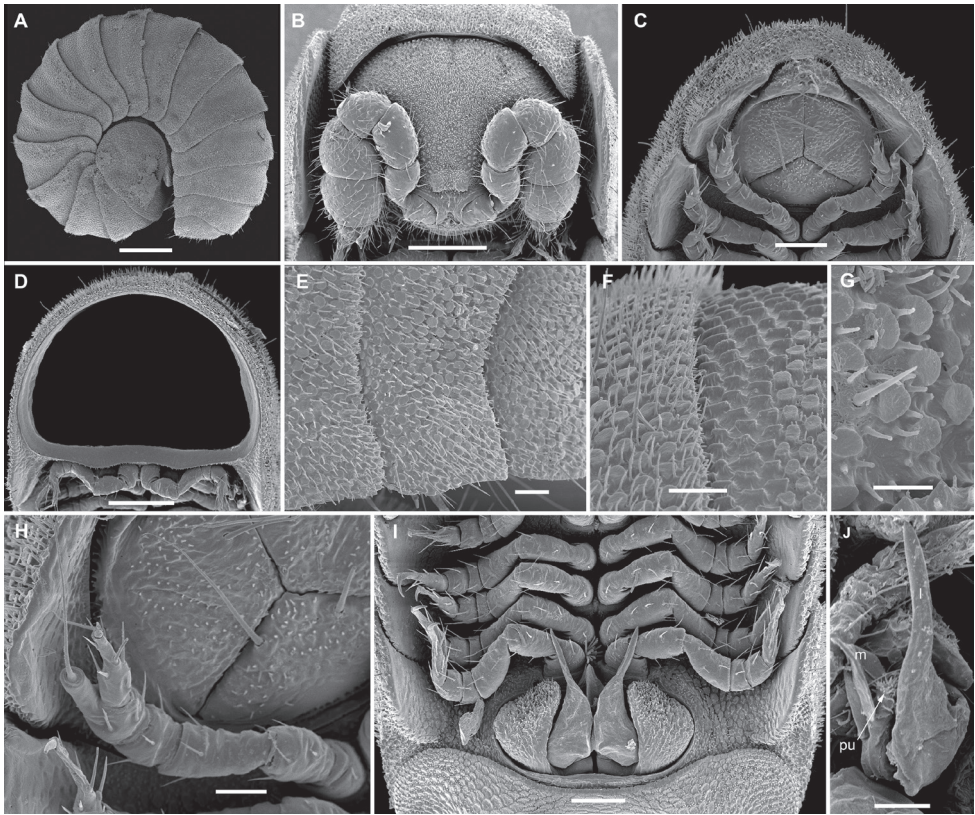


Figure 1. *Ammodesmus congoensis* sp. n., a 18-segmented ♂ paratype. **A** habitus of male, lateral view **B** head, ventral view **C** posterior part of body, caudal view **D** caudal view of a midbody segment, caudal view **E** midbody paraterga, lateral view **F**, **G** tegument texture, dorsal view **H** last left leg, lateral view; **I** both gonopods *in situ*, ventral view **J** left gonopod, submesal view. Scale bars: **A** = 200 µm; **B**, **D** = 100 µm; **C**, **I** = 50 µm; **E**, **F** = 20 µm; **G**, **J** = 10 µm. (**I** lateral finger-shaped branch, **m** mesal finger-shaped branch, **pu** pulvillus).

Description. Length of adults 1.5–2.1 mm, width 0.6–0.9 mm, ♂ usually a little smaller than ♀. Adult body with 18 or 19 segments (17+1+T) (♂, ♀). Entire dorsal surface covered with a thin layer of secretions (= cerategument) borne by microvilli, often also a dirt crust, under which the body integument is uniformly yellowish. Body shape as in Figs 1A, 3A, with caudal body end tapering towards a relatively small telson, the latter not being concealed by last paraterga (Figs 1C, 3F). Head small, only partly concealed under front edge of collum (Figs 1B, 3B); upper half of head densely granulate, lower part smooth and densely setose. Interantennal isthmus about as wide as antennomere 1 or antennal socket diameter (Fig. 1B). Antennae very strongly clavate due to subequal antennomeres 5 and 6 (Fig. 1B). Collum subquadrate, slightly impressed along longitudinal axis (Fig. 3B); tergum 2 as usual, hypertrophied, with strongly enlarged, spatuliform paraterga concealing the head in lateral view (Figs 1A, 3A, C). Lim-

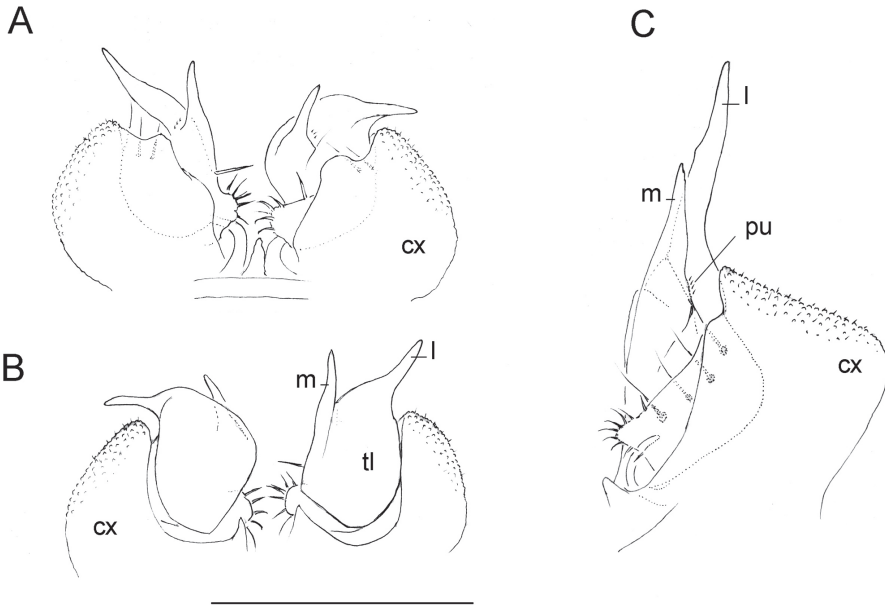


Figure 2. Gonopods of a 18- (**A, B**) and a 19-segmented ♂ paratype (**C**). **A, B** both gonopods *in situ*, frontal and caudal views, respectively **C** left gonopod, frontal view. Scale bar: 1.0 mm (**cx** coxae, **l** lateral finger-shaped branch, **m** mesal finger-shaped branch, **pu** pulvillus, **tl** telopodite).

bus nearly smooth, at most with sparse, well separated, short spicules. Metaterga either regularly convex and uniformly very densely pilose throughout, with only few scattered longer setae (♂, including juveniles) (Fig. 1E, F, G) or nearly smooth, showing a deep transverse gutter in anterior 1/3, the latter supplied with ca 10–18 especially long, microspiculate setae at bottom and bearing a small pit marking ventral end of gutter about midheight of paraterga (♀, including juveniles) (Fig. 3A, D). Prozonae and stricture thereafter beset with round scales with peripheral hair-like cuticular outgrowths (Fig. 1F, G). Paraterga vertical, continuing the highly convex outline of dorsum, their ends rounded, projecting far below venter/coxae (Figs 1E, 3E), increasingly angular towards telson (Fig. 3E). Anteroventral edges of paraterga 3 to 15 each with a notch forming a groove for paratergum 2 to hinge into during volvation. Ozopores absent. Telson small (Figs 1C, 3F). Hypoproct triangular (Figs 1C, 3F).

Legs rather slender, but short, barely reaching tips of paraterga (Fig. 1C, I); femora and tarsi subequal in length, longer than other podomeres; claw normal, simple, very slightly curved ventrad; last pair of ♂ and ♀ legs modified, typical of *Ammodesmus*, with a long distodorsal flagellum borne on a stump on tibia (Figs 1H, 3G).

Gonopods (Figs 1I, J, 2) relatively simple. Coxae small, globulose, micropapillate and microsetose laterally. Telopodite long and well-exposed beyond gonocoxae, divided into two finger-shaped branches: a shorter mesal (**m**) and a longer lateral (**l**); a small hairy pulvillus (**pu**) marking the orifice of a short seminal groove at base between **m** and **l**. A solenomere absent.

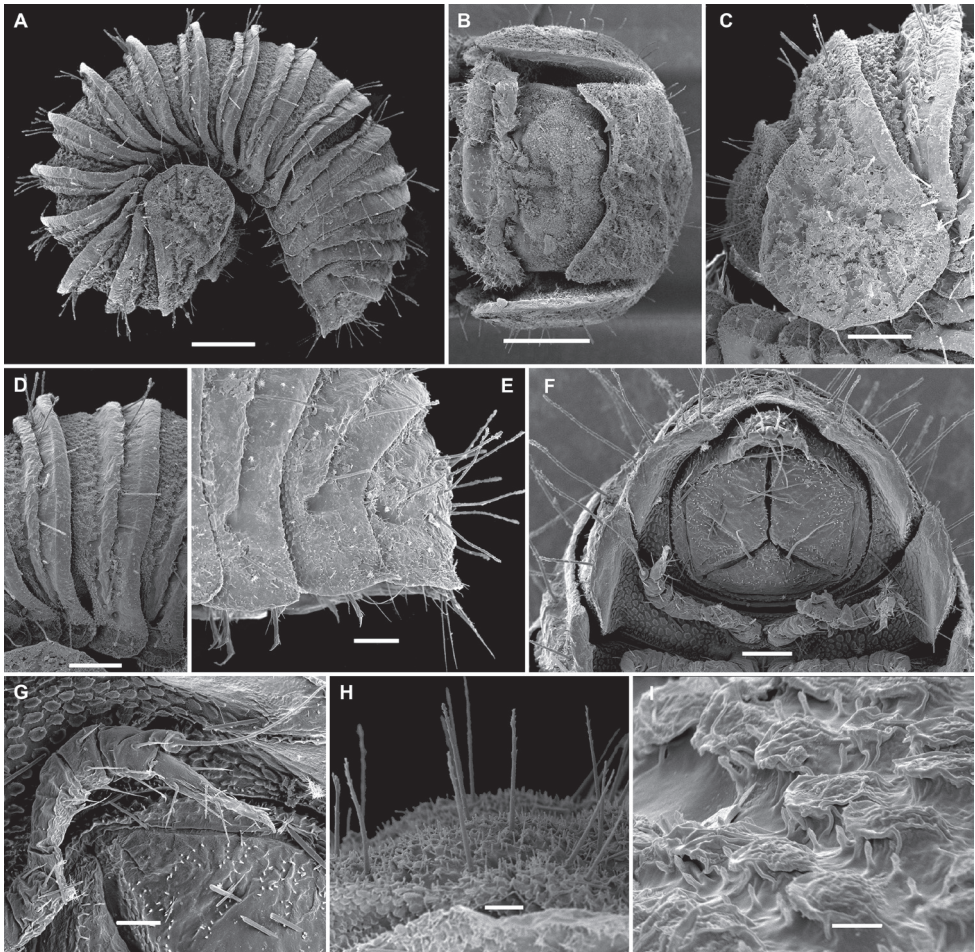


Figure 3. *Ammodesmus congoensis* sp. n., a 19-segmented ♀ paratype. **A** habitus, lateral view **B** head and collum, dorsal view **C, D, E** anterior, middle and caudal parts of body, respectively, lateral view **F** posterior part of body, caudal view **G** last left leg, lateral view **H** tergal setae, dorsal view **I** tegument texture, dorsal view. Scale bars: **A, B** = 200 µm; **C, D** = 100 µm; **E, F** = 50 µm; **G, H** = 20 µm; **I** = 5 µm.

Remarks. The total absence of ozopores in *A. congoensis* sp. n. is well documented by Fig. 1A which shows an adult ♂ with 18 segments clean enough to be certain. In both other *Ammodesmus* species, in addition to the pits near the base of the paraterga, which are also observed in the new species, ozopores are clearly visible closer to the ventral ends of paraterga 5, 7, 9, 10, 12, 13, 15–17(18). A similar pore formula is observed in *Elassystremma* species: 5, 7, 9, 12, 13, 15–17(18). As variation in ozopore distribution in Ammodesmidae is a proven fact, we are reluctant to create a separate, new genus for *A. congoensis* sp. n. only because it totally lacks ozopores. The most important character that brings the new species together with *A. granum* and *A. nimba* is the strangely modified last leg-pair.

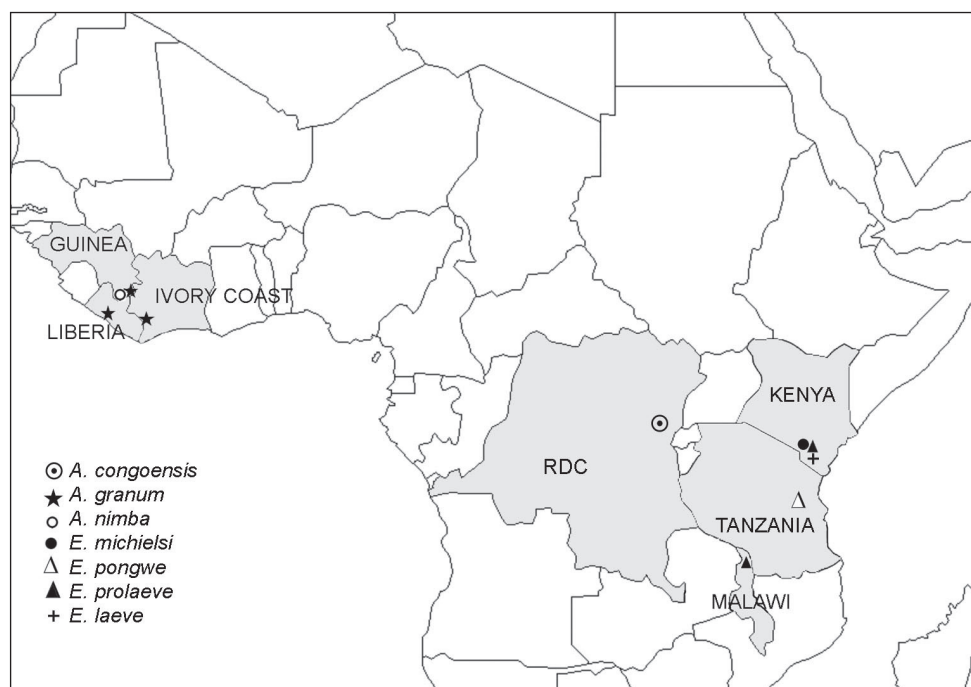


Figure 4. Updated distribution of the family Ammodesmidae.

Variation in adults of both sexes showing either 18 or 19 segments is another piece of evidence bringing *A. congoensis* sp. n. especially close to *A. granum*. The latter has hitherto remained the only species of Polydesmida where the number of segments varies regardless of sex. As in the ♂ the size of the body likewise correlates positively with gonopod size (Fig. 1I), an additional molt of the 18-segmented adult turning it into the 19-segmented one is obviously implied.

Key to *Ammodesmus* species

- 1 Metaterga smooth, either densely pilose and/or sparsely setose (Figs 1A–F, 3A, D). Gonopods simple, telopodites biramous (Figs 1I, J, 2A–C). Central Africa.....***A. congoensis* sp. n.**
- A transverse row of large, flat, low bosses or high tubercles located in caudal 1/3 of metaterga, the latter neither setose nor pilose. Gonopods different. Western Africa.....**2**
- 2 No sexual dimorphism in tergal sculpture. Gonopods complex, with extremely large coxae concealing telopodites inside a deep gonocoel***A. nimba***
- Drastic sexual dimorphism in tergal sculpture: ♂ with, ♀ without, high tubercles across metaterga. Gonopods simple, telopodites uniramous, mostly represented by solenomeres.....***A. granum***

Conclusion

Fig. 4 shows an updated distribution of the known species of Ammodesmidae. *Ammodesmus* is more widespread, occurring both in western and central Africa. Only *A. granum* is relatively widespread, whereas the other two congeners seem to be highly local in distribution. In contrast, *Elassystremma* seems to be confined to eastern Africa. All four *Elassystremma* species (*E. pongwe* Hoffman & Howell, 1981, *E. michielsi* VandenSpiegel & Golovatch, 2004, *E. laeve* VandenSpiegel & Golovatch, 2004 and *E. prolaeve* VandenSpiegel & Golovatch, 2004) are slightly larger than *Ammodesmus* (up to 5 mm long), and their gonopods are invariably complex, sunken inside a deep gonocoel (VandenSpiegel and Golovatch 2004). Likewise, only one species, *E. prolaeve*, is widespread, occurring not only in Kenya and Malawi, but probably also in between in Tanzania.

Acknowledgements

Sergei Golovatch is most obliged to the Royal Museum for Central Africa, Tervuren, Belgium for the invitation to work on this project. Thanks are also due to Jean-Pierre Michiels for his technical assistance.

References

- Hoffman RL (1993) Biogeography of East African montane forest millipedes. In: Lovett JC, Wasser SK (Eds) Biogeography and ecology of the rain forests of eastern Africa, 103–114.
- Hoffman RL, Howell KM (1981) An ammodesmid millipede from Tanzania (Polydesmida). *Revue de Zoologie africaine* 95(1): 227–233.
- VandenSpiegel D, Golovatch SI (2004) Review of the East African millipede genus *Elassystremma* Hoffman & Howell, 1981 (Diplopoda: Polydesmida: Ammodesmidae), with descriptions of three new species. *Arthropoda Selecta* 12(3–4): 183–191. [for 2003] http://zmmu.msu.ru/files/images/spec/journals/12_3%20183_191%20Van%20Der%20Spiegel.pdf
- VandenSpiegel D, Golovatch SI (2012) The millipede family Ammodesmidae (Diplopoda, Polydesmida) in western Africa. *ZooKeys* 221: 1–17. doi: 10.3897/zookeys.221.3739

Revised concept of the fossil genus *Oviparosiphum* Shaposhnikov, 1979 with the description of a new genus (Hemiptera, Sternorrhyncha, Aphidomorpha)

Dagmara Żyła¹, Agnieszka Homan², Barbara Franielczyk², Piotr Wegierek²

¹ Department of Natural History, Upper Silesian Museum, Plac Jana III Sobieskiego 2, 41–902 Bytom, Poland

² Department of Zoology, University of Silesia, Bankowa 9, 40–007 Katowice, Poland

Corresponding author: Dagmara Żyła (zyladagmara@gmail.com)

Academic editor: R. Blackman | Received 6 November 2014 | Accepted 9 February 2015 | Published 19 February 2015

<http://zoobank.org/CB36F3AA-C7E0-47D1-B38F-E3CB0A046DBA>

Citation: Żyła D, Homan A, Franielczyk B, Wegierek P (2015) Revised concept of the fossil genus *Oviparosiphum* Shaposhnikov, 1979 with the description of a new genus (Hemiptera, Sternorrhyncha, Aphidomorpha). *ZooKeys* 483: 9–22. doi: 10.3897/zookeys.483.8902

Abstract

This paper presents a revision of the aphid genus *Oviparosiphum*, which is known from the Cretaceous period. Redescriptions of two species: *O. jakovlevi* Shaposhnikov, 1979 and *O. baissense* Shaposhnikov & Wegierek, 1989 are made, and an updated diagnosis of this genus is provided. *Oviparosiphum baissense* is the type species of a newly described genus *Archeoviparosiphum* **gen. n.** Five other species of *Oviparosiphum* are also transferred to the new genus. The basis for their separation from *Oviparosiphum* is the structure of the siphunculi and ovipositor. A key is provided to the genera of Oviparosiphidae.

Keywords

Aphids, fossils, Cretaceous, Oviparosiphidae, *Archeoviparosiphum* gen. n., morphology

Introduction

One aphid family known only from fossils is Oviparosiphidae. Representatives of this family are known from several localities (China, Germany, Mongolia, Russia) but originated within a relatively short time span, from the Early/Middle Jurassic to the end of the Early Cretaceous. The oldest genus is *Grimmenaphis* Ansorge, 1996, described

from the Lower Jurassic deposit of Grimmen (Germany). However, it is known only from an isolated wing (Ansorge 1996). The oldest undoubted representative is *Khotontaphis* Shaposhnikov & Wegierek, 1989 from the Upper Jurassic/Lower Cretaceous Khotont deposit (Mongolia). More Oviparosiphidae are known from the Early Cretaceous: *Acanthotrichaphis* Shaposhnikov & Wegierek, 1989, *Dinaphis* Shaposhnikov & Wegierek, 1989, *Expansaphis* Hong & Wang, 1990, *Oviparosiphum*, *Sinoviparosiphum* Ren, 1995 and *Vitimaphis* Shaposhnikov & Wegierek, 1989, but they are absent from Upper Cretaceous sediments (Heie and Wegierek 2011).

This family is highly diverse morphologically, but the simultaneous occurrence of the ovipositor and siphunculi constitutes its most characteristic feature (Shaposhnikov 1979). The first described aphid with both these structures visible was *Oviparosiphum jakovlevi* from the Lower Cretaceous Bon–Tsagan deposit (Mongolia), which is the type species of the genus *Oviparosiphum* (Shaposhnikov 1979). To date, the genus includes seven species. The present paper revises the species originally placed in *Oviparosiphum*. It also emends its diagnosis and describes a new genus.

Material and methods

The material consisted of 44 aphid fossil specimens borrowed from the collection of the Institute of Palaeontology, Russian Academy of Sciences in Moscow. The fossils were preserved in the form of two imprints – “obverse” and “reverse”, marked as ±. The material was analyzed using standard palaeontological research methods (Rasnitsyn 2002). Specimens were photographed using a Nikon SMZ1500 stereoscopic microscope and a Nikon Eclipse E600 polarized light microscope. Selected body parts were photographed using Philips XL 30 TMP ESEM and Tescan Vega scanning electron microscopes (with the backscattered electron detector (BSE) in the low–vacuum mode) for better analysis of their morphology. Photographs and measurements were made in the NIS-Elements program. The figures are based on the combined drawings of reverse and obverse imprints, while the photographs represent only one imprint. All measurements are given in mm.

The imprints were collected from two localities: Baissa, Russia and Bon–Tsagaan, Mongolia. Both of them are Lower Cretaceous deposits.

Geological settings

Baissa is one of the richest deposits and most important localities of fossil insects from the Early Cretaceous. More than 10 000 specimens of insects have been collected from there (Rasnitsyn and Zherikhin 2002). It is located in the Asian part of Russia, in Transbaikalia, in the Buryat Republic, on the left bank of the Vitim River (Kania and Wegierek 2008). The Baissa deposit belongs to the Zaza Formation of approximately Berriasian age (Rasnitsyn et al. 1998). This lithostratigraphic unit is characteristic of

the Lower Cretaceous sediments throughout western Transbaikalia. It is built mainly of sandstone, limestone, marl and bituminous shale (Zherikhin et al. 1999).

Bon–Tsagan (= Bon–Tsagaan) is one of the richest Mesozoic insect remains deposits in Mongolia, and one of the best known and richest in the world. Numerous outcrops of mudstone and marls are widely distributed in Central Mongolia, south of the recent Lake Bon–Tsagaan–Nur (Rasnitsyn and Zherikhin 2002). The exact age of the lacustrine sediments of Bon–Tsagaan is estimated at the Early Cretaceous, probably the Aptian. Fossils are well preserved in lacustrine sediments of the lake, which was situated in a mountain valley (Ponomarenko 2013).

Systematic palaeontology

Key to the genera of the family Oviparosiphidae:

- | | | |
|---|--|--|
| 1 | Less than seven antennal segments..... | 2 |
| – | Seven antennal segments..... | 3 |
| 2 | Secondary rhinaria round and irregular. <i>Expansaphis</i> Hong & Wang, 1990 | |
| – | Secondary rhinaria annular..... | <i>Sinoviparosiphum</i> Ren, 1995 |
| 3 | Siphunculi in the form of short truncate cones..... | 4 |
| – | Siphunculi in form of pores..... | 6 |
| 4 | Ovipositor large and well-developed. <i>Oviparosiphum</i> Shaposhnikov, 1979 | |
| – | Ovipositor rudimentary..... | 5 |
| 5 | Cubital veins with separate bases..... | |
| | <i>Vitimaphis</i> Shaposhnikov & Wegierek, 1989 | |
| – | Cubital veins leave the main vein Sc + R + M from one point..... | |
| | <i>Khotontaphis</i> Shaposhnikov & Wegierek, 1989 | |
| 6 | Vein CuA ₁ not connected with the main vein Sc + R + M..... | |
| | <i>Daoaphis</i> Huang, Wegierek, Żyła & Nel, 2014 | |
| – | Vein CuA ₁ connected with the main vein Sc + R + M..... | 7 |
| 7 | Pterostigma long, at least 5.5 times longer than wide..... | |
| | <i>Dinaphis</i> Shaposhnikov & Wegierek, 1989 | |
| – | Pterostigma short, at most 5 times longer than wide..... | 8 |
| 8 | Abdomen with setae..... | <i>Acanthotrichaphis</i> Shaposhnikov & Wegierek, 1989 |
| – | Abdomen without setae..... | <i>Archeoviparosiphum</i> gen. n. |

Genus *Oviparosiphum* Shaposhnikov, 1979

Type species. *Oviparosiphum jakovlevi* Shaposhnikov, 1979

Emended diagnosis. Seven antennal segments. Secondary rhinaria slightly ellipsoidal, large. Siphunculi in the form of short truncate cones. Ovipositor large with valvae I and III well developed.

***Oviparosiphum jakovlevi* Shaposhnikov, 1979**

Figs 1, 2, 3, 4

Holotype. 3559/51, Paleontological Institute, Russian Academy of Sciences, Moscow; Bon–Tsagaan locality (Mongolia); Early Cretaceous (Aptian); alate female

Emended diagnosis. As for genus.

Redescription. Body (2.49) thick (Figs 1A–C, 3A). Epicranial suture present (Fig. 4A), connected in the middle of the epicranium with lateral sutures. On head, narrow oblique slats running from front and lateral edges to the posterior part of the head. Diameter of ocelli 0.05; distance between ocelli 0.24. Segment I of antennae (0.05) shorter than segment II (0.08) (Fig. 4B). Secondary rhinaria arranged in transverse rows (Fig. 2A). Praescutum length 0.37; width 0.52. Femora thick. Fore tibia (1.07) about 2.5 times longer than fore femur (0.38). Length of middle tibia 1.02. Middle tarsus (0.26) (Fig. 2B) about one fourth of middle tibia length. Length of hind coxa 0.11. Hind tibia (1.18) about twice as long as the hind femur (0.53). Hind tibiae about half the body length. Fore wing (4.76) (Figs 2D, 3B) longer than body length. Base of the wing narrow. Vein surface scaly (Figs 3C, D). Distance from base of wing to end of pterostigma 3.33. Bases of cubital veins very close to each other. CuA_1 (1.46) slightly arched distally, separating from main vein at a 45° angle, slightly shorter than CuA_2 . Vein CuA_2 (1.16) separating from main vein at mid-length between base of the wing and base of vein Rs, at a 70° angle. Vein M with three branches. Base of vein M directed to base of pterostigma, not connected with main vein. Branches of M form a wide (50°) fork. Base of fork of M_{1+2} and M_{3+4} behind base of vein Rs. Common stem of vein M (0.89) longer than M_{1+2} length (0.63) and equal to M_{3+4} length. Vein Rs (1.67) slightly curved, leaving proximal part of pterostigma at an angle of 25° and running close to it. Pterostigma pointed, short and wide; 3 times longer (0.93) than wide (0.31). Hind wing with two cubital vein. Apical part of abdomen slightly sclerotized (Figs 2C, 4C). Basal diameter of siphunculus 0.13 (Fig. 4D). Diameter of siphunculus aperture 0.10. Ovipositor with valvae I and III well preserved (Fig. 4E). Tergite IX of abdomen clearly visible. Subgenital plate wider than base of ovipositor, 5 times wider than long. In the middle part, its anterior edge forms an indentation reaching half of the length of the plate.

Genus *Archeoviparosiphum* gen. n.

<http://zoobank.org/B46E2C8B-351B-4392-ADA9-E786234AB825>

Type species. *Archeoviparosiphum baissense* (Shaposhnikov & Wegierek, 1989), comb. n.

Diagnosis. Seven antennal segments. Secondary rhinaria slightly ellipsoidal, smaller than secondary rhinaria of *Oviparosiphum*. Vein CuA_1 connected with the main vein $Sc + R + M$. Pterostigma short, at most 5 times longer than wide. Abdomen without setae. Siphunculi in form of pores. Ovipositor small and rudimentary.

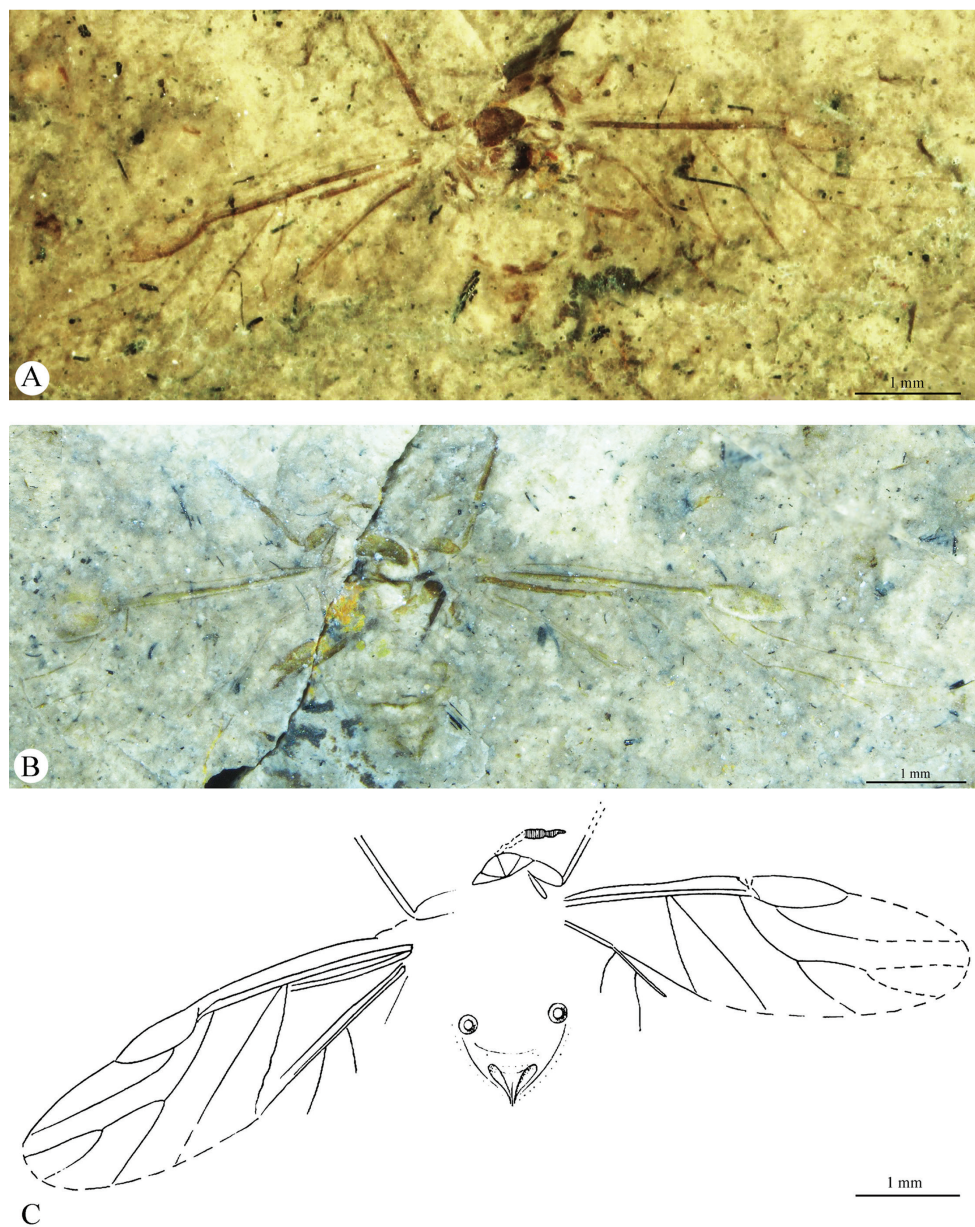


Figure 1. *Oviparosiphum jakovlevi* Shaposhnikov, 1979; PIN 3559/51, holotype. **A** body, ventral view **B** body, dorsal view **C** original reconstruction (after Shaposhnikov 1979).

Etymology. The name is a combination of the Greek word *archaios* (meaning ‘ancient’) and the genus *Oviparosiphum*.

Gender. Neuter.

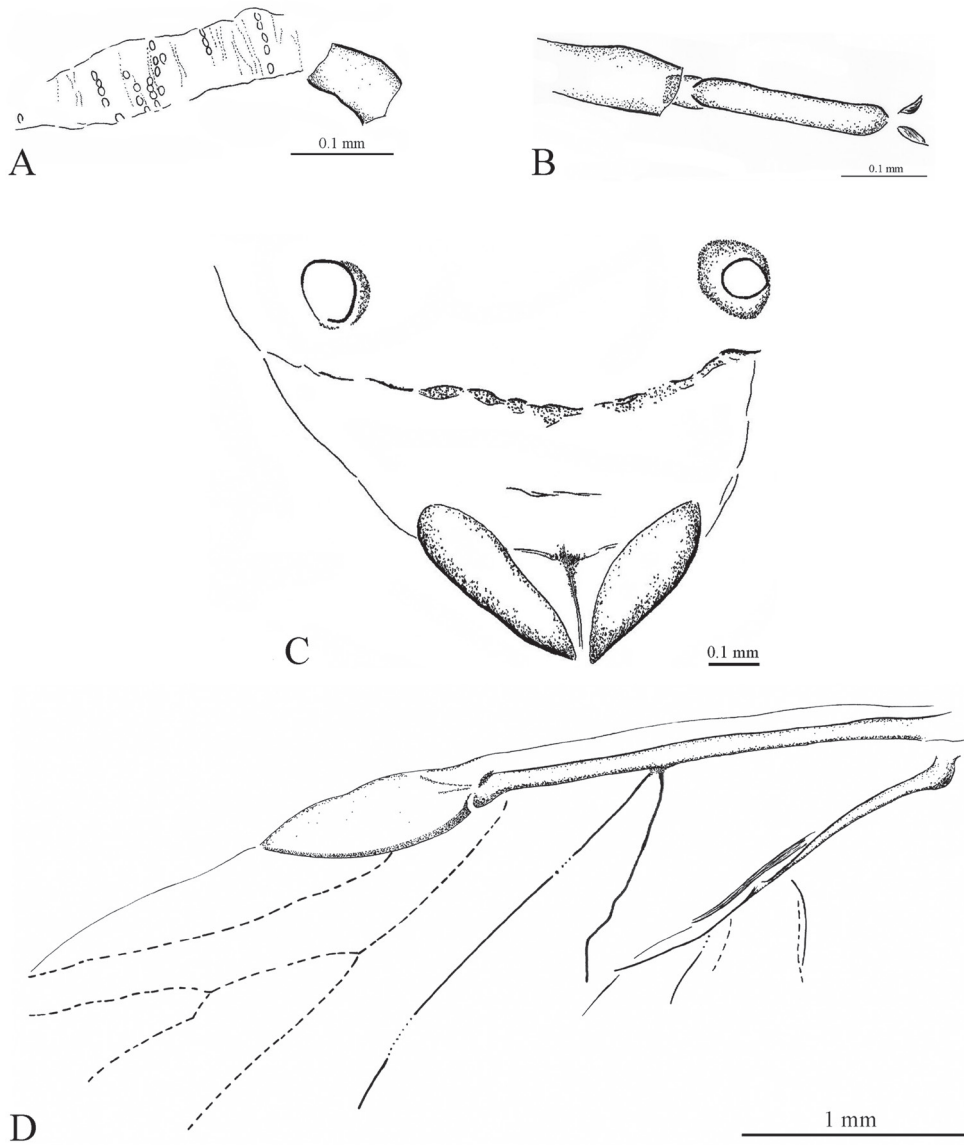


Figure 2. *Oviparosiphum jakovlevi* Shaposhnikov, 1979; PIN 3559/51, holotype. **A** fragment of right antenna with secondary rhinaria, dorsal view **B** middle tarsus **C** apical part of abdomen **D** reconstruction of fore wing.

Archeoviparosiphum baissense (Shaposhnikov & Wegierek, 1989), comb. n.

Figs 5, 6

Holotype. 4210/2623±, Paleontological Institute, Russian Academy of Sciences, Moscow; Baissa locality (Russia); Early Cretaceous; alate female

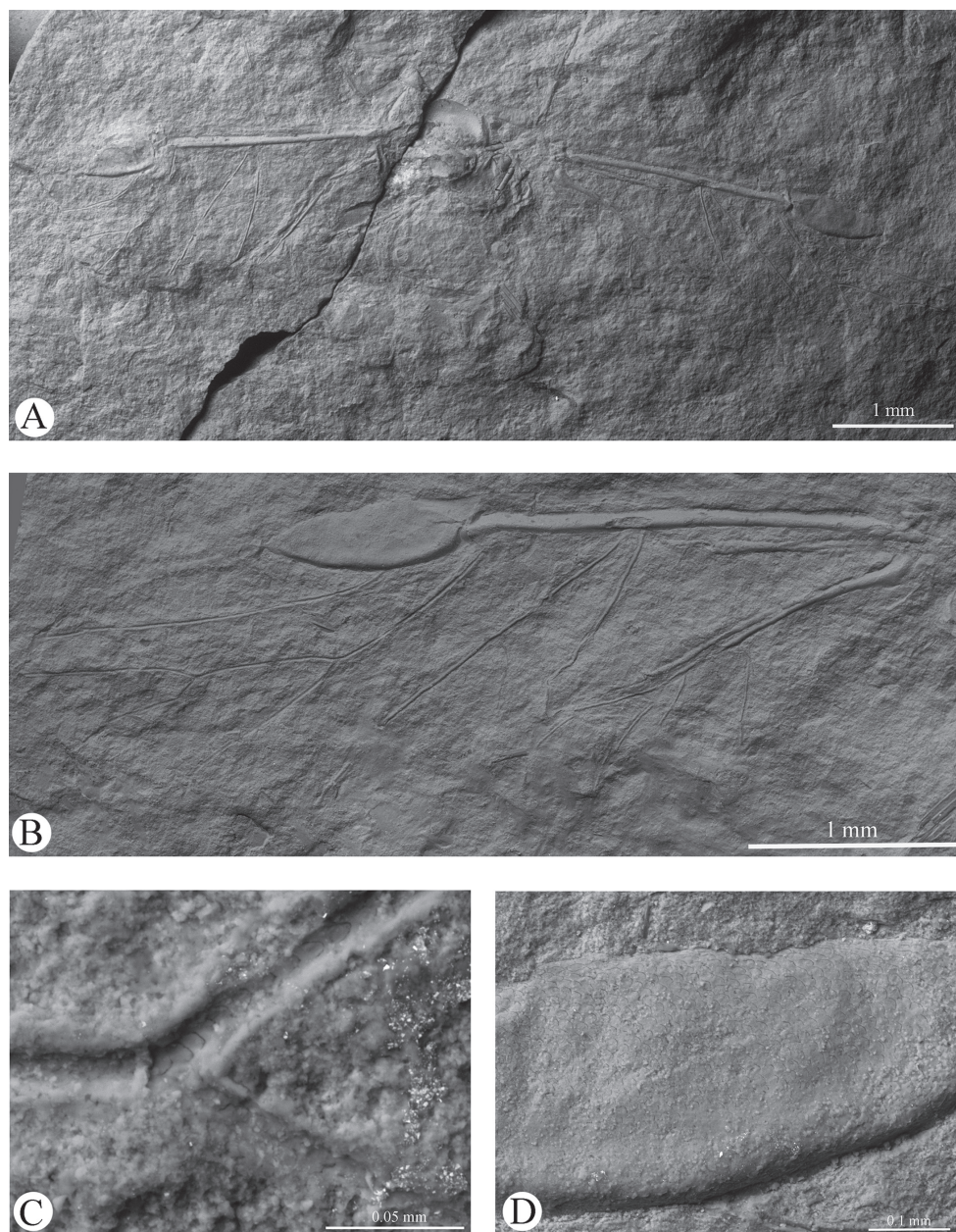


Figure 3. *Oviparosiphum jakovlevi* Shaposhnikov, 1979; PIN 3559/51, holotype, scanning electron micrographs. **A** body, dorsal view **B** fore wing **C** scaly surface of veins **D** scaly surface of pterostigma.

Paratypes. 3064/2107; 3064/2108(2273); 3064/2161(2164); 3064/2165; 3064/2166; 3064/2171(5138); 3064/2181; 3064/2184; 3064/2193(2210); 3064/2203; 3064/2205; 3064/2213±; 3064/2309(2311); 3064/2310(2312);

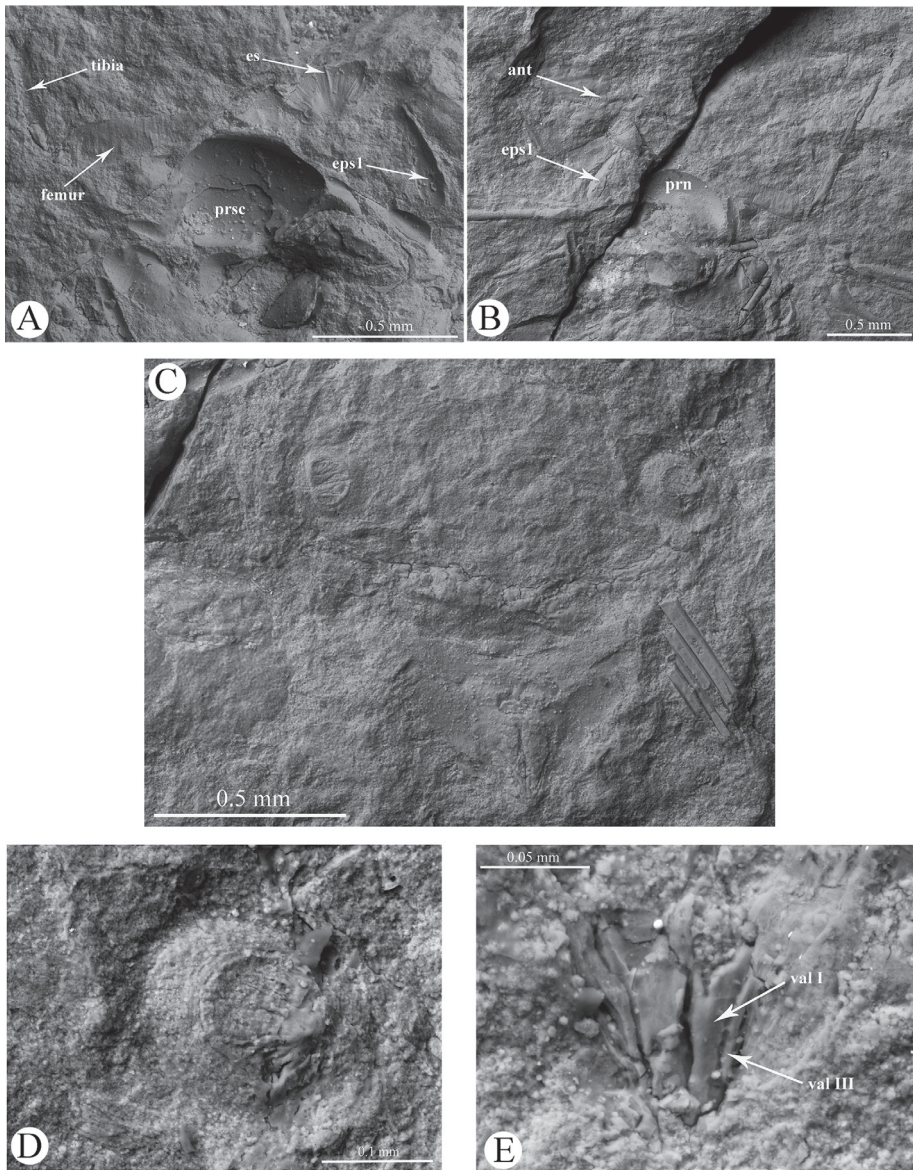


Figure 4. *Oviparosiphum jakovlevi* Shaposhnikov, 1979; PIN 3559/51, holotype, scanning electron micrographs. **A** head and thorax, ventral view **B** head and thorax, dorsal view **C** apical part of abdomen **D** siphunculi; **E** ovipositor. ant – antenna, epsI – proepisternum, es – epicranial suture, prn – pronotum, prsc – praescutum, val – valvae.

3064/2313(4846); 3064/2314; 3064/2315(2316); 3064/3978; 3064/4765;
 3064/4775; 3064/4816; 3064/4911; 3064/4915; 3064/4916(4922); 3064/4970;
 3064/4975; 3064/5031; 3064/5110; 4210/2521±; 4210/2624±; 4210/2625;
 4210/2771; 4210/2801±; 4210/2802; 4210/2803

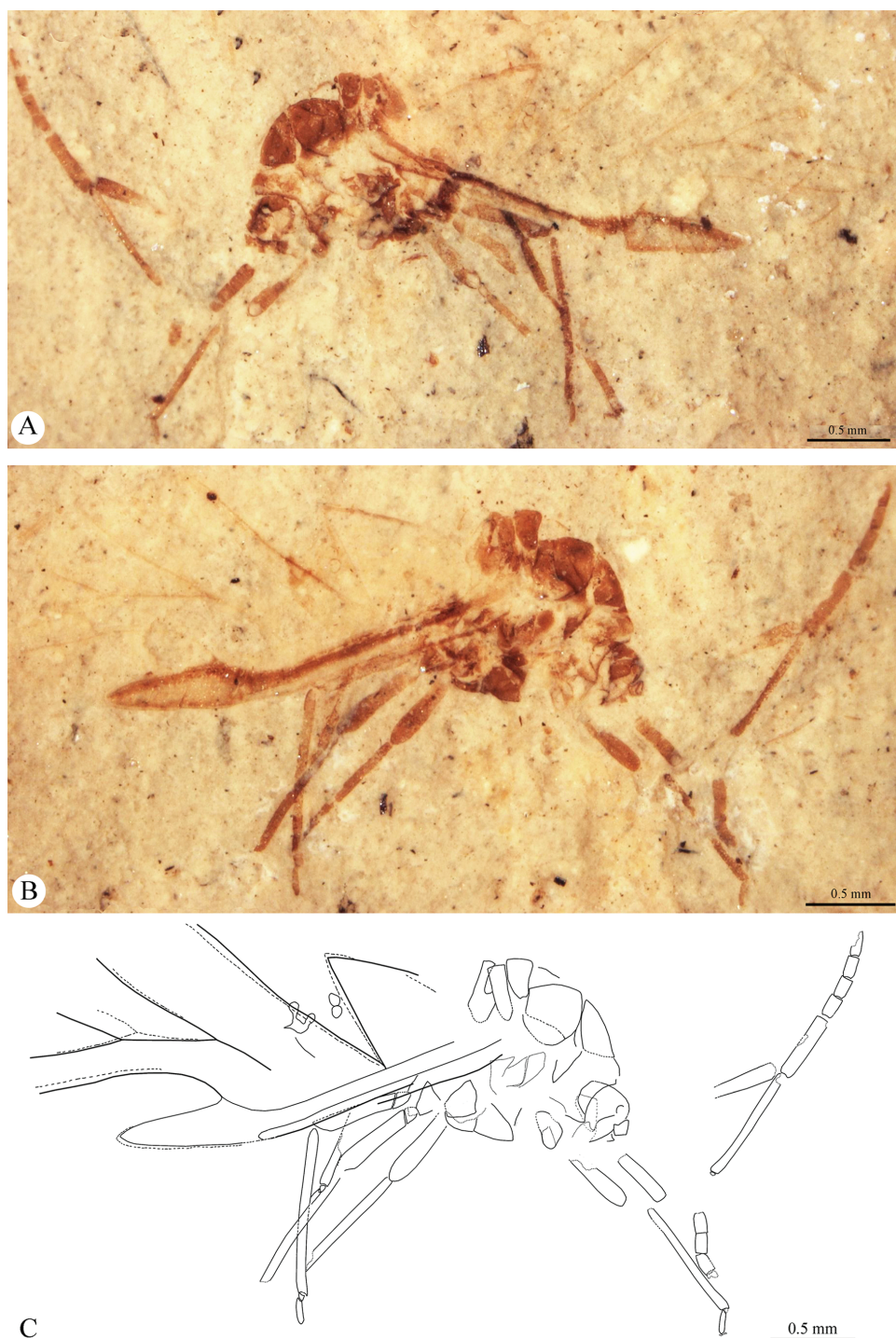


Figure 5. *Archeoviparosiphum baissense* (Shaposhnikov & Wegierek, 1989), comb. n.; PIN 4210/2623±, holotype. **A, B** body, lateral views **C** reconstruction of body.

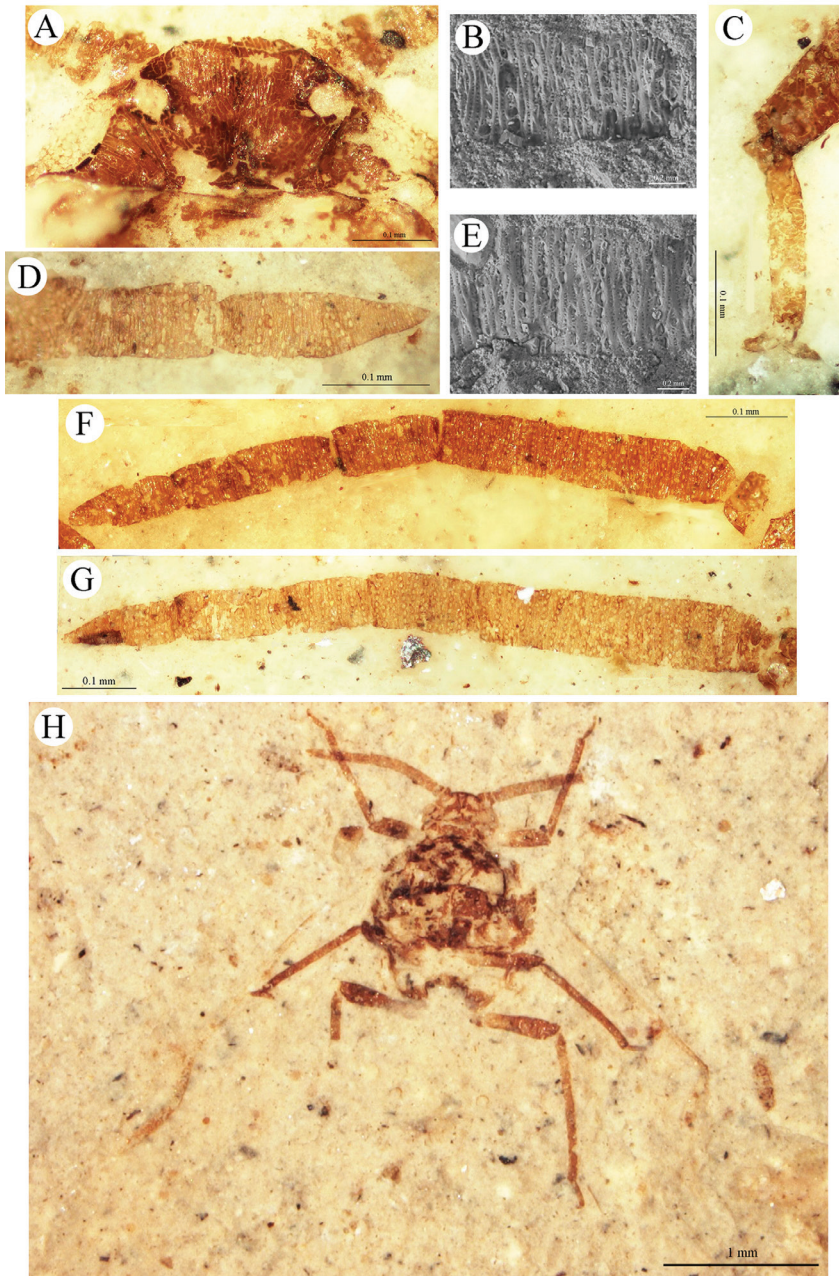


Figure 6. *Archeoviparosiphum baissense* (Shaposhnikov & Wegierek, 1989), comb. n. **A** PIN 3064/2213±, paratype, head, dorsal view **B** PIN 3064/2284, additional material, fragment of antennal segment V with secondary rhinaria, scanning electron micrograph **C** PIN 3064/2310(2312), paratype, hind tarsus **D** PIN 3064/2203, paratype, antennal segment VI and VII with secondary rhinaria **E** PIN 3064/2284, additional material, fragment of antennal segment III with secondary rhinaria, scanning electron micrograph **F** PIN 3064/2108(2273), paratype, right antenna **G** PIN 3064/2310(2312), paratype, left antenna **H** PIN 3064/2213±, paratype, body, ventral view.

Additional material. 1989/1072; 3064/2160; 3064/2173(4751); 3064/2225; 3064/2276; 3064/2278; 3064/2284; 3064/4825; 3064/4870; 3064/4990; 3064/5023; 3064/5113; 3064/5130a; 4210/2548; 4210/4120±; 4210/4365±; 4210/4629±; 4210/5553±; 4210/5588±; 4210/5590±; 4210/5618±; 4210/5630±; 4210/5654; 4210/5659; 4210/5661; 4210/5665; 4210/5669; 4210/5674; 4210/5675; 4210/6889±; 4210/6893±; 4210/6894±; 4210/6896±; 4210/6899±; 4210/6900±; 4210/6908; 4210/6911; 4210/6912a; 4210/6915; 4210/7577a±; 4210/7577b±; 4210/7580±; 4210/7584±

Emended diagnosis. Bases of cubital veins leaving the main vein at the same point.

Description. Body (1.9–2.7) thick (Figs 5A–C, 6H). Anterior margin of head (Fig. 6A) straight. Length of the head (0.19–0.25); width (0.35–0.40). Epicranial suture present, sometimes not clearly visible. Lateral sutures present. On head, additional narrow oblique slats running from front and lateral edges to the posterior part of the head. Distance between ocelli 0.18–0.20. Antennae (0.94–1.40) (Figs 6F, G) half of body length, and longer or equal to hind tibiae length. Segments I 0.05–0.06 and II 0.04–0.06 in length. Segment III (0.34–0.42) shorter than the cumulative length of subsequent segments; about 3–4 times longer than wide. Segment IV (0.11–0.14) as long as wide, equal to segment V and VI. Segment VII (0.15–0.18) slightly longer than the previous segment, about twice as long as wide, narrowed in the apical part. Secondary rhinaria arranged in dense, transverse rows (Figs 6B, D, E), on segment III in 24–30 rows; segments IV–VI in 7–10 rows; segment VII in 5–8 rows. 8–11 secondary rhinaria in one row on segment III. Rostrum relatively long, reaching to the hind coxae. Length of mesoscutellum 0.13–0.15; width 0.39–0.45. Length of mesothoracic sternite 0.41–0.46; width 0.68–0.72. Length of fore femur 0.34; fore tibia 0.61–0.71; segment I of fore tarsus 0.03; segment II 0.13–0.14. Length of middle femur 0.39–0.49; middle tibia 0.68–0.78; segment I of middle tarsus 0.03; segment II 0.15–0.17. Length of hind coxa 0.15–0.16; hind trochanter 0.10; hind femur 0.48–0.53; hind tibia 0.89–1.28; segment I of hind tarsus 0.04 (Fig. 6C); segment II 0.17–0.19. Hind tibiae about half the body length. Fore wing (3.10–3.60) longer than body length. Distance from base of wing to end of pterostigma 2.50–2.70. Vein CuA_1 about twice as long as CuA_2 . Vein M three branched, its base directed to base of pterostigma, not connected with main vein. M furcates to M_{1+2} and M_{3+4} behind Rs base. Common stem of vein M longer than M_{1+2} . Vein Rs slightly curved, leaving proximal part of the pterostigma and running far away from it. Pterostigma pointed, long and narrow; 4 times longer than wide. Hind wing (2.70) with two cubital veins. Apical part of abdomen slightly sclerotized. Diameter of siphunculus 0.07–0.08.

Discussion

The first species of the genus *Oviparosiphum*, *O. jakovlevi* was described in 1979 by Shaposhnikov and assigned to a new family Oviparosiphidae. The diagnostic features

were the following: antennae with annular secondary rhinaria, siphunculi in the form of truncated cones with a height less than the diameter of the wide aperture, and a large conical ovipositor, most likely composed of four valvae (Shaposhnikov 1979). New techniques made a detailed study possible, confirming the presence of these features and allowing to redescribe the type species of the genus *Oviparosiphum*. Additionally, analysis of the antennal morphology showed that the secondary rhinaria of *Oviparosiphum jakovlevi* are slightly ellipsoidal and occur in dense, transverse rows. The second species assigned to this genus was *O. baissense* from the Baissa deposit (Lower Cretaceous, Russia), described on the basis of a single imprint (Shaposhnikov and Wegierek 1989). The large number of specimens available for the present study permitted a very accurate redescription of the species. The presence of pore-shaped siphunculi has been clearly demonstrated, in contrast to the original description, which highlighted the short cone-shaped siphunculi. The characteristics that distinguish these two species of the genus *Oviparosiphum* from other genera in the family are similar length of both cubital veins and vein Rs leaving proximal part of the pterostigma. These features remain valid but more attention is paid to the abdomen structure. Only one other genus – *Khotonaphis* – has clearly truncate conical siphunculi, but its ovipositor is not as well developed as in *Oviparosiphum jakovlevi* (Shaposhnikov and Wegierek 1989). The species *Oviparosiphum latum*, described from the Early Cretaceous of China, is more problematic because vein Rs leaves the distal part of the pterostigma, and the fact that the exact structure of the secondary rhinaria is unknown (Hong and Wang 1990). However, the drawings suggest that the siphunculi are pore-shaped, which enables it to be reclassified as a member of the new genus.

In the original description of *Paroviparosiphum* syn. n. and *Mesoviparosiphum* syn. n. the authors indicated 5-segmented antennae, annular secondary rhinaria and pore-shaped siphunculi as being diagnostic features of both genera (Zhang et al. 1989). However, on the basis of drawings, it could be stated that the antennae are 7-segmented, typical of the Oviparosiphidae, and that the secondary rhinaria are most likely ellipsoidal. Nevertheless the siphunculi seem to be pore-shaped, which makes it possible to include these genera also in *Archeoviparosiphum*.

The composition of the new genus is thus as follows:

Archeoviparosiphum baissense (Shaposhnikov & Wegierek, 1989), comb. n.
Oviparosiphum baissensis Shaposhnikov & Wegierek, 1989: 49 (original combination)

Archeoviparosiphum camptotropum (Zhang, Zhang, Hou & Ma, 1989), comb. n.
Paroviparosiphum camptotropum Zhang, Zhang, Hou & Ma, 1989: 31 (original combination)
Oviparosiphum camptotropum (Zhang, Zhang, Hou & Ma, 1989) (synonym by Heie and Wegierek 2011: 49)

Archeoviparosiphum latum (Hong & Wang, 1990), comb. n.
Oviparosiphum latum Hong & Wang, 1990: 80 (original combination)

Archeoviparosiphum malacum (Zhang, Zhang, Hou & Ma, 1989), comb. n.
Mesoviparosiphum malacum Zhang, Zhang, Hou & Ma, 1989: 33 (original combination)
Oviparosiphum malacum (Zhang, Zhang, Hou & Ma, 1989) (synonym by Heie and Wegierek 2011: 49)

Archeoviparosiphum opimum (Zhang, Zhang, Hou & Ma, 1989), comb. n.
Paroviparosiphum opimum Zhang, Zhang, Hou & Ma, 1989 : 29 (original combination)
Oviparosiphum opimum (Zhang, Zhang, Hou & Ma, 1989) (synonym by Heie and Wegierek 2011: 49)

Archeoviparosiphum tuanwangense (Zhang, Zhang, Hou & Ma, 1989), comb. n.
Mesoviparosiphum tuanwangense Zhang, Zhang, Hou & Ma, 1989: 32 (original combination)
Oviparosiphum tuanwangense (Zhang, Zhang, Hou & Ma, 1989) (synonym by Heie and Wegierek 2011: 49)

Conclusion

Previously the genus *Oviparosiphum* consisted of seven species. It is now limited to a single species, *O. jakovlevi*, with clearly truncate conical siphunculi and a well-developed ovipositor. The other species have been transferred to a new genus *Archeoviparosiphum* gen. n.; all these species have pore-shaped siphunculi and a rudimentary ovipositor.

Acknowledgements

We wish to thank Dr. Dimitrij E. Shcherbakov and Dr. Roman Rakitov from the Palaeontological Institute, Russian Academy of Sciences, Moscow for allowing us to use the specimen and for their help with the SEM photographs. We also want to thank the reviewers for comments that greatly improved the manuscript. We are grateful to Marzena Zmarzły (Department of Zoology, University of Silesia) for the technical assistance, and Peter Senn for kindly checking the English language of the manuscript.

References

- Ansorge J (1996) Insekten aus dem Oberen Lias von Grimmen (Vorpommern, Norddeutschland). Neue Paläontologische Abhandlungen 2: 132.
 Heie OE, Wegierek P (2011) A list of fossil aphids (Hemiptera, Sternorrhyncha, Aphidomorpha). Monographs of the Upper Silesian Museum, 82 pp.
 Hong YC, Wang WL (1990) Fossil insects from the Laiyang basin, Shandong province. In: Regional Geological Surveying Team, Shandong Bureau of Geology and Mineral Resources

- (Eds) The stratigraphy and palaeontology of Laiyang Basin, Shandong province. Geological Publishing House, Beijing, 44–189. [in Chinese with English summary]
- Kania I, Wegierek P (2008) Palaeoaphididae (Hemiptera, Sternorrhyncha) from Lower Cretaceous Baissa deposits. Morphology and classification. Instytut Systematyki i Ewolucji Zwierząt Polskiej Akademii Nauk, Kraków, 133 pp.
- Ponomarenko AG (2013) Review of the locations of fossil insects in Mongolia. Palaeontology in Russia. Arthropod Lab, Paleontological Institute, Moscow. http://palaeontolog.ru/Collections/mong_loc.html [25 November 2013]
- Rasnitsyn AP (2002) Special Features of the Study of Fossil Insects. In: Rasnitsyn AP, Quicke DLJ (Eds) History Of Insects. Kluwer Academic Publishers, Dordrecht, 8–12. doi: 10.1007/0-306-47577-4
- Rasnitsyn AP, Jarzembowski EA, Ross AJ (1998) Wasps (Insecta: Vespida=Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and paleoenvironmental significance. *Cretaceous Research* 19(3–4): 329–391. doi: 10.1006/cres.1997.0114
- Rasnitsyn AP, Zherikhin VV (2002) Impression fossils. In: Rasnitsyn AP, Quicke DLJ (Eds) History Of Insects. Kluwer Academic Publishers, Dordrecht, 437–444. doi: 10.1007/0-306-47577-4_4
- Shaposhnikov GK (1979) Late Jurassic and Early Cretaceous aphids. *Paleontological Journal* 13: 449–461. [in Russian]
- Shaposhnikov GCh, Wegierek P (1989) New aphids of the late Mesozoic (Oviparosiphidae, Homoptera). *Paleontological Journal* 3: 42–50. [in Russian]
- Zhang JF, Zhang S, Hou F, Ma G (1989) Late Jurassic aphids (Homoptera, Insecta) from Shandong Province, China. *Geology of Shandong* 5: 28–46. [in Chinese with English summary]
- Zherikhin VV, Mostovski MB, Vrsansky P, Blagoderov VA, Lukashevich ED (1999) The unique Lower Cretaceous locality Baissa and other contemporaneous fossil insect sites in North and West Transbaikalia. *Proceedings of the First International Palaeontological Conference, Moscow, 1998*, 185–191.

Palearctic elements in the old world tropics: a taxonomic revision of the ant genus *Temnothorax* Mayr (Hymenoptera, Formicidae) for the Afrotropical biogeographical region

Matthew Prebus¹

¹ Department of Entomology & Nematology, University of California Davis, Davis, CA 95616

Corresponding author: Matthew Prebus (mmprebus@ucdavis.edu)

Academic editor: Brian Fisher | Received 11 December 2014 | Accepted 3 February 2015 | Published 20 February 2015

<http://zoobank.org/9323F207-90A7-465B-8486-3468E839BC32>

Citation: Prebus M (2015) Palearctic elements in the old world tropics: a taxonomic revision of the ant genus *Temnothorax* Mayr (Hymenoptera, Formicidae) for the Afrotropical biogeographical region. ZooKeys 483: 23–57. doi: 10.3897/zookeys.483.9111

Abstract

Four new Afrotropical species of the ant genus *Temnothorax* are described and illustrated, all from Kenya. Based upon high resemblance to taxa known from the North African and Iberian territories of the Mediterranean region, these new tropical elements are placed into known Palearctic species complexes. Specifically, *T. brevidentis* **sp. n.**, *T. mpala* **sp. n.** and *T. rufus* **sp. n.** are placed in the *laurae* species group, and *T. solidinodus* **sp. n.** is placed in the *angustulus* species group. Two already known *Temnothorax* species from the region, *T. cenatus* (Bolton, 1982) and *T. megalops* (Hamann & Klemm, 1967), are also placed into the *laurae* species group based on the high number of shared morphological characters. Diagnoses for the African representatives of *laurae* and *angustulus* species groups of the Afrotropical biogeographical region are provided. A key to workers of the six *Temnothorax* species known to occur in the Afrotropical biogeographical region is provided, as well as diagnoses of morphologically similar myrmecine genera.

Keywords

Afrotropical region, Formicoxenini, Kenya, Laikipia, Sudan, taxonomy, *Temnothorax*

Introduction

Temnothorax Mayr, 1861 is a genus of small, generally inconspicuous ants found in habitats ranging from deserts to tropical rainforests. Many of the species belonging to this genus are positively thigmotactic, nesting in preformed cavities such as the shells of rotten nuts, beetle-carved chambers in wood, between cracks in stone, and in the soil. Colonies are typically quite small, often with fewer than 100 workers per nest (Beckers et al. 1989). The diet and foraging habits of these ants are mostly unknown, but they are suspected to be trophic generalists; a few studies have recorded instances of granivory and consumption of elaiosomes (Espadaler 1997, Fokuhl et al. 2012).

With more than 350 named species (Bolton 2014), *Temnothorax* is a large genus with a predominantly Holarctic distribution. A few notable exceptions to this general distribution include a large radiation in Meso-America, including the islands of the Caribbean (Kempf 1959; Baroni-Urbani 1978), two undescribed species from mountainous northern Vietnam (Eguchi 2011) and two described species from sub-Saharan Africa (Bolton 1982). Below, four new species of *Temnothorax* are described from the latter region, all from within Kenya.

In the last revision of the genus *Leptothorax* of the Afrotropical biogeographic region, Bolton (1982) described three new species, bringing the number of described species to 11. In 2003 Bolton revived the genera *Temnothorax* and *Nesomyrmex* from synonymy with *Leptothorax*; nine of the Afrotropical species were transferred to *Nesomyrmex*, while the remaining two were transferred to *Temnothorax*. One of these species, *T. megalops*, has been noted by several authors to have close affinities to members of the *laurae* species group (Emery 1884, Tinaut 1995, Cagniant and Espadaler 1997), predominantly of northern Africa and southern Europe. Although a comprehensive revision of this group is beyond the scope of this paper, I propose that *T. mpala* sp. n. is also a member of this group, differing from most of the other members by the absence of a distinct metanotal groove. The species of *T. cenatus*, *T. brevidentis* and *T. rufus* also appear to be members of this group, especially when considering *T. crepuscularis* and *T. caesari* of the Iberian peninsula.

The paucity of *Temnothorax* species in the Afrotropics led Bolton (1982) to speculate that this may be a result of direct competition from members of the genus *Tetramorium*, which are extremely diverse in sub-Saharan Africa. The genera *Nesomyrmex* and *Tetramorium*, which are not particularly closely related to *Temnothorax* (Ward et al. 2014), are often confused with this genus due to convergence in general habitus. Table 1, updated from Bolton 1982, will aid in separating these genera from *Temnothorax*.

Abbreviations of depositories

The collection abbreviations follow Evenhuis (2009). The material upon which this study is based is located and/or was examined at the following institutions:

BMNH The Natural History Museum (British Museum, Natural History), London

Table 1. Diagnostic characters of three sympatric and morphologically similar myrmicine genera.

Character	<i>Temnothorax</i>	<i>Nesomyrmex</i>	<i>Tetramorium</i>
Sting with apical or apicodorsal lamelliform appendage	no	no	yes
Maxillary palp segments	5	5	3 or 4
Lateral clypeal lobes raised into a narrow ridge or shield-wall in front of antennal insertions	no	no	yes
Median clypeal lobe in the form of an apron that fits tightly over the base of the mandibular dorsum in profile	no	yes	no
Number of mandibular teeth	5	5	6 to 7

CASC California Academy of Sciences, San Francisco, USA

HLMD Hessisches Landmuseum, Darmstadt, Germany

LACM Los Angeles County Museum of Natural History, Los Angeles, USA

MHNG Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland

NHMW Naturhistorisches Museum Wien, Vienna, Austria

Material and methods

The material used in this study is relatively scarce. Much of it has come from collections made by Roy Snelling at the LACM. The type material of the new species and all imaged specimens can be uniquely identified with specimen-level codes affixed to each pin (e.g. CASENT0078328). Types of all new species described below will be deposited at the institutions mentioned above. Digital color images were created using a JVC KY-F75 digital camera and Syncroscope Auto-Montage software (version 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (version 3.8). All images presented are available online and can be seen on AntWeb (<http://www.antweb.org>).

The measurements and indices used in this study are based on Bolton (1982), Radchenko (2004), Hita Garcia and Fisher (2011), Schulz et al. (2007), Seifert (2006), and Bharti et al. (2011). The measurements were taken with a Leica MZ 12.5 equipped with an orthogonal pair of micrometers at a magnification of up to 115×. Measurements and indices are presented as minimum and maximum values with arithmetic means in parentheses. In addition, all measurements are expressed in mm to three decimal places. See Figure 1 for illustrations of the following measurements.

EL Eye length: maximum diameter of compound eye including all structurally visible ommatidia irrespective of the pigmentation status, measured in oblique lateral view.

FRS Distance of the frontal carinae immediately caudal of the posterior intersection points between frontal carinae and the lamellae dorsal of the torulus. If these dorsal lamellae do not laterally surpass the frontal carinae, the deepest point of scape corner pits may be taken as reference line. These pits take up the inner corner of scape base when the scape is fully switched caudad and produce a

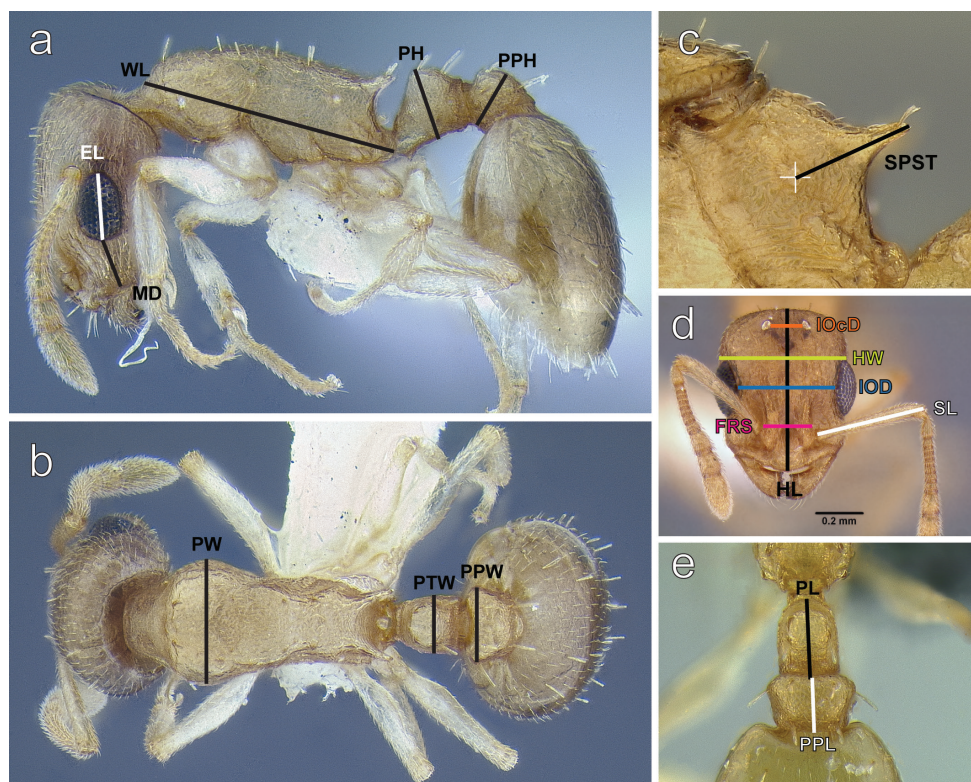


Figure 1. **a** *Temnothorax mpala* sp. n. worker (LACMENT323183) in lateral view illustrating measurements used: malar distance (MD), eye length (EL) Weber's length (WL), petiole height (PH), postpetiole height (PPH) **b** *T. mpala* sp. n. worker (LACMENT323183) in dorsal view: pronotal width (PW), petiole width (PTW), postpetiole width (PPW) **c** *Temnothorax mpala* sp. n. dealate gyne (LACMENT323184) in lateral view illustrating propodeal spine length (SPST) **d** *T. mpala* sp. n. dealate gyne (LACMENT323183) in full face view: interocellar distance (IOcD), head width (HW), interocular distance (IOD), frontal carina distance (FRS), scape length (SL) **e** *T. mpala* sp. n. worker (LACMENT323183) in dorsal view: petiole length (PL), postpetiole length (PPL).

dark triangular shadow in the lateral frontal lobes immediately posterior of the dorsal lamellae of scape joint capsule (Seifert 2006).

- HL Head length: maximum distance from the mid-point of the anterior clypeal margin to the mid-point of the posterior margin of head, measured in full-face view. Impressions on anterior clypeal margin and posterior head margin reduce head length.
- HW Head width: width of head directly behind the eyes, measured in full-face view.
- IOcD Inter-ocellar distance: minimum distance between the posterior-most pair of ocelli. Applies to queens and males.
- IOD Inter-ocular distance: minimum distance between the compound eyes, measured in full-face view.

MD	Malar distance: the minimum distance between the anterior margin of the compound eye and the base of the mandible
PH	Petiole height: The maximum height of the petiole, measured from the apex of the node to ventral edge of petiole, parallel to the anterior margin of the petiole (Bharti et al. 2012).
PL	Petiole length: the maximum length of the petiole is measured in dorsal view from the anterior notch close to the propodeum to the articulation with the postpetiole. Both points must be in focus (Schulz et al. 2007).
PPH	Postpetiole height: maximum height of the postpetiole measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node.
PPL	Postpetiole length: maximum length of postpetiole measured in dorsal view, excluding helcium.
PPW	Postpetiole width: maximum width of postpetiole measured in dorsal view.
PTW	Petiole width: maximum width of petiole measured in dorsal view.
PW	Pronotal width: maximum width of pronotum measured in dorsal view.
SL	Scape length: maximum scape length excluding basal condyle and neck.
SPST	Distance between the center of the propodeal stigma and spine tip. The stigma center refers to the midpoint defined by the outer cuticular ring but not to the center of stigma opening, which may be positioned eccentrically (Seifert 2006).
WL	Weber's length: diagonal length of mesosoma in lateral view from the postero-ventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck.

Indices

CI	Cephalic index: $HW / HL \times 100$
DPeI	Dorsal petiole index: $PTW / PTL \times 100$
DPpI	Dorsal postpetiole index: $PPW / PPL \times 100$
LPpI	Lateral postpetiole index: $PPL / PPH \times 100$
OI	Ocular index: $EL / HW \times 100$
PeNI	Petiolar node index: $PTW / PW \times 100$
PPI	Postpetiole index: $PPW / PTW \times 100$
PpNI	Postpetiolar node index: $PPW / PW \times 100$
PSLI	Propodeal spine index: $SPST / HL \times 100$
SI	Scape index: $SL / HL \times 100$

The varying degree of inclination of pubescence and pilosity are often of high diagnostic value throughout a broad spectrum of ant genera. In this context I use the terms “erect”, “suberect”, “subdecumbent”, “decumbent”, and “appressed” following Wilson (1955).

Species concept

Due to the severe paucity of specimens of this genus from tropical Africa, especially of entire nest collections, the species concept used in this article is loosely based on the biological species concept. The specimens described in this article, based upon their close geographical proximity and their distinct morphology in relation to each other, hypothetically represent reproductively isolated species.

Species-group affinities

Many of the *Temnothorax* species of sub-Saharan Africa bear close morphological resemblance to the ants of the *laurae* species group of North Africa and southern Europe as described by Cagniant and Espadaler 1997, primarily in having large eyes and, with the exception of *T. mpala* sp. n., bearing a metanotal groove. *T. cenatus*, *T. brevidentis* sp. n. and *T. rufus* sp. n. are morphologically similar to members of the *laurae* group from the Iberian peninsula in their coarsely striate sculpture and impressed metanotal groove. *T. mpala* sp. n. and *T. megalops* appear to be closely related to one another, differing mainly in the morphology of the head and mesosoma. However, none of the *laurae*-group species presented in this article display micropilosity between the facets of the compound eye, which is one of the distinguishing features of this species group on the Iberian peninsula and North Africa. *T. solidinodus* sp. n., on the other hand, bears a close resemblance to *T. angustulus* of the North African and Iberian regions. Differing primarily in the morphology of the petiolar node (dorsally angulate in *T. angustulus*, massive and blunt dorsally in *T. solidinodus* sp. n.), both species are apparently arboreal.

Diagnosis of the species groups of *Temnothorax* in the Afrotropical region

laurae group: Eyes large relative to the length of the head capsule: $OI > 30$. Head capsule elongate: $CI < 85$. Postpetiole more or less trapezoidal in dorsal view; widest anterior to the midlength of the segment. Antennal scape variable relative to head capsule length: $68 < SI < 97$.

angustulus group: Eyes small relative to the length of the head capsule: $OI < 30$. Head capsule nearly equal in maximum length and width: $CI > 85$. Postpetiole widest at the midlength of the segment in dorsal view. Antennal scape short relative to head capsule length: $SI > 70$.

Biogeographical notes

Due to close affinities to the species of the Mediterranean and southern Palearctic biogeographical region, the species presented in this article are most likely relict fauna

which may have become isolated in the sub-Saharan region following the African Humid Period (deMenocal et al. 2000) or a similar event, during which the Sahara desert was mostly vegetated. Alternatively, the ancestral species of the present fauna may have migrated from Northern Africa into sub-Saharan region via the Great Rift Valley. Subsequently, these species may have been prevented from radiating in the African tropics due to the ecologically similar, diverse and successful species of the genus *Tetramorium*, as hypothesized by Bolton (1982).

Synopsis of Afrotropical *Temnothorax* species

Temnothorax brevidentis Prebus, **sp. n.**

Temnothorax cenatus (Bolton, 1982)

Temnothorax megalops (Hamann & Klemm, 1967)

Temnothorax mpala Prebus, **sp. n.**

Temnothorax rufus Prebus, **sp. n.**

Temnothorax solidinodus Prebus, **sp. n.**

Key to the afrotropical *Temnothorax* based on workers

- 1 Compound eyes moderate in size: OI < 30. Head square CI > 8.....
..... ***T. solidinodus* sp. n.**
- Compound eyes large: OI > 30. Head elongate CI < 85 **2**
- 2 In full-face view antennal scapes short, distinctly failing to reach posterior margin of head (Fig. 2a); SI < 80. In dorsal view postpetiole trapezoidal, widest at the anterior 1/4 of the segment (Fig. 2c) **3**
- In full face view antennal scapes long, surpassing posterior margin of head by at least the length of the first funicular segment (Fig. 2b); SI > 80. In dorsal view, postpetiole widest at the anterior 1/3 of the segment (Fig. 2d) **4**
- 3 Metanotal groove present (Fig. 3a); posterior margin of head shallowly but distinctly impressed (Fig. 3c) ***T. megalops* (Hamman & Klemm)**
- Metanotal groove absent (Fig. 3b), barely visible as an indistinct break in the sculpture dorsally in some specimens; posterior margin of head flat (Fig. 3d) ...
..... ***T. mpala* sp. n.**
- 4 Propodeal spines short: PSLI < 23 (Fig. 4a) ***T. brevidentis* sp. n.**
- Propodeal spines moderately long and acute: PSLI > 23 (Fig. 4b) **4**
- 5 Antennal scapes long; surpassing the posterior margin of the head by the length of the first two funicular segments when fully retracted: SI 94–97 (Fig. 4c) ***T. rufus* sp. n.**
- Antennal scapes shorter; surpassing the posterior margin of the head by the length of the first funicular segment when fully retracted: SI 84 (Fig. 4d)
..... ***T. cenatus* (Bolton)**

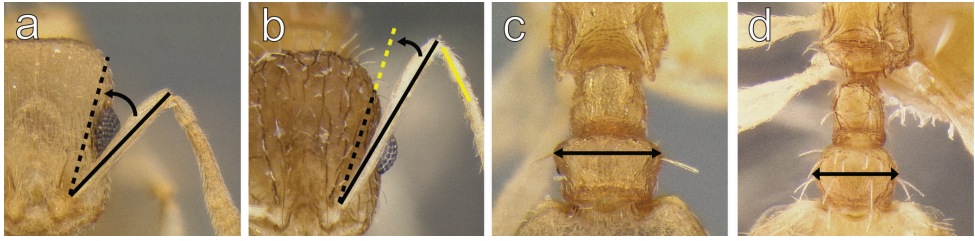


Figure 2. **a** *Temnothorax mpala* sp. n. (LACMENT323183) in full face view **b** *T. rufus* sp. n. (CASENT0712675) in full face view **c** *T. mpala* sp. n. (LACMENT323183) in dorsal view **d** *T. rufus* sp. n. (CASENT0712675) in dorsal view.

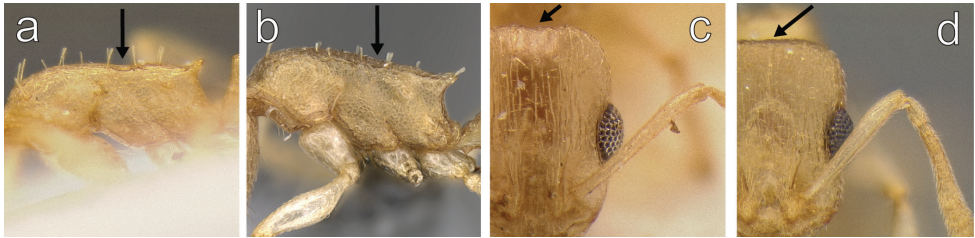


Figure 3. **a** *Temnothorax megalops* (CASENT0712601) in lateral view **b** *T. mpala* sp. n. (LACMENT323183) in lateral view **c** *T. megalops* (CASENT0712601) in full face view **d** *T. mpala* (LACMENT323183) in full face view.

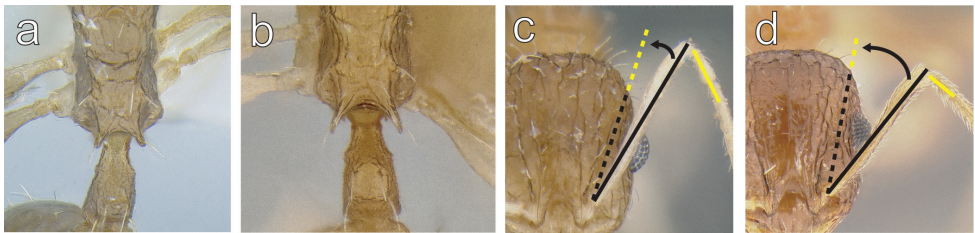


Figure 4. **a** *Temnothorax brevidentis* sp. n. (CASENT0712603) in dorsal view **b** *T. cenatus* (CASENT0900308) in dorsal view **c** *T. rufus* sp. n. (CASENT0712675) in full face view **d** *T. cenatus* (CASENT0900308) in full face view.

***Temnothorax brevidentis* Prebus, sp. n.**

<http://zoobank.org/F4C3293E-92D1-4AA9-9473-BFC285D2E0D8>

Figs 4a, 5

Type material. Holotype worker, KENYA, Laikipia District, Mpala Research Centre, 1650 m, 0.29°N, 36.90°E, Acacia woodland, stray in litter, collection code #99-056, 24.IX.1999 (*R.R. Snelling*) (BMNH: CASENT0712603).

Diagnosis. *Temnothorax brevidentis* is easily distinguishable from the other Afro-tropical species by the following character combination:

Antennal scapes surpassing the posterior margin of the head by the length of the first funicular segment; postpetiole widest at the anterior 1/3 of the segment; setae on the posterior margin of the first gastric tergite separated by about their own length; posterior margin of head rounded; metanotal groove shallowly impressed; compound eyes moderate in size; propodeal spines short.

Worker measurements (n = 1). EL 0.155; FRS 0.185; HL 0.633; HW 0.479; IOD 0.422; IOcD N/A; MD 0.172; PH 0.186; PL 0.243; PPH 0.196; PPL 0.196; PPW 0.245; PTW 0.144; PW 0.355; SL 0.573; SPST 0.136; WL 0.802.

Indices: CI 75.7; DPel 59.3; DPpI 125; LPeI 131; LPpI 100; OI 32.4; PeNI 40.6; PpNI 69; PPI 170; PSLI 21.5; SI 90.5.

Worker description. Head longer than wide (CI 76); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin convex and posterior corners of head broadly rounded. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae developed: extending posteriorly about one-half the length of the compound eye. Antennae 12-segmented, antennal scapes relatively long, extending past the posterior margin of the head by the length of the first funicular segment (SI 120). Eyes moderate in size (OI 32), 8 ommatidia in longest row.

Mesosoma relatively slender (WL 1.26 times HL); promesonotal suture absent. Metanotal groove narrowly and shallowly impressed. Propodeal spines short and acute (PSLI 21.5); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low (LPeI 131), and uniformly rounded, without distinct angles between anterior, dorsal, and posterior faces. In dorsal view petiole elongate (DPel 59). Postpetiole in profile globular (LPpI 100) and roughly the same height as the petiole. Postpetiole in dorsal view transversely elongate-oval, widest at 1/3 of the total postpetiole length from anterior margin (DPpI 125), widest at 1/3 of the total postpetiole length from the anterior margin, and 1.7 times wider than petiole (PPI 170).

Mandibular sculpture: longitudinally striate along entire length. Clypeus smooth and shiny, bearing 9 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum smooth and shining, with overlying well developed, widely spaced longitudinal rugae, which develop cross-linking rugae on the vertex. In profile, head coarsely reticulate; genae with irregular punctures anterior to the compound eye. Sculpture of mesosoma in dorsal view coarsely rugo-reticulate, with interspaces shining. Space between propodeal spines with a single well developed, arcuate transverse carina, which divides the propodeal dorsum from the declivity. Propodeal declivity irregularly shallowly punctate, bordered laterally by weak carinae which run from the ventral margins of the propodeal spines to the propodeal lobes. In

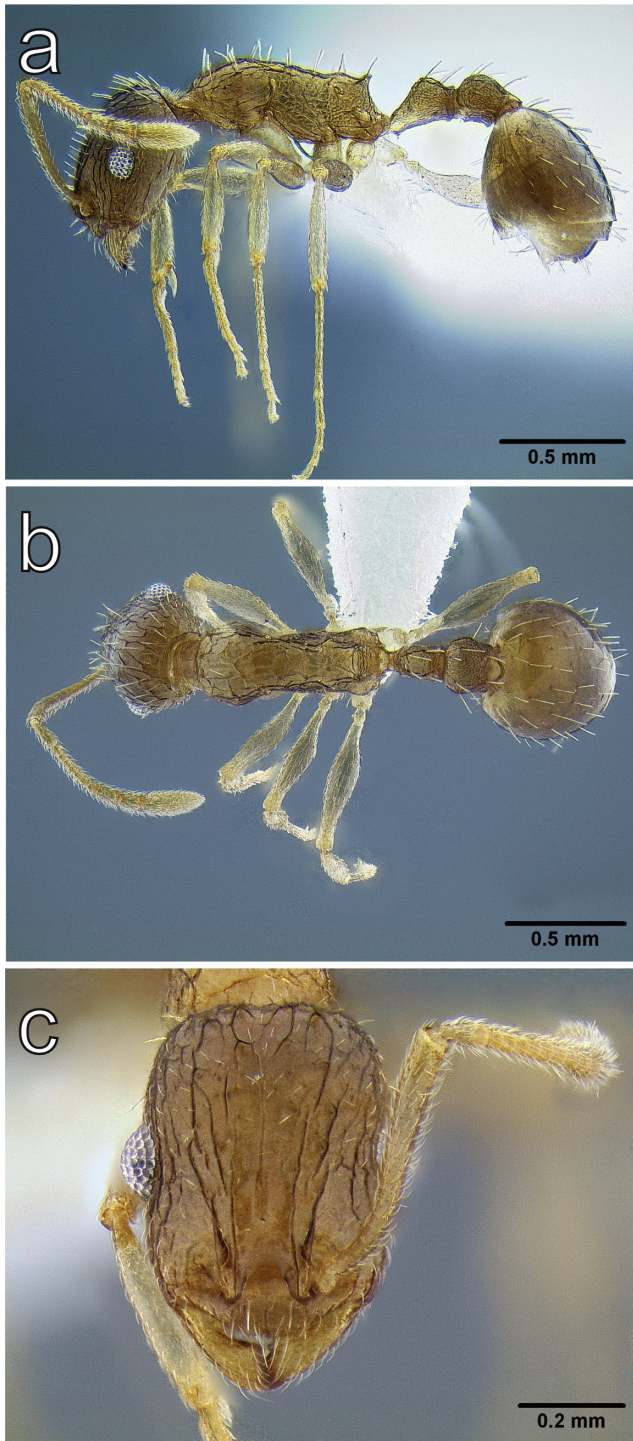


Figure 5. *Temnothorax brevidentis* sp. n., worker (CASENT0712603) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

profile, mesosoma predominantly finely rugo-reticulate; pronotum with coarse longitudinal rugae. Petiole and postpetiole finely punctate, with fine reticulation present on the dorsal surface of the petiolar node, and faint longitudinal rugae on the postpetiole. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Head and mandibles nearly uniformly covered in a fine, yellowish pubescence. Dorsal surface of the head, including clypeus, frons and posterior margin of the head equipped with long, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Antennal scapes with short, sharp-tipped suberect pilosity. Pronotal “neck” and pronotal humeri with short, fine yellowish pubescence. Propleurae and procoxae with long, flexous, sharp-tipped pilosity. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, moderately long, abundant and blunt-tipped setae, their bases spaced from each other by the length of the setae or less. Bases of the setae on the posterior margin of first gastral tergite separated by about the length of the setae arising from them. Ventral surface of the gaster with sparse pilosity like that of the propleuron. Ventral surface of the post petiole free of pilosity.

Queen. Unknown

Male. Unknown

Color. Worker: Overall light reddish brown, with head and gaster slightly darker.

Distribution and ecology. *T. brevidentis* is known only from acacia woodland leaf litter at the type locality, Mpala Research Centre.

Taxonomic notes. *T. brevidentis* appears to be very closely related to both *T. cenatus* and *T. rufus*, differing primarily from these in having short propodeal spines.

***Temnothorax cenatus* (Bolton, 1982)**

Figs 4b and d; 6

Leptothorax cenatus: Bolton 1982: 327.

Temnothorax cenatus: Bolton 2003: 271.

Type material. Holotype worker, KENYA, Lake Nakuru National Park, leaf litter, 6.XI.1974 (*V. Mahnert*) (MHNG) [examined]. Paratype, 1 worker from KENYA, Nakuru, Lake Elmenteita, 1800 m, 7.XI.1977 (*V. Mahnert & J.-L. Perret*) (BMNH: CASENT0900308) [examined].

Diagnosis. The following character combination distinguishes *T. cenatus* from the other Afrotropical genus members:

Antennal scapes surpassing the posterior margin of the head by the length of the first funicular segment; postpetiole widest at the anterior 1/3 of the segment; posterior margin of head rounded; metanotal groove shallowly impressed; compound eyes moderate in size; propodeal spines moderately long.

Worker measurements (n = 1). EL 0.174; FRS 0.222; HL 0.698; HW 0.558; IOD 0.468; IOcD N/A; MD 0.184; PH 0.219; PL 0.29; PPH 0.211; PPL 0.209; PPW 0.281; PTW 0.172; PW 0.398; SL 0.584; SPST 0.195; WL 0.922.

Indices: CI 79.9; DPeI 59.3; DPpI 134; LPeI 132; LPpI 99.1; OI 31.2; PeNI 43.2; PpNI 70.6; PPI 163; PSLI 27.9; SI 83.7.

Worker description. Head longer than wide (CI 79.9); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin broadly convex and posterior corners of head broadly rounded. Anterior clypeal margin convex, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae developed: extending posteriorly to about midlength of the compound eye, after which they become indistinguishable from the ground rugulae of the head. Antennae 12-segmented, antennal scapes relatively long, surpassing the posterior margin of the head by about the length of the first funicular segment (SI 105). Eyes moderate in size (OI 31.2), with 11 ommatidia in longest row.

Mesosoma relatively slender (WL 1.32 times HL); promesonotal suture not impressed, barely visible as a darkened line in dorsal view, but not indicated by a break in the sculpture. Metanotal groove shallowly impressed; visible as a broad, shallow concavity in lateral view. Propodeal spines acute and moderately long (PSLI 27.9); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, petiole with a low carina running transversely from the petiolar spiracle to the posterior margin; the anterior face of node forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low, with anterior and posterior faces broadly rounded (LPeI 132). In dorsal view petiole elongate (DPeI 59.3). Postpetiole in profile globular, nearly equal in height to petiolar node and relatively elongate (LPpI 99.1); in dorsal view transversely elongate-oval, widest at 1/3 of the total postpetiole length from anterior margin (DPpI 134) and 1.6 times wider than petiole (PPI 163).

Mandibular sculpture: distinctly longitudinally striate along entire length. Clypeus smooth and shiny, bearing 9 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum predominantly longitudinally rugose, with transverse rugae incompletely connecting longitudinal rugae. In profile, sides of head coarsely rugo-reticulate; coarse punctures visible between rugae, particularly postero-ventrally to the compound eye. Sculpture of mesosoma in dorsal view with predominately longitudinal rugae on pronotum and mesonotum, becoming increasingly reticulate on the propodeum. Space between propodeal spines with several fine transverse rugae, propodeal declivity finely punctate. In profile, mesosoma rugo-reticulate; longitudinal rugae stronger on pronotum, becoming increasingly reticulate on mesopleuron, and giving way to coarse punctation on metapleuron. Petiole and postpetiole finely punctate, with weak overlying rugosity. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Mandibles, lateral and ventral regions of the head nearly uniformly covered in a fine, yellowish pubescence. Dorsal surface of the head, including clypeus, frons and posterior margin of the head equipped with long, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Antennal scape pilosity abundant, sharp-tipped and decumbent.

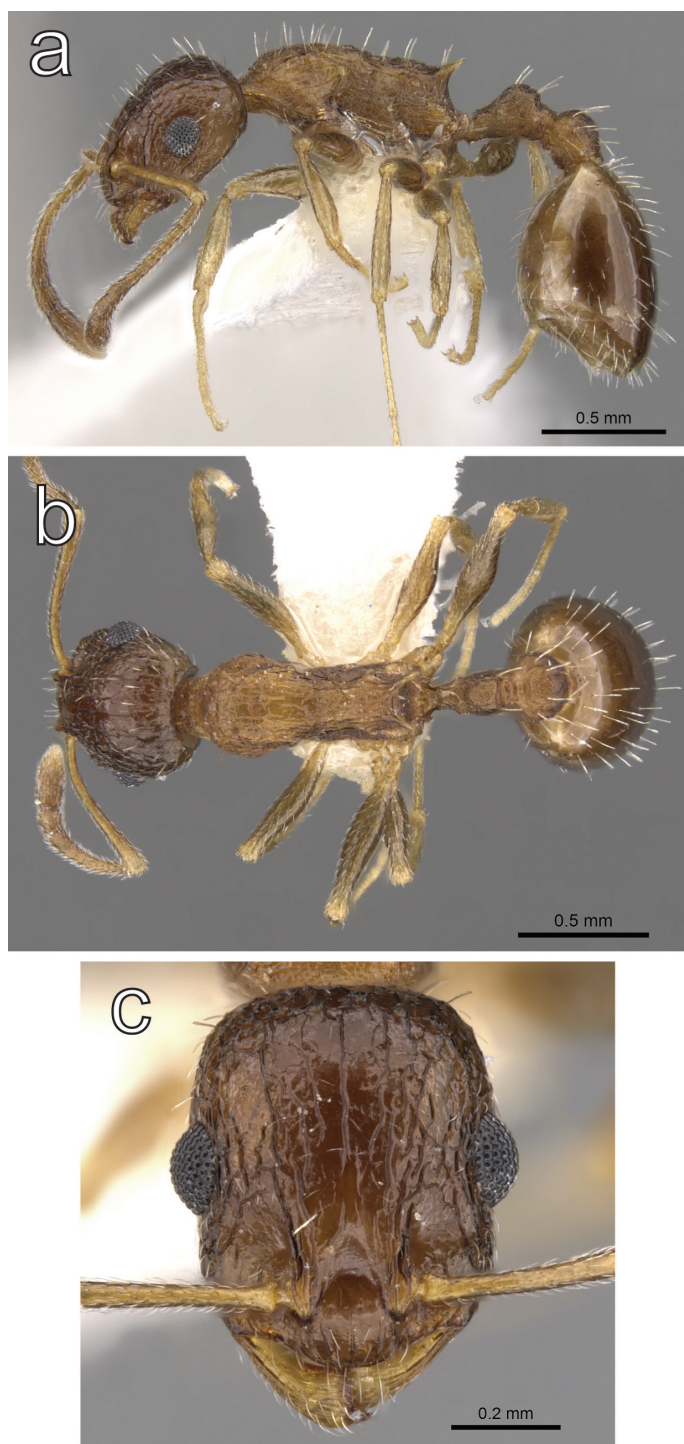


Figure 6. *Temnothorax cenatus* (Bolton, 1982) paratype worker (CASENT0900308) **a** body in lateral view **b** body in dorsal view **c** head in full face view. Photographer: Zach Lieberman.

Pronotal “neck” and pronotal humeri with short, fine yellowish pubescence. Propleurae and upper half of procoxae with long, flexous, sharp-tipped pilosity. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, moderately long, abundant and blunt-tipped setae, their bases spaced from each other by the length of the setae or less. Ventral surfaces of the post-petiole and gaster with sparse pilosity like that of the propleuron.

Queen. Unknown

Male. Unknown

Color. Worker : Overall light reddish brown, with head and gaster slightly darker.

Distribution and ecology. So far, *T. cenatus* is only known from few localities in Central Kenya, all of which are savannah.

The holotype was collected from leaf litter, suggesting that this may be a ground nesting species.

***Temnothorax megalops* (Hamann & Klemm, 1967)**

Figs 3a and c, 7, 8

Leptothorax megalops: Hamann and Klemm 1967: 417.

Temnothorax megalops (Hamann & Klemm): Bolton 2003: 271

Type material. Holotype worker, SUDAN, Wadi Halfa, feuchter Graben, 28.I.1962 (*H. Hamann & W. Klemm*) (NHMW: CASENT0712601) [examined]. Paratype, 1 dealate queen with same data as holotype (NHMW: CASENT0712600) [examined].

Diagnosis. The following character combination clearly separates *T. megalops* from the other Afrotropical *Temnothorax* species: Antennal scapes short, distinctly failing to reach the posterior margin of the head; compound eyes large; post petiole trapezoidal in dorsal view, widest at the anterior 1/5 of the segment; metanotal groove present; head subrectangular; posterior margin of head shallowly but distinctly impressed; setae on the posterior margin of the first gastric tergite separated by about their own length; pilosity of antennal scapes short and adpressed.

Worker measurements (n = 1). EL 0.174; FRS 0.175; HL 0.636; HW 0.465; IOD 0.376; IOcD N/A; MD 0.141; PH 0.183; PL 0.208; PPH 0.178; PPL 0.127; PPW 0.192; PTW 0.139; PW 0.327; SL 0.505; SPST 0.145; WL 0.728.

Indices: CI 73.1; DPel 66.8; DPpI 151; LPel 114; LPpI 71.3; OI 37.4; PeNI 42.5; PpNI 58.7; PPI 138; PSli 22.8; SI 79.4.

Worker description. Head subrectangular, longer than wide (CI 73.1); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin with a broad, shallow median impression; posterior corners of head broadly rounded. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae poorly developed: extending posteriorly about one-quarter the length of the compound eye. Antennae 12-segmented, antennal scapes

relatively short, failing to reach the posterior margin of the head (SI 109). Eyes large (OI 37.4); 11 ommatidia in the longest row.

Mesosoma relatively compact (WL 1.14 times HL); promesonotal suture absent. Metanotal groove shallowly but distinctly impressed; visible as a shallow concavity in lateral view, and as a narrowing of the dorsal surface of the mesosoma in dorsal view. Propodeal declivity steep. Propodeal spines blunt and relatively short (PSLI 22.8); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low and cuneate (LPeI 113), junction of anterior and posterior faces forming a 90° angle; without differentiated dorsal and posterior faces. In dorsal view petiole elongate (DPeI 66.8). Postpetiole in profile with proximal half of dorsal margin evenly rounded, and distal half forming an even declivity; nearly equal in height to petiolar node and laterally compressed (LPpI 71.3). In dorsal view postpetiole trapezoidal and wider than long (DPpI 151), widest at 1/4 of the total postpetiole length from anterior margin, and 1.4 times wider than petiole (PPI 138).

Mandibular sculpture: longitudinally irregularly striate along entire length. Clypeus smooth and shiny, bearing 5 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum smooth and shiny with weak, closely spaced longitudinal rugae, becoming sparse medially. In profile, gena anterior to the compound eye reticulate but otherwise similar to sculpture on dorsum. Sculpture of mesosoma in dorsal view punctate, becoming weak on pronotum, with overlying weak, longitudinal rugae which become stronger in the metanotal suture. Space between propodeal spines with a single fine, arcuate transverse carina, which divides the propodeal dorsum from the declivity. Propodeal declivity shallowly punctate and shining. In profile, mesosoma predominantly longitudinally rugose; humeri weakly reticulate, propodeum finely punctate. Petiole and postpetiole finely punctate, with a couple of weak longitudinal rugae visible on dorsum of postpetiole. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Mandibles and ventral region of the head with a short, fine yellowish pubescence. Posterior margin of clypeus with two pairs of short, stout setae flanking each side of the median lobe. Frontal carinae with one stout seta each, located at the level of the anterior margin of the compound eye. Posterior margin of the head equipped with several short, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Scapes with abundant, short, subdecumbant pilosity. Propleurae with several short, sharp-tipped setae. Pronotal "neck" and pronotal humeri, and procoxae free of pubescence. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, short, sparse and blunt-tipped bristle-like setae; their bases spaced from each other by more than the length of the setae which arise from them. Ventral surfaces of the post-petiole and gaster free of pilosity.

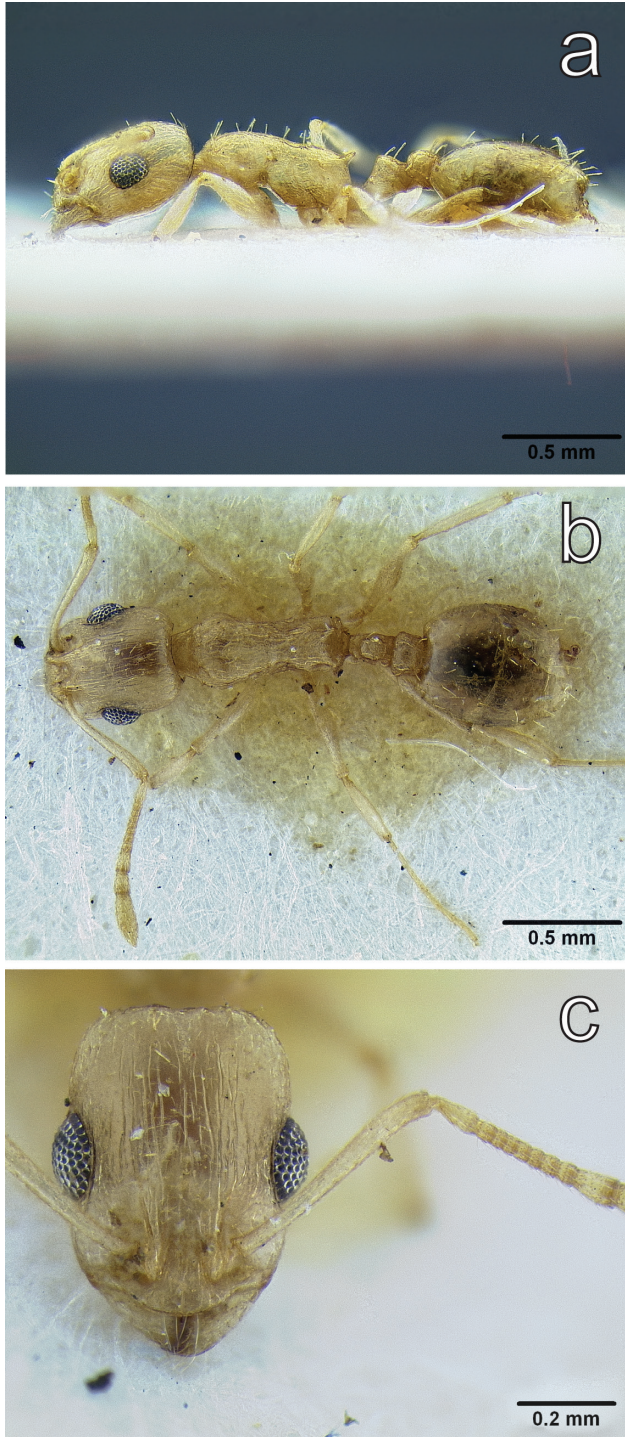


Figure 7. *Temnothorax megalops* (Hamman & Klemm, 1967) holotype worker (CASENT0712601) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

Queen measurements ($n = 1$). EL 0.205; FRS 0.204; HL 0.661; HW 0.506; IOD 0.407; IOcD 0.135; MD 0.147; PH 0.21; PL 0.233; PPH 0.177; PPL 0.153; PPW 0.241; PTW 0.177; PW 0.422; SL 0.536; SPST 0.188; WL 0.904.

Indices: CI 76.6; DPel 76; DPpI 158; LPeI 111; LPpI 86.4; OI 40.5; PeNI 41.9; PpNI 57.1; PPI 136; PSLI 28.4; SI 81.1.

Queen description. Head subrectangular, longer than wide (CI 76.6); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin with a broad, shallow median impression and posterior corners of head broadly rounded. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae poorly developed: extending posteriorly about one-half the length of the compound eye. Antennae 12-segmented, antennal scapes relatively short, failing to reach the posterior margin of the head (SI 106). Eyes large (OI 40.5); 13 ommatidia in the longest row. Three ocelli present.

Body more massive than the worker; mesosoma somewhat elongate (WL 1.37 times HL). Scutum and scutellum forming an even, flat surface in profile, broken only by the suture between the two tergites. Propodeal declivity steep. Propodeal spines blunt and slightly longer than in the worker (PSLI 28.4); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low and cuneate (LPeI 111), junction of anterior and posterior faces forming a 90° angle; without differentiated dorsal and posterior faces. In dorsal view petiole elongate (DPel 76). Postpetiole in profile with proximal half of dorsal margin evenly rounded, and distal half forming an even declivity; nearly equal in height to petiolar node and laterally compressed (LPpI 86.4). In dorsal view postpetiole trapezoidal and wider than long (DPpI 158); widest in the anterior 1/4, and 1.4 times wider than petiole (PPI 136).

Mandibular sculpture: longitudinally irregularly striate along entire length. Clypeus smooth and shiny, bearing 5 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum with closely spaced longitudinal rugae, extending the entire length of the head, but becoming weak between the compound eyes and ocelli. In profile, gena anterior to the compound eye strongly reticulate. Scutum and scutellum with longitudinal rugae; propodeum reticulate. Space between propodeal spines with a single strong, arcuate transverse carina, which divides the propodeal dorsum from the declivity. Propodeal declivity with longitudinal rugae. In profile, mesosoma predominantly longitudinally rugose; anterior of pronotum reticulate; sculpture weakened on mesopleuron. Petiole and postpetiole finely punctate, with longitudinal rugae on dorsum of postpetiole. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Mandibles and ventral region of the head with a short, fine yellowish pubescence. Posterior margin of clypeus with two pairs of short, stout setae flanking each side of the median lobe. Frontal carinae with one stout seta each, located at the level of the



Figure 8. *Temnothorax megalops* (Hamman & Klemm, 1967) allotype dealate gyne (CASENT0712600)
a body in lateral view **b** body in dorsal view **c** head in full face view.

anterior margin of the compound eye. Dorsal surface of head equipped with several short, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Scapes with abundant, short, subdecumbant pilosity. Propleurae with several short, sharp-tipped setae. Pronotal “neck” and pronotal humeri with short, stout and sparse setae. Procoxae with short, thin and sparse setae. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, sparse and blunt-tipped bristle-like setae which is longer than in the worker. Ventral surfaces of the post-petiole free of pilosity; ventral surface of gaster with short, fine, yellowish pilosity.

Male. Unknown

Color. Worker: Yellow overall with gaster slightly infuscated at the posterior margin of the first tergite.

Queen: Same as worker.

Distribution and ecology. Known only from the type material, which was collected from Wadi Halfa, Sudan.

***Temnothorax mpala* Prebus, sp. n.**

<http://zoobank.org/1C409951-D8D2-4FD6-B0BD-D4577BD54284>

Figs 1, 2a and c, 3b and d, 9, 10, 11

Type material. Holotype worker: 1 worker: KENYA, Laikipia District, Mpala Research Centre, 0.28°N, 36.87°E, 1700m, 18.III.2001 “Black Cotton” ex. pitfall trap in No. enclosure (*D. Misurelli*) (BMNH: LACMENT323183). Paratypes: 1 dealate queen: same data as previous (CASENT0733785). 1 worker, 1 dealate queen: same data as previous (NHMW: LACMENT323184). 1 male, 1 dealate queen: same data as previous (BMNH: LACMENT323185). 2 workers, 1 dealate queen: same data as previous (HLMD: LACMENT323186). KENYA, Laikipia District, Mpala Research Centre, 1650 m, 0.29°N, 36.90°E, Acacia woodland, ex pitfall trap near centre, collection code #01-225, 12.IV.2001 (*R.R. Snelling*) (BMNH: CASENT0280870). 1 worker, 1 dealate queen: same data as previous (LACM: CASENT0712602).

Diagnosis. *Temnothorax mpala* is easily distinguishable from the other Afrotropical species by the following character combination:

Antennal scapes short, distinctly failing to reach the posterior margin of the head; compound eyes large; post petiole trapezoidal in dorsal view, widest at the anterior 1/5 of the segment; metanotal groove absent; head subrectangular; posterior margin of head flat; setae on the posterior margin of the first gastric tergite separated by about their own length; pilosity on antennal scape short and adpressed.

Worker measurements (n = 6). EL 0.168–0.193 (0.185); FRS 0.175–0.19 (0.182); HL 0.598–0.67 (0.631); HW 0.445–0.488 (0.465); IOD 0.343–0.372 (0.355); IOcD N/A; MD 0.134–0.157 (0.142); PH 0.195–0.22 (0.205); PL 0.2–0.233 (0.218); PPH 0.172–0.185 (0.179); PPL 0.125–0.154 (0.142); PPW 0.216–0.239 (0.227); PTW 0.156–0.174 (0.162); PW 0.34–0.373 (0.354); SL 0.43–0.467 (0.443); SPST 0.161–0.183 (0.166); WL 0.705–0.772 (0.733).

Indices: CI 72.8–75.9 (73.6); DPeI 71.1–83 (74.5); DPpI 150.7–178.4 (160.7); LPeI 95–112 (107); LPpI 71.4–83.7 (79.2); OI 37–41.6 (39.8); PeNI 45–46.8 (45.9); PpNI 62.2–65.8 (64.1); PPI 134.9–145.1 (139.7); PSLI 25.4–27.3 (26.3); SI 68.3–72.6 (70.2).

Worker description. Head subrectangular, longer than wide (CI 72.8–75.9); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin flat and posterior corners of head broadly rounded. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae poorly developed: extending posteriorly about one-quarter the length of the compound eye. Antennae 12-segmented; antennal scapes short, failing to reach the posterior margin of the head (SI 91.3–98.9). Eyes large (OI 37.0–41.6). with 11 ommatidia in longest row.

Mesosoma compact (WL 1.17 times HL); promesonotal suture absent. Metanotal groove not impressed, but marked by a faint narrowing of the dorsal surface of the mesosoma in dorsal view. Propodeal spines acute and relatively short (PSLI 25.4–27.3); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node forming a very shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile low (LPeI 95.0–112), with dorsal and posterior faces joined by a rounded 120° angle. Subpetiolar process is in the form of a small tooth in the anterior 1/4 of the petiole. In dorsal view petiole somewhat elongate (DPeI 71.1–83.0). Postpetiole in profile with proximal half of dorsal margin evenly rounded, and distal half forming an even declivity; slightly shorter than petiolar node and laterally compressed (LPpI 71.4–83.7). In dorsal view postpetiole trapezoidal and wider than long (DPpI 151–153), widest in the anterior 1/4, and 1.4–1.5 times wider than petiole (PPI 135–145).

Mandibular sculpture: longitudinally striate along entire length. Clypeus smooth and shiny, bearing 9 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum reticulate, with transverse rugae becoming weaker posterior to the level of the compound eyes. In profile, head irregularly reticulate-punctate. Sculpture of mesosoma in dorsal view punctate, with overlying weak reticulation on pronotum. Space between propodeal spines with a single extremely fine, arcuate transverse carina, which divides the propodeal dorsum from the declivity. Propodeal declivity uniformly punctate, bordered laterally by carinae which run from the ventral margins of the propodeal spines to the propodeal lobes. In profile, mesosoma predominantly irregularly punctate; humeri weakly reticulate. Petiole and postpetiole finely punctate. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Head, including mandibles, with a short, sparse, adpressed fine yellowish pubescence. Mandibles with longer setae along the distal margins. Posterior margin of clypeus with one pair of short, stout setae directly below the antennal insertions. Frontal

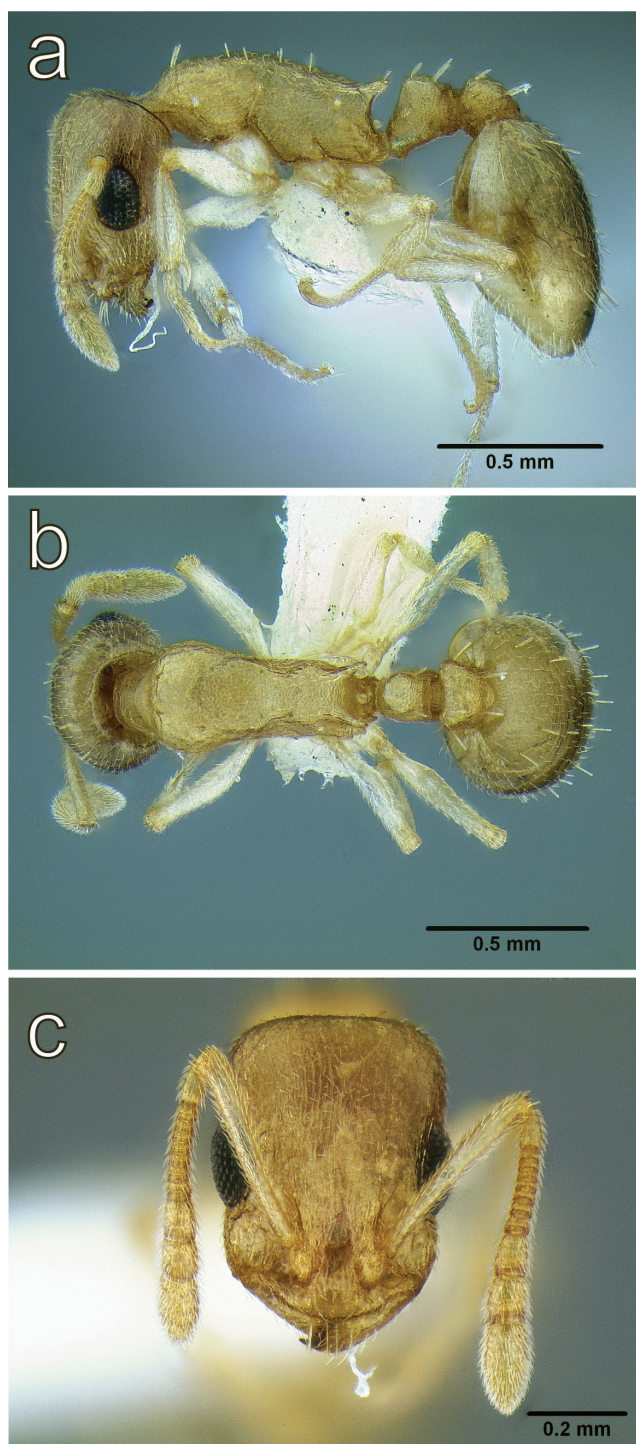


Figure 9. *Temnothorax mpala* sp. n., worker (LACMENT323183) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

carinae with three pairs of stout setae, located at the level of the antennal insertions, anterior margin of the compound eye, and midway up the compound eye. Region of the head posterior to the level of the compound eyes equipped with three pairs of short, blunt-tipped setae: one located medially, posterior to the level of the compound eyes and two pairs on the posterior margin of the head. Anterior clypeal margin with two pairs of long setae flanking the median carina. Scapes with abundant, short sub-decumbant pilosity. Pronotal “neck” with pubescence similar to that which is found on the head. Propleurae with several short, sharp-tipped setae. Procoxae with short, adpressed and abundant pilosity. Pronotal humeri free of pubescence. Dorsal surfaces of mesosoma and waist segments with uniformly erect, short, sparse and spatulate setae; their bases spaced from each other by more than the length of the setae which arise from them. All surfaces of gaster covered in sparse, evenly spaced short pilosity. Dorsal surface of first gastral tergite largely free of setae longer than the ground pilosity, save for several irregularly spaced stout setae. Anterior margins of all gastral tergites with evenly spaced short, stout setae. Ventral surfaces of the post-petiole with several short, fine setae. Ventral surface of gaster with abundant long fine pilosity.

Queen measurements (n = 4). EL 0.241–0.248 (0.245); FRS 0.212–0.218 (0.214); HL 0.68–0.71 (0.699); HW 0.534–0.551 (0.543); IOD 0.411–0.427 (0.421); IOcD 0.139–0.148 (0.142); MD 0.131–0.143 (0.139); PH 0.232–0.259 (0.246); PL 0.242–0.29 (0.265); PPH 0.224–0.232 (0.228); PPL 0.162–0.177 (0.169); PPW 0.277–0.295 (0.283); PTW 0.192–0.207 (0.201); PW 0.484–0.501 (0.491); SL 0.459–0.489 (0.481); SPST 0.214–0.221 (0.217); WL 1.029–1.07 (1.054).

Indices: CI 76.8–78.5 (77.7); DPel 71.4–83.1 (76.2); DPpI 163.9–172.8 (167.7); LPel 98–116 (108); LPpI 71.1–76.3 (74); OI 45–45.4 (45.1); PeNI 39.7–41.8 (41); PpNI 57.1–58.9 (57.7); PPI 136.6–144.3 (140.8); PSLI 30.5–31.5 (31.1); SI 67.5–69.4 (68.8).

Queen description. Head subrectangular, longer than wide (CI 76.8–78.5); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin flat; posterior corners of head more broadly rounded than in the worker. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae developed: extending posteriorly to about one-half the length of the compound eye. Antennae 12-segmented; antennal scapes short, failing to reach the posterior margin of the head (SI 86.0–89.9). Eyes large (OI 45.0–45.5). with 14–16 ommatidia in longest row. Three ocelli present.

Mesosoma more massive and elongate than in the worker (WL 1.51 times HL). Scutum and scutellum forming an even, flat surface in profile, broken only by the suture between the two tergites. Propodeal declivity steep. Propodeal spines acute and slightly longer than in the worker (PSLI 30.5–31.5); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node not forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low and truncate (LPel 98.0–116), junction of anterior and dorsal faces forming a rounded 120° angle; dorsal and posterior faces differen-

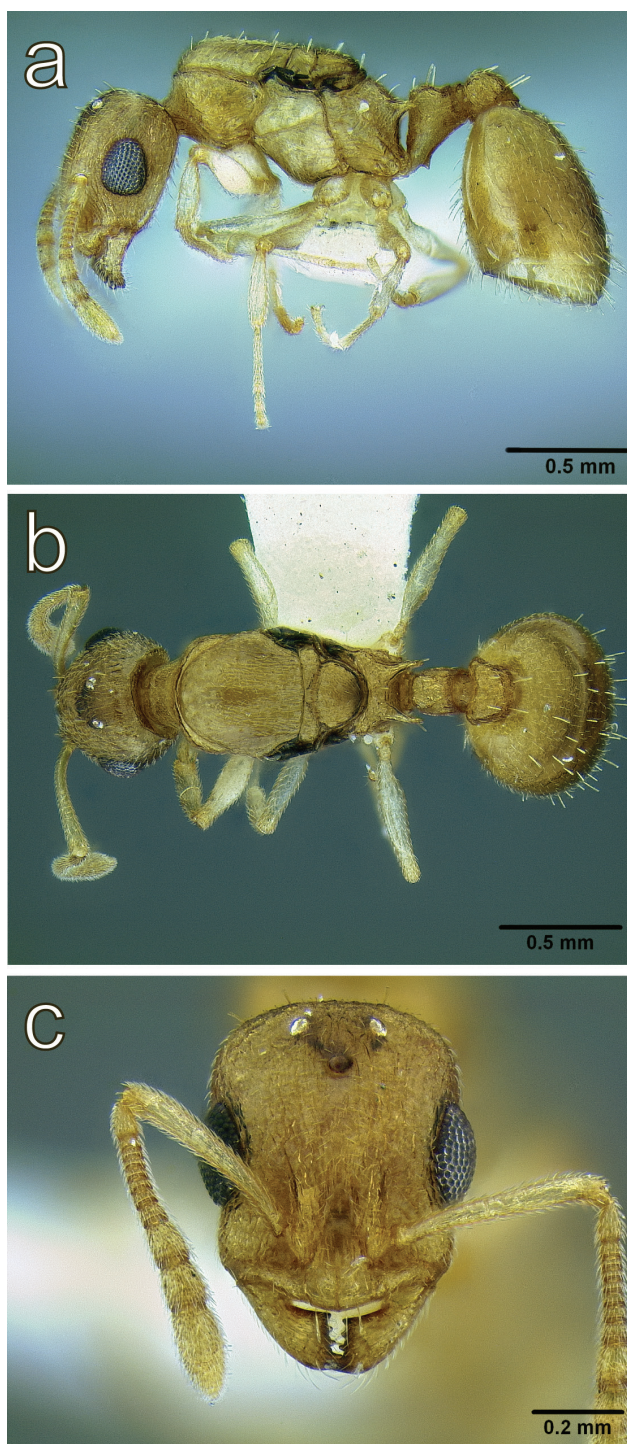


Figure 10. *Temnothorax mpala* sp. n., dealate gyne (LACMENT323183) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

tiated by a rounded 135° angle. Subpetiolar process is in the form of a small tooth at the anterior $1/4$ of the petiole. In dorsal view petiole elongate (DPeI 71.4–83.1). Postpetiole in profile with proximal half of dorsal margin evenly rounded, and distal half forming an even declivity; slightly shorter than petiolar node and laterally compressed (LPpI 71.1–76.3). In dorsal view postpetiole trapezoidal and wider than long (DPpI 164–173); widest in the anterior $1/4$, and 1.4 times wider than petiole (PPI137–144).

Mandibular sculpture: longitudinally irregularly striate along entire length. Clypeus smooth and shiny, bearing 5 longitudinal rugae and a few irregular rugae on posteriorly; median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum with closely spaced longitudinal rugae, extending the entire length of the head. In profile, gena anterior to the compound eye strongly reticulate. Scutum and scutellum with light longitudinal rugae and shallow foveae, becoming smooth and polished on the anterior of the scutum in some specimens; propodeum reticulate. Space between propodeal spines with a single arcuate transverse carina, which divides the propodeal dorsum from the declivity. Propodeal declivity weakly reticulate. In profile, mesosoma predominantly longitudinally rugose; anterior of pronotum reticulate; sculpture weakening slightly on mesopleuron. Petiole and postpetiole finely punctate; dorsum of postpetiole reticulate. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Head, including mandibles, with a short, sparse, adpressed fine yellowish pubescence. Mandibles with longer setae along the distal margins. Posterior margin of clypeus with one pair of short, stout setae directly below the antennal insertions. Frontal carinae with three pairs of stout setae, located at the level of the antennal insertions, anterior margin of the compound eye, and midway up the compound eye. Posterior of head equipped with three pairs of short, blunt-tipped setae; one flanking the anterior ocellus, and two pairs on posterior margin of the head. Anterior clypeal margin with two pairs of long setae flanking the median carina. Scapes with abundant, short, subdecumbant pilosity. Pronotal “neck” with pubescence similar to that which is found on the head. Propleurae with several short, fine setae. Coxae with short, thin and sparse setae. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, sparse and blunt-tipped bristle-like setae. Dorsum of mesosoma with fine, short, sparse yellowish setae. Ventral surface of the petiole free of pilosity, but post-petiole has a pair of hairs latero-ventrally. All surfaces of gaster with short, fine, yellowish pilosity which becomes longer ventrally.

Male measurements (n = 1). EL 0.222; FRS 0.123; HL 0.498; HW 0.419; IOD 0.271; IOcD 0.131; MD 0.044; PH 0.151; PL 0.22; PPH 0.151; PPL 0.142; PPW 0.196; PTW 0.14; PW 0.487; SL 0.262; SPST N/A; WL 0.957.

Indices: CI 84.1; DPeI 63.6; DPpI 138; LPeI 146; LPpI 94; OI 53; PeNI 28.7; PpNI 40.2; PPI 140; PSLI N/A; SI 52.6.

Male description. Head globular, small and somewhat longer than wide (CI 84.1); head sides rounding broadly into the posterior of the head. Anterior clypeal margin convex and entire, with the median clypeal lobe projecting strongly beyond the lateral clypeal lobes. Frontal carinae developed: extending posteriorly to the posterior margin

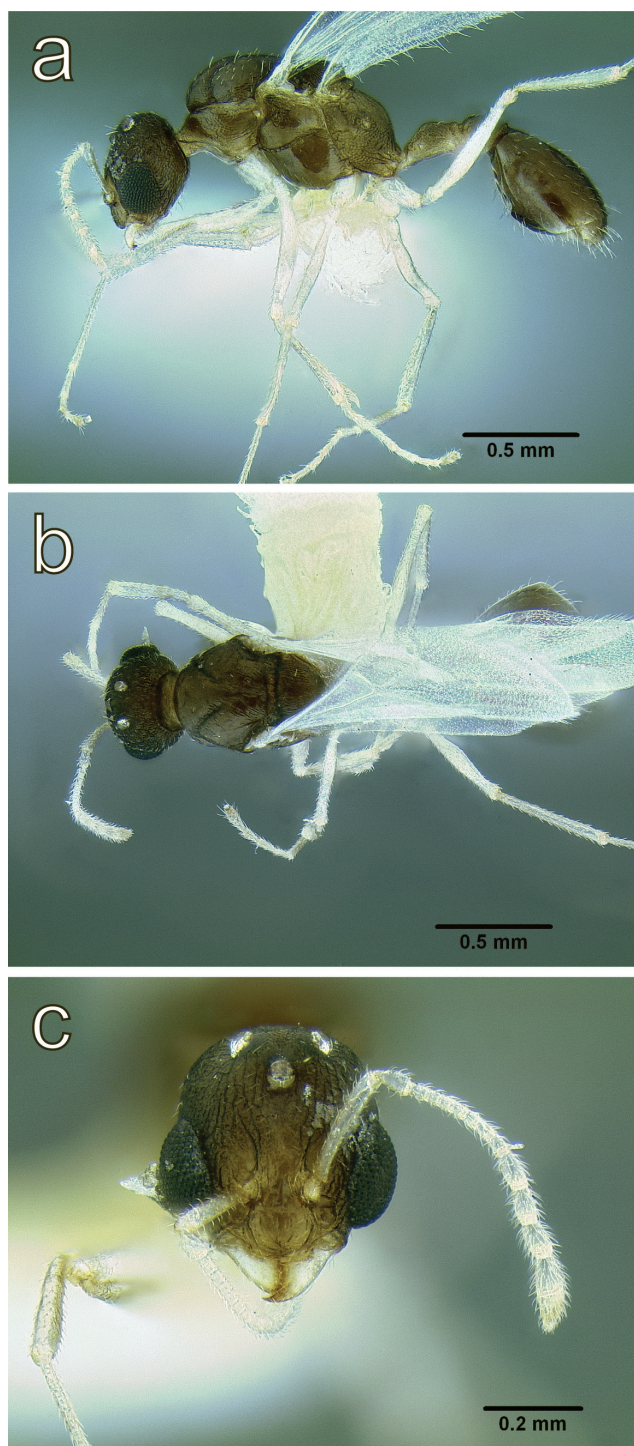


Figure 11. *Temnothorax mpala* sp. n., male (LACMENT323186) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

of the compound eye. Antennae 13-segmented, with a four-segmented club; antennal scapes very short, failing to reach the posterior margin of the head (SI 62.5). Eyes very large (OI 53) and close to the mandibular insertions (MD 0.044). 20 ommatidia in longest row. Three ocelli present.

Mesosoma more massive and elongate than in the worker (WL 1.92 times HL). Scutum and scutellum forming an even, flat surface in profile, broken only by the suture between the two tergites. Dorsal surface of propodeum rounding evenly into the propodeal declivity. Propodeal spines absent.

Petiole without a differentiated peduncle. In profile, petiolar node indistinct, forming a low mass (LPeI 146). Subpetiolar process reduced to a small bump in the anterior 1/4 of the petiole in profile. In dorsal view petiole elongate (DPeI 63.6). Postpetiole in profile with proximal half of dorsal margin evenly rounded, and distal half forming an even declivity; slightly shorter than petiolar node (LPpI 94). In dorsal view postpetiole weakly trapezoidal and slightly wider than long (DPpI 138); slightly wider in the anterior half, and 1.4 times wider than petiole (PPI 140).

Mandibular sculpture: smooth and shiny along their entire length. Clypeus smooth and shiny, bearing several irregular rugae. Cephalic dorsum with closely spaced longitudinal rugae with slightly weaker reticulations and punctuations between them. Scutum and scutellum with light longitudinal rugae, becoming smooth and polished on the anterior half of the scutum; propodeum weakly reticulate over a punctate ground sculpture. Propodeal declivity weakly punctate. In profile, mesosoma predominantly smooth and shiny; anterior of pronotum, dorsal margin of the anepisternum and propodeum weakly punctate. Petiole and postpetiole finely punctate; dorsum of postpetiole smooth and weakly punctate. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Head, including mandibles, with a short, sparse, adpressed fine yellowish pubescence. Mandibles with longer setae along the distal margins. Posterior margin of clypeus with one pair of short, stout setae directly below the antennal insertions. One pair of short, blunt-tipped setae flank the anterior ocellus. Scapes with abundant, short, subdecumbant pilosity. Pronotal “neck” with pubescence similar to that which is found on the head. Propleurae with several short, fine setae. Coxae with short, thin and sparse setae. Dorsal surfaces of mesosoma and waist segments with uniformly erect, sparse and blunt-tipped bristle-like setae. Dorsum of mesosoma with fine, short, and very sparse setae. Ventral surface of the petiole free of pilosity, but post-petiole has a pair of hairs latero-ventrally. All surfaces of gaster with fine, yellowish, sparse pilosity which becomes longer ventrally.

Color. Worker : Overall light brownish-yellow, with slightly darker head and gaster and lighter legs (including coxae).

Queen : Same as worker, but with dorsum of mesosoma same color as head and mesosoma.

Male : Overall dark reddish brown, with ventral surfaces of waist segments slightly lighter. Extremities, including antennae, mouthparts, legs and coxae cream-colored.

Distribution and ecology. *Temnothorax mpala* is only known from the leaf litter of acacia woodland at the type locality, Mpala Research Centre. Curiously, workers, dealate gynes as well as one male were recovered from pitfall traps, suggesting that these collection events captured a nest migration.

Taxonomic notes. The word “mpala” comes from a Bantu name for a type of antelope that was kept by chiefs of the Bunganda kingdom. *T. mpala* is not expected to be particularly swift in its movements; the only known specimens were collected at the above mentioned Mpala Research Centre in Laikipia, Kenya.

***Temnothorax rufus* Prebus, sp. n.**

<http://zoobank.org/F2293A69-0C37-4A51-9095-BAAEFBD1B0D3>

Figs 2b and d, 4c, 12

Type material. Holotype worker, KENYA, Kora National Park, “Salvadora pitfall”, collection code no. 18, 1983 N.M. Collins & M. Ritchie (BMNH: CASENT0712675). Paratype, 1 worker with same data as holotype (HLMD: CASENT0733784).

Diagnosis. *Temnothorax rufus* is easily distinguishable from the other Afrotropical species by the following character combination:

Antennal scapes surpassing the posterior margin of the head by the length of the first two funicular segments; postpetiole widest at the anterior 1/3 of the segment; posterior margin of head rounded; promesonotal suture shallowly impressed; compound eyes moderate in size; propodeal spines moderately long.

Worker measurements (n = 2). EL 0.162–0.164 (0.163); FRS 0.191–0.196 (0.194); HL 0.654–0.664 (0.659); HW 0.517–0.527 (0.522); IOD 0.446–0.455 (0.451); IOcD N/A; MD 0.167–0.18 (0.174); PH 0.19–0.213 (0.202); PL 0.286–0.299 (0.293); PPH 0.21–0.222 (0.216); PPL 0.204–0.211 (0.208); PPW 0.257–0.278 (0.268); PTW 0.156–0.176 (0.166); PW 0.375–0.386 (0.381); SL 0.626–0.633 (0.63); SPST 0.169–0.177 (0.173); WL 0.863–0.868 (0.866).

Indices: CI 79.1–79.4 (79.2); DPel 54.5–58.9 (56.7); DPpI 122–136 (129); LPel 140–151 (145); LPpI 91.9–100.5 (96.2); OI 31.1–31.3 (31.2); PeNI 41.6–45.6 (43.6); PpNI 68.5–72 (70.3); PPI 158–165 (161); PSLI 25.8–26.7 (26.2); SI 94–96.8 (96).

Worker description. Head longer than wide (CI 79.1–79.4); head sides parallel, but converging toward the mandibular insertions anteriorly beyond the level of the antennal insertions in full-face view; posterior head margin broadly convex and posterior corners of head broadly rounded. Anterior clypeal margin convex, with the median clypeal lobe projecting slightly beyond the lateral clypeal lobes. Frontal carinae developed: extending posteriorly to about midlength of the compound eye, after which they become indistinguishable from the ground rugulae of the head. Antennae 12-segmented, antennal scapes long, surpassing the posterior margin of the head by about the length of the first two funicular segments (SI 119–122). Eyes moderate in size (OI 31.1–31.3), 11 ommatidia in longest row.

Mesosoma relatively slender (WL 1.31–1.32 times HL); promesonotal suture not impressed. Metanotal groove shallowly impressed; visible as a broad, shallow concavity in lateral view. Propodeal spines acute and moderately long (PSLI 25.8–26.7); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, petiole with a low carina running transversely from the petiolar spiracle to the posterior margin; the anterior face of node forming a shallow concavity anteriorly as it joins the anterior portion of the petiole. Petiolar node in profile relatively low, with anterior and posterior faces broadly rounded (LPel 140–151). In dorsal view petiole elongate (DPel 54.5–58.9). Postpetiole in profile globular, nearly equal in height to petiolar node and relatively elongate (LPpI 91.9–100.5); in dorsal view transversely elongate-oval, widest at 1/3 of the total postpetiole length from anterior margin (DPpI 122–136) and 1.6 times wider than petiole (PPI 158–165).

Mandibular sculpture: distinctly longitudinally striate along entire length. Clypeus smooth and shiny, bearing 9 longitudinal rugae, with median ruga strongly developed and running posteriorly from the anterior clypeal margin to the level of antennal insertions before weakening. Cephalic dorsum predominantly longitudinally rugose, with transverse rugae incompletely connecting longitudinal rugae. In profile, sides of head coarsely rugoreticulate; coarse punctures visible between rugae, particularly postero-ventrally to the compound eye. Sculpture of mesosoma in dorsal view with predominately longitudinal rugae on pronotum and mesonotum, becoming increasingly reticulate on the propodeum. Space between propodeal spines with several fine transverse rugae, propodeal declivity finely punctate. In profile, mesosoma rugo-reticulate; longitudinal rugae stronger on pronotum, becoming increasingly reticulate on mesopleuron, and giving way to coarse punctation on metapleuron. Petiole and postpetiole finely punctate, with weak overlying rugosity. Gaster smooth and shining except for small, widely spaced piligerous punctures.

Head, including mandibles and ventral regions nearly uniformly covered in a fine, whitish pubescence. Dorsal surface of the head, including clypeus, frons, posterior margin of the head and occipital corners equipped with long, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Antennal scape pilosity abundant, sharp-tipped and subdecumbent. Pronotal “neck”, pronotal humeri, propleurae and upper half of procoxae with short, fine whitish pubescence. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, long, abundant, blunt-tipped whitish setae, their bases spaced from each other by the length of the setae or less. Bases of the setae on the posterior margin of first gastral tergite separated by less than the length of the setae. Ventral surfaces of the post-petiole and gaster with sparse pilosity like that of the propleuron.

Queen. Unknown

Male. Unknown

Color. Worker : Overall yellowish-orange with extremities, including antennae, legs, coxae, mouthparts and gaster (excluding first tergite) yellowish-white.

Distribution and ecology. *T. rufus* is known only from the type locality, Kora National Park, which includes acacia bushland and riverine forests. The type specimens were collected via pitfall traps; presumably this is a ground-nesting species.

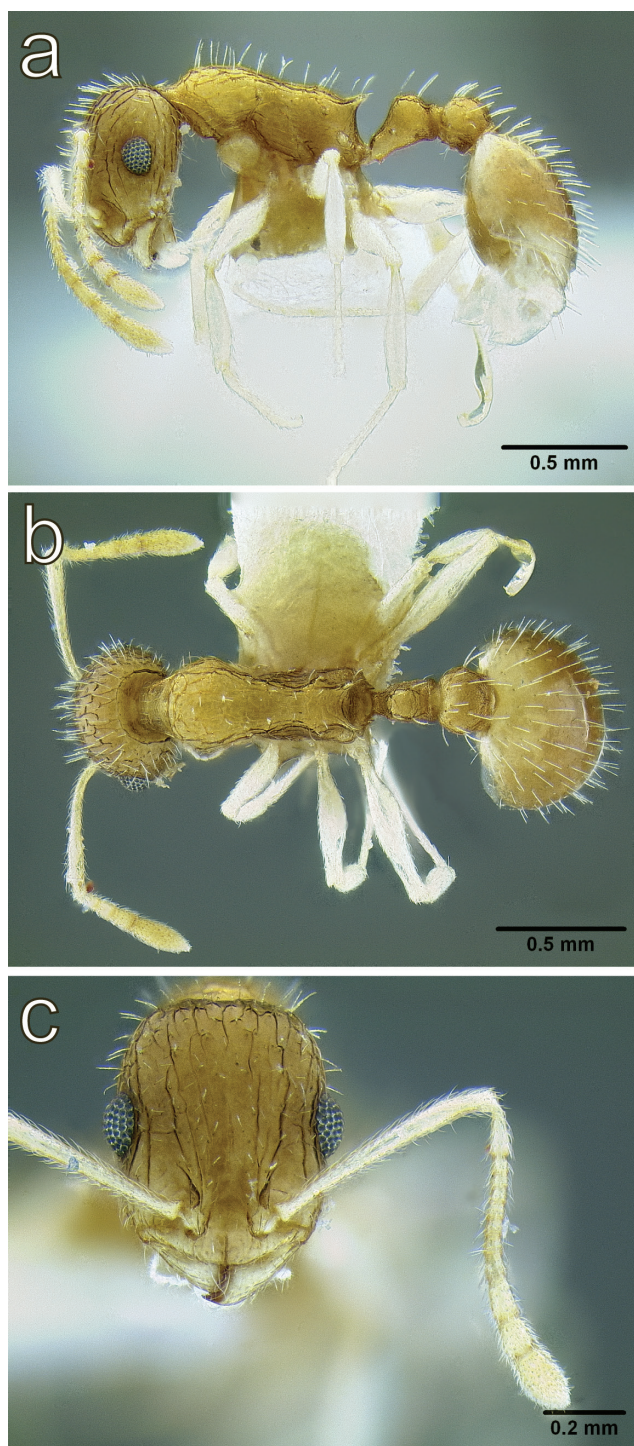


Figure 12. *Temnothorax rufus* sp. n., worker (CASENT0712675) **a** body in lateral view **b** body in dorsal view **c** head in full face view.

Taxonomic notes. The only known specimens of *T. rufus* exhibit coloration unique among the species of the Afrotropical region, having light orange head, mesosoma and gaster and pale extremities.

***Temnothorax solidinodus* Prebus, sp. n.**

<http://zoobank.org/6BC6BA04-F0E3-4714-957F-B62A2D7D60A4>

Fig. 13

Type material. Holotype worker: KENYA, Kakamega Forest, Colobus. 0.27°N, 34.88°E, 1600 m. Rainforest, canopy fogging *Teclea nobilis* “101”. x.2002. leg. W. Freund. (HLMD: CASENT0906153).

Diagnosis. *Temnothorax solidinodus* is easily distinguishable from the other Afrotropical species by the following character combination:

Antennal scapes short, distinctly failing to reach the posterior margin of the head; compound eyes moderate in size ($OI < 30$); post petiole globular in dorsal view, widest at the midpoint of the segment; metanotal groove shallowly impressed; head subrectangular ($CI > 85$); posterior margin of head flat.

Worker measurements (n = 1). EL 0.185; FRS 0.257; HL 0.728; HW 0.664; IOD 0.575; IOcD N/A; MD 0.153; PH 0.295; PL 0.298; PPH 0.248; PPL 0.198; PPW 0.265; PTW 0.215; PW 0.45; SL 0.507; SPST 0.232; WL 0.921.

Indices: CI 91.2; DPel 72.1; DPpI 134; LPel 101; LPpI 79.8; OI 27.9; PeNI 47.8; PpNI 58.9; PPI 123; PSli 31.9; SI 69.6.

Worker description. Head sub rectangular (CI 91.2); head sides converging toward the mandibular insertions anterior to the compound eyes in full-face view; posterior margin of head flat, occipital corners rounded. Anterior clypeal margin slightly concave medially, with the median clypeal lobe rounding evenly into the lateral clypeal lobes. Frontal carinae developed: extending posteriorly to about midlength of the compound eye, after which they become indistinguishable from the ground rugulae of the head. Antennae 12-segmented, antennal scapes short, falling short of the posterior margin of the head by about the length of the first funicular segment (SI 69.6). Eyes moderate in size (OI 27.9), 13 ommatidia in longest row.

Mesosoma relatively slender (WL 1.27 times HL); promesonotal suture very shallowly impressed and marked a distinct break in sculpture. Metanotal groove shallowly impressed; visible as a broad, shallow concavity in lateral view and lending a slightly peaked appearance to the propodeum. Propodeal spines long, straight and acute ($PSli$ 31.9); propodeal lobes small and rounded.

Petiole without a differentiated peduncle. In profile, the anterior face of node sloping evenly into the anterior portion of the petiole. Petiolar node in profile low, with anterior and posterior faces broadly rounded ($LPel$ 79.8). In dorsal view petiole elongate ($DPel$ 72.1). Postpetiole in profile globular, nearly equal in height to petiolar node, laterally compressed ($LPpI$ 79.8); in dorsal view transversely elongate-rectangular, widest at the midpoint ($DPpI$ 134) and 1.2 times wider than petiole (PPI 123).

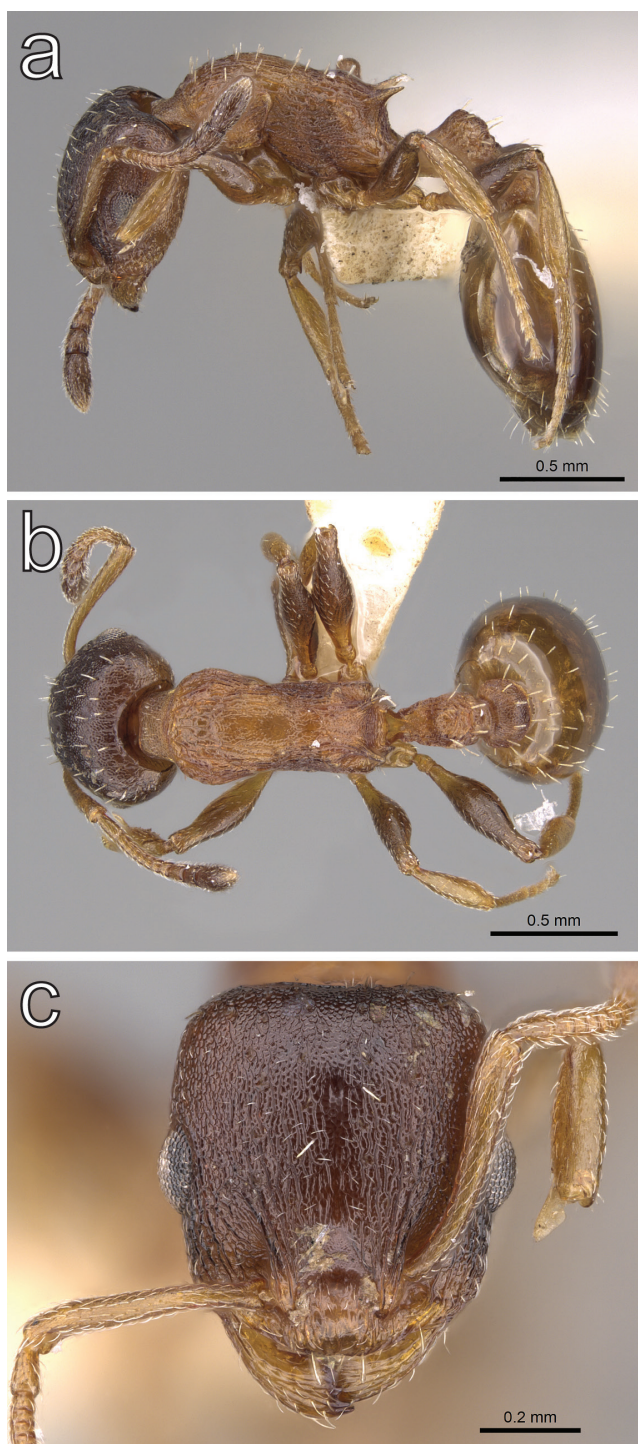


Figure 13. *Temnothorax solidinodus* sp. n., worker (CASENT0906153) **a** body in lateral view **b** body in dorsal view **c** head in full face view. Photographer: Michele Esposito.

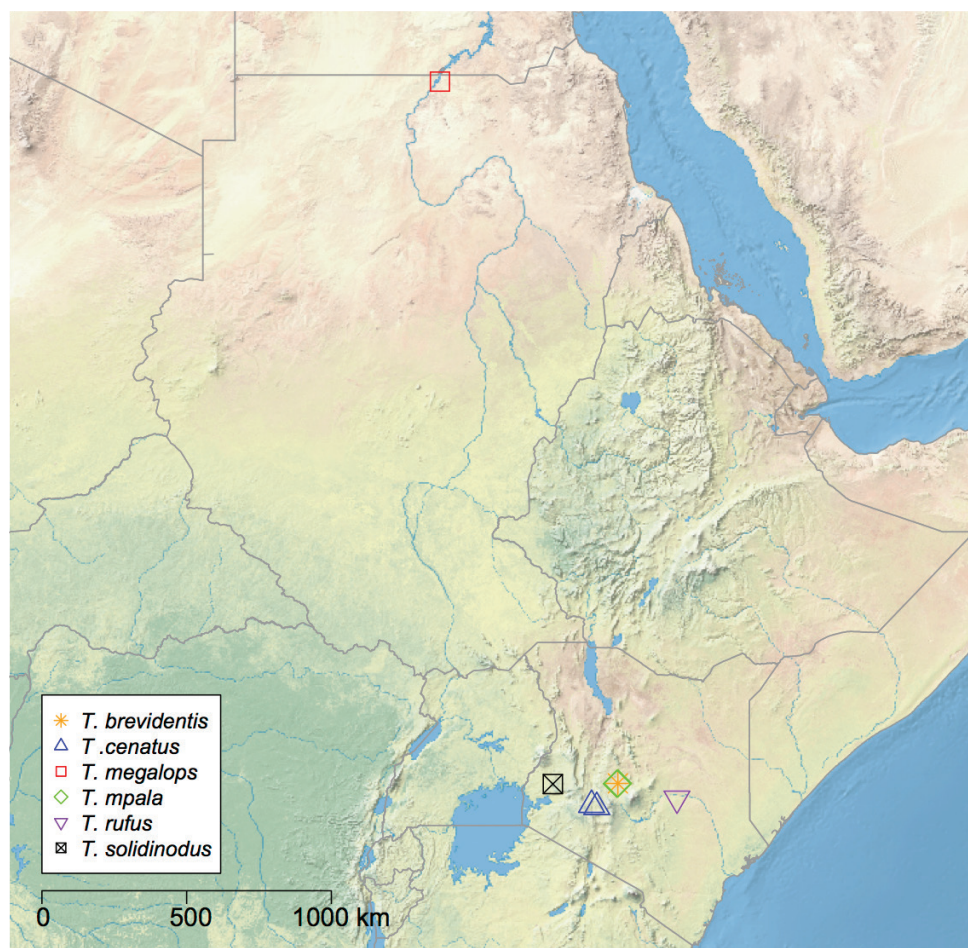


Figure 14. Distribution of the Afrotropical species of *Temnothorax*. Area depicted ranges from southern Egypt to northern Tanzania.

Mandibles distinctly longitudinally striate along their entire length. Clypeus smooth and shiny, bearing 13 longitudinal rugae which become weaker medially. Cephalic dorsum predominantly longitudinally rugose, overlying punctate sculpture that weakens medially. In profile, sides of head coarsely reticulate between the compound eye and mandible. Sculpture of mesosoma in dorsal view with predominately longitudinal rugae on pronotum; mesonotum punctate on the anterior half, weakening the posterior half; propodeum predominantly longitudinally rugose. Space between propodeal spines strongly punctate, propodeal declivity with several weak transverse rugae. In profile, mesosoma, petiole and post petiole strongly rugo-reticulate over a punctate ground sculpture. Gaster smooth and shining.

Dorsal surface of the head, including clypeus, frons, posterior margin of the head and occipital corners equipped with short (less than the length of the pedicel), yellow-

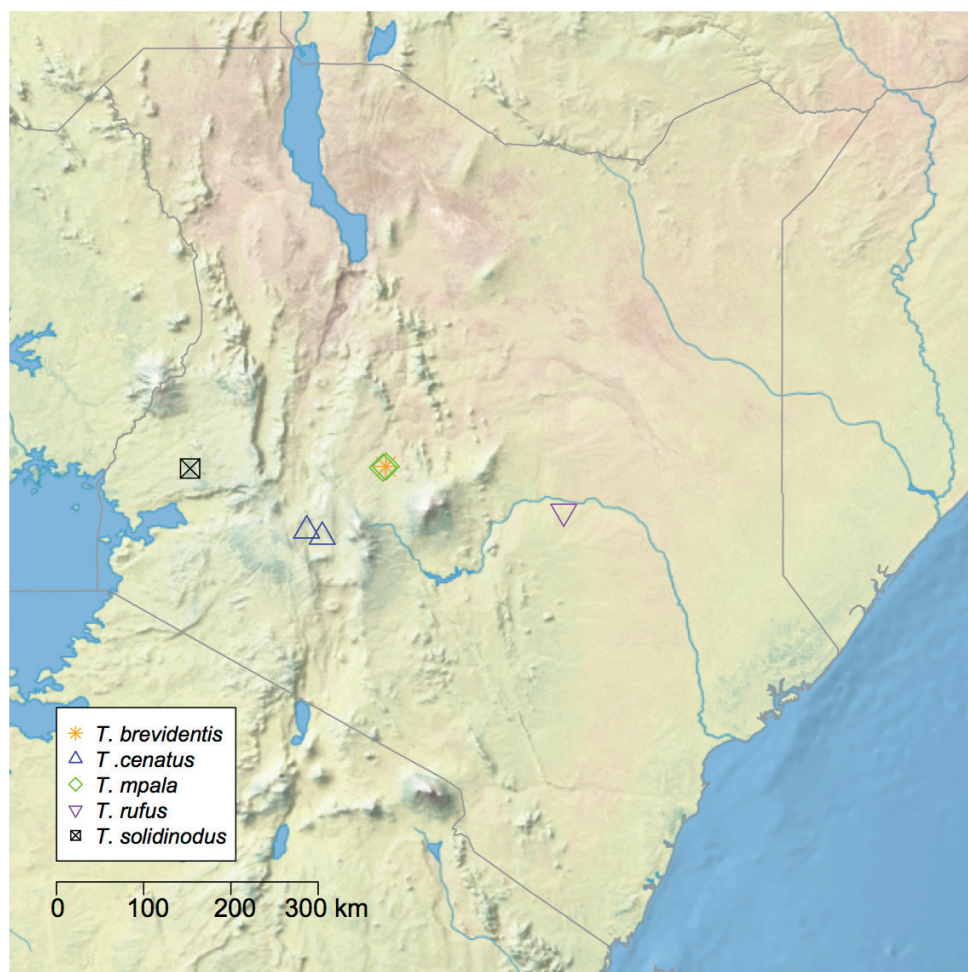


Figure 15. Detail of the distribution of *Temnothorax* species in sub-Saharan Africa. Area depicted includes Kenya and bordering countries

ish, blunt-tipped setae. Anterior clypeal margin with two pairs of long setae flanking the median carina. Antennal scape pilosity abundant, sharp-tipped and subdecumbent. Pronotal “neck” and procoxae with short, fine yellowish pubescence. Dorsal surfaces of mesosoma, waist segments and gaster with uniformly erect, short, abundant, blunt-tipped yellowish setae, their bases spaced from each other by the length of the setae or more. Bases of the setae on the posterior margin of first gastral tergite separated by more than the length of the setae.

Dorsal surface of head, excluding the antennae, clypeus and mandibles, dark brown. Antennae, clypeus, mandibles, mesosoma and waist segments uniformly light brown. Gaster transitions from light brown to dark brown along the anteroposterior axis.

Queen. Unknown

Male. Unknown

Distribution and ecology. One worker of *T. solidinodus* was collected via canopy fogging of *Teclea nobilis* in Kakamega Forest. Presumably this is an arboreal species.

Color. Worker: Overall chestnut-brown, with head and gaster posterior to the midlength of the first tergite darker.

Taxonomic notes. *T. solidinodus*, in relation to *T. angustulus* and other species within the *angustulus* group bears a very large petiolar node.

Acknowledgements

Many thanks to Francisco Hita Garcia for providing specimens for this study and helpful feedback during the writing of this manuscript; to Barry Bolton and an anonymous reviewer for providing valuable suggestions that improved this work; to Brian Brown, Weiping Xie and Giar-Ann Kung at the LACM for being amiable hosts during a visit to the collections, and to Phil Ward for comments on this manuscript and mentorship.

References

- Baroni Urbani C (1978) Materiali per una revisione dei *Leptothorax* neotropicali appartenenti al sottogenere *Macromischa* Roger, n. comb. (Hymenoptera: Formicidae). *Entomologica Basiliensia* 3: 395–618.
- Beckers R, Goss S, Deneubourg JL, Pasteels JM (1989) Colony Size, Communication and Ant Foraging Strategy. *Psyche* 96: 239–256. doi: 10.1155/1989/94279
- Bharti H (2011) List of Indian Ants (Hymenoptera: Formicidae). *Halteres* 3: 79–87.
- Bolton B (1982) Afrotropical species of the myrmicine ant genera *Cardiocondyla*, *Leptothorax*, *Melissotarsus*, *Messor* and *Cataulacus* (Formicidae). *Bulletin of the British Museum (Natural History)*. *Entomology* 45: 307–370.
- Bolton B (2003) Synopsis and classification of Formicidae. *Memoirs of the American Entomological Institute* 71: 1–361.
- Bolton B (2014) An online catalog of the ants of the world. <http://antcat.org> [accessed 5 June 2014]
- Cagniant H, Espadaler X (1997) Les *Leptothorax*, *Epimyrma* et *Chalepoxenus* du Maroc (Hymenoptera: Formicidae). Clé et catalogue des espèces. *Annales-Société Entomologique de France* 33: 259–284.
- Eguchi K, Bui TV, Yamane S (2011) Generic synopsis of the Formicidae of Vietnam (Insecta: Hymenoptera), part I – Myrmicinae and Pseudomyrmecinae. *Zootaxa* 2878: 1–61.
- Emery C (1884) Materiali per lo studio della fauna Tunisina raccolti da G. e L. Doria. III. Rassegna delle formiche della Tunisia. *Annali del Museo Civico di Storia Naturale* 21: 373–384.
- Espadaler X (1997) *Leptothorax caesari* sp. n. (Insecta: Hymenoptera: Formicidae), a granivore with apterous males. *Annalen des Naturhistorischen Museums in Wien* 99(B): 145–150.

- Evenhuis NL (2009) The insect and spider collections of the world website. <http://hbs.bishop-museum.org/codens> [accessed 5 June 2014]
- Fokuhl G, Heinze J, Poschlod P (2012) Myrmecochory by small ants- Beneficial effects through elaiosome nutrition and seed dispersal. *Acta Oecologica* 38: 71–76. doi: 10.1016/j.actao.2011.09.007
- Hamann HHF, Klemm W (1967) Ergebnisse der zoologischen Nubien-Expedition 1962. Teil XXXIV. Hymenoptera – Formicidae. *Annalen des Naturhistorischen Museums in Wien* 70: 411–421.
- Hita Garcia F, Fisher B (2011) The ant genus *Tetramorium* Mayr (Hymenoptera: Formicidae) in the Malagasy region: introduction, definition of species groups, and revision of the *T. bicarinatum*, *T. obesum*, *T. sericeiventris* and *T. tosii* species groups. *Zootaxa* 3039: 1–72.
- Kempf WW (1959) A synopsis of the New World species belonging to the Nesomyrmex-group of the ant genus *Leptothorax* Mayr (Hymenoptera: Formicidae). *Studia Entomologica* 2: 391–432
- Radchenko AG (2004) A review of the ant genera *Leptothorax* Mayr and *Temnothorax* Mayr (Hymenoptera, Formicidae) of the eastern Palearctic. *Acta Zoologica Academiae Scientiarum Hungaricae* 50: 109–137.
- Schulz A, Heinze J, Pusch K (2007) Description of two new *Temnothorax* species (Hymenoptera: Formicidae) from Italy. *Zootaxa* 1471: 1–14.
- Seifert B (2006) *Temnothorax saxonicus* (Seifert, 1995) stat. n., comb. n. – a parapatric, closely-related species of *T. sordidulus* (Müller, 1923) comb. n. and description of two new closely-related species, *T. schoedli* sp. n. and *T. artvinense* sp. n., from Turkey (Hymenoptera: Formicidae). *Myrmecologische Nachrichten* 8: 1–12.
- Tinaut A (1995) Nueva especie de *Leptothorax* (Mayr, 1855) del grupo *laurae* Emery, 1884 *Leptothorax crepuscularis* n. sp. (Hymenoptera, Formicidae). *Zoologica Baetica* 5: 89–98.
- Ward PS, Brady SG, Fisher BL, Schultz TR (2014) The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). *Systematic Entomology* 40: 61–81. doi: 10.1111/syen.12090

The paleoenvironments of azhdarchid pterosaurs localities in the Late Cretaceous of Kazakhstan

Alexander Averianov^{1,2}, Gareth Dyke^{3,4}, Igor Danilov⁵, Pavel Skutschas⁶

1 Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab. 1, 199034 Saint Petersburg, Russia **2** Department of Sedimentary Geology, Geological Faculty, Saint Petersburg State University, 16 liniya VO 29, 199178 Saint Petersburg, Russia **3** Ocean and Earth Science, National Oceanography Centre, Southampton, University of Southampton, Southampton SO14 3ZH, UK **4** MTA-DE Lendület Behavioural Ecology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, 4032 Debrecen, Egyetem tér 1, Hungary **5** Zoological Institute of the Russian Academy of Sciences, Universitetskaya nab. 1, 199034 Saint Petersburg, Russia **6** Department of Vertebrate Zoology, Biological Faculty, Saint Petersburg State University, Universitetskaya nab. 7/9, 199034 Saint Petersburg, Russia

Corresponding author: Alexander Averianov (dzharakuduk@mail.ru)

Academic editor: Hans-Dieter Sues | Received 3 December 2014 | Accepted 30 January 2015 | Published 20 February 2015

<http://zoobank.org/C4AC8D70-1BC3-4928-8ABA-DD6B51DABA29>

Citation: Averianov A, Dyke G, Danilov I, Skutschas P (2015) The paleoenvironments of azhdarchid pterosaurs localities in the Late Cretaceous of Kazakhstan. ZooKeys 483: 59–80. doi: 10.3897/zookeys.483.9058

Abstract

Five pterosaur localities are currently known from the Late Cretaceous in the northeastern Aral Sea region of Kazakhstan. Of these, one is Turonian-Coniacian in age, the Zhirkindek Formation (Tyulkili), and four are Santonian in age, all from the early Campanian Bostobe Formation (Baibishe, Akkurgan, Buroinak, and Shakh Shakh). All so far collected and identifiable Late Cretaceous pterosaur bones from Kazakhstan likely belong to Azhdarchidae: *Azhdarcho* sp. (Tyulkili); *Aralazhdarcho bostobensis* (Shakh Shakh); and *Samrukia nessovi* (Akkurgan). These latter two taxa, both from the Bostobe Formation might be synonyms. *Azhdarcho* sp. from the Zhirkindek Formation lived in a tropical-to-subtropical relatively humid climate on the shore of an estuarine basin connected to the Turgai Sea. Known fossils were collected in association with brackish-water bivalves and so the overall paleoenvironment of this pterosaur was likely an estuarine marsh as indicated by the dominance of conifers and low relative counts of ferns and angiosperms. *Aralazhdarcho bostobensis*, from the Bostobe Formation, lived on a coastal fluvial plain along the Turgai Sea. This paleoenvironment was either floodplain (Akkurgan, Buroinak, and Shakh Shakh) or

estuarine (Baibishe). In the Santonian – early Campanian, shallow waters near this coastal plain were sites for the intensive accumulation of phosphates under upwelling conditions caused by strong winds from the ancient Asian landmass. These winds also caused significant aridization of the climate during this time. We speculate that pterosaurs may have been attracted to this area by the abundant resources in the bio-productive estuaries and nearshore upwelling waters.

Keywords

Pterosauria, Azhdarchidae, Late Cretaceous, Kazakhstan, distribution, paleoenvironments

Introduction

In Kazakhstan two regions are known to have yielded the skeletal remains of pterosaurs: 1) the Upper Jurassic (Oxfordian-Kimmeridgian) Karabastau Formation in the Karatau Mountains of southern Kazakhstan, and; 2) several sites within the Late Cretaceous Zhirkindek (Turonian-Coniacian) and Bostobe (Santonian – lower Campanian) formations in the northeastern Aral Sea region of western Kazakhstan (Fig. 1). Of these, the latter has yielded isolated bones of large pterodactyloid pterosaurs while the former is a Konservat-Lagerstätte known to contain exceptionally well-preserved skeletons with soft tissues of the non-pterodactyloid pterosaurs *Batrachognathus volans* and *Sordes pilosus* (Riabinin 1948; Sharov 1971; Unwin and Bakhurina 1994).

The first pterosaur bones from the northeastern Aral Sea region of Kazakhstan were described by Nesov (1984). Subsequently, two taxa have been described from the



Figure 1. Map to show the northeastern Aral Sea region of Kazakhstan and the approximate positions of known Late Cretaceous pterosaur localities (1 Tyulkili 2 Baibishe 3 Akkurgan 4 Buroinak 5 Shakh-Shakh). The lakes in the western part of the map are remnants of the Aral Sea, relics of the Turgai Strait that once connected the Tethys and Arctic oceans.

Bostobe Formation: *Aralazhdarcho bostobensis* (Averianov 2004, 2007a) and *Samrukia nessovi* (Buffetaut 2011; Naish et al. 2012). Here we review all previous finds of pterosaurs from the northeastern Aral Sea region, report on additional specimens collected on our expedition in 2012, and discuss the paleoenvironment of the pterosaurs that lived in this region.

Institutional abbreviations: CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; SMNK PAL, Staatliches Museum für Naturkunde, Karlsruhe, Germany; WDC, the Wyoming Dinosaur Center, Thermopolis, USA; ZIN PH and ZIN PO, Paleoherpertological and Paleornithological collections of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Late Cretaceous pterosaur localities in Kazakhstan

Tyulkili

The Tyulkili [=Tjulkeli] hills (known in the paleobotanical literature as the Kankazgan locality) are located about 80 km north of Dzhusaly railway station in northeastern Kazakhstan (Fig. 1). Here the Zhirkindek Formation is exposed and is composed of sands interbedded with clays and silts (Shilin 1998; Kordikova et al. 2001). The ferruginous sandstone at the bottom of the Zhirkindek Formation section at Tyulkili hills has yielded numerous plant remains, including 36 species of fossil angiosperms (Shilin 1982, 1986, 1998). The next bed up-sequence, consisting of yellow-grey and grey clays, represents an ingression of brackish waters. It has produced fossilized wood, numerous remains of crustaceans, shark teeth (*Protolamna* sp., *Scapanorhynchus* sp.) and coprolites, the isolated bones of lindholmemydid and trionychid turtles, crocodyliforms, ornithopods (*Hadrosauroidea* indet.), possible sauropods, and laterally compressed teeth of theropods (*Tyrannosauroida* indet.) (Nesov 1995, 1997). Indeed, in 2012 the tooth of a marine shark *Cretodus longiplicatus* was found at this level, a species characteristic of the Cenomanian of the Tethys region (Werner 1989; Kennedy et al. 2008; Underwood et al. 2011). According to Sokolov (1978), this species [= *Semiplicatodus sulcatus* in his usage] is widely distributed in late Albion – Cenomanian deposits of the Mangyshlak Peninsula and western Turkmenistan but is rare in the Turonian of Kazakhstan.

The main fossiliferous horizon at the Tyulkili locality is confined to the middle sandstone bed, about 18 m above the base of the Zhirkindek Formation (Kordikova et al. 2001). In 1982, Nesov collected the remains of plesiosaurs, crocodyliforms, pterosaurs (cf. Azhdarchidae) and dinosaurs (*Ankylosauridae* indet., *Hadrosauroidea* indet., *Neoceratopsia* indet., *Sauropoda* indet., *Tyrannosauroida* indet., *Ornithomimidae* indet., and *Therizinosauroida* indet.) at this level (Nesov 1995, 1997; Averianov 2007b, 2009; Averianov and Sues 2009). Martinson (1990b, 1997) reported six species of bivalves (*Trigonoidea* and *Unionoidea*) from unspecified levels of the Zhirkindek Formation at Tyulkili (Kankazgan). Much later, Kordikova et al. (2001) reported gastropods, bivalves, brachiopods, crustaceans, selachians, osteichthyans, amphibians,

varanoid lizards, trionychid turtles, crocodyliforms (cited as “*Turanosuchus aralensis*” [= *Kansajsuchus borealis*]) and ornithomimid, tyrannosaurid, and dromaeosaurid theropods from this horizon. In 2012, we collected a microvertebrate sample from this level that included shark teeth and spines (*Hybodus* sp., *Polyacrodus* sp.), numerous gar scales and bones (Lepisosteidae indet.), rare dinosaur teeth and salamander bones (Skutschas 2013). Further up in the section, at the top part of the middle sandy bed, there are also shark teeth and spines (Hybodontidae indet., Odontaspididae indet., *Scapanorhynchus* sp.), holostean (Lepisosteidae indet.), teleostean bones and scales, bones of lindholmemydid and trionychid turtles, crocodyliforms, dinosaurs, and fragments of pterosaur hollow bones (Nesov 1997). The upper part of the Zhirkindek Formation at Tyulkili hills is composed of light grey clays from which abundant plant remains as well a bird feather have been collected (Shilin 1986: fig. 3; Nesov 1992a).

The flora known from the lowermost sandstone bed of the Zhirkindek Formation at Tyulkili is dominated by *Platanus* species and thermophilous conifers (Shilin 1998) and likely corresponds to the early Turonian thermal maximum (Nesov 1993). A similar Turonian flora has been collected from the Zhirkindek Formation at Karakumzholy at the eastern end of the Tyulkili hills (Shilin 2008). East from the Tyulkili hills, in the lower Syr Darya area below the Zhirkindek Formation, there are marine early Turonian deposits with inoceramids and fossilized wood (Geology of the USSR 1970). The lower clayey part of the Zhirkindek Formation corresponds to the early Turonian marine transgression in the region and the upper sandy part may be of the late Turonian – Coniacian age (Nesov 1997; Kordikova et al. 2001).

The pterosaur specimens collected by Nesov in 1982 at Tyulkili include ZIN PH 54/43, a dorsal vertebra (Averianov 2007a: fig. 1), ZIN PH 38/43, a poorly preserved distal fragment of radius or ulna and ZIN PH 13/43, a small fragment of the first wing phalanx (?). In 2012 a well preserved distal fragment of juvenile ulna (ZIN PH 56/43; Fig. 2) was also collected from the lower part of this section. This specimen is about half the size of ZIN PH 14/44, a distal ulna fragment of *Azhdarcho lancicollis* from the upper Turonian Bissekty Formation of the Kyzylkum Desert, Uzbekistan (Averianov 2010: fig. 25F–J): its distal width is 25.3 mm compared with 41.0 mm in the specimen from the Bissekty Formation. ZIN PH 14/44 could be from an adult but is not the largest specimen from the Bissekty Formation as ZIN PH 86/44, an ulna lacking its distal end, is distinctly larger. In spite of these size differences, the morphology of both bones is almost identical: in each the shaft is hollow, with a maximum wall thickness around 1 mm, and is oval in cross section with a dorsoventral long axis (Fig. 2a). The shaft flares towards the distal end and is more pronounced on the ventral side compared with the dorsal side; the distal end is more than twice as expanded dorsoventrally compared with the preserved proximal end. The distal articulation surface for the proximal syncarpal is skewed towards the longitudinal axis of the shaft at an angle $\sim 76^\circ$. This surface is composed of the dorsal articulation surface, middle tuberculum, and ventral fovea (Fig. 2). The dorsal articulation surface is slightly convex and crescentic in distal view (Fig. 2f) and has a tongue-like extension on its posterior surface. This extension occupies almost

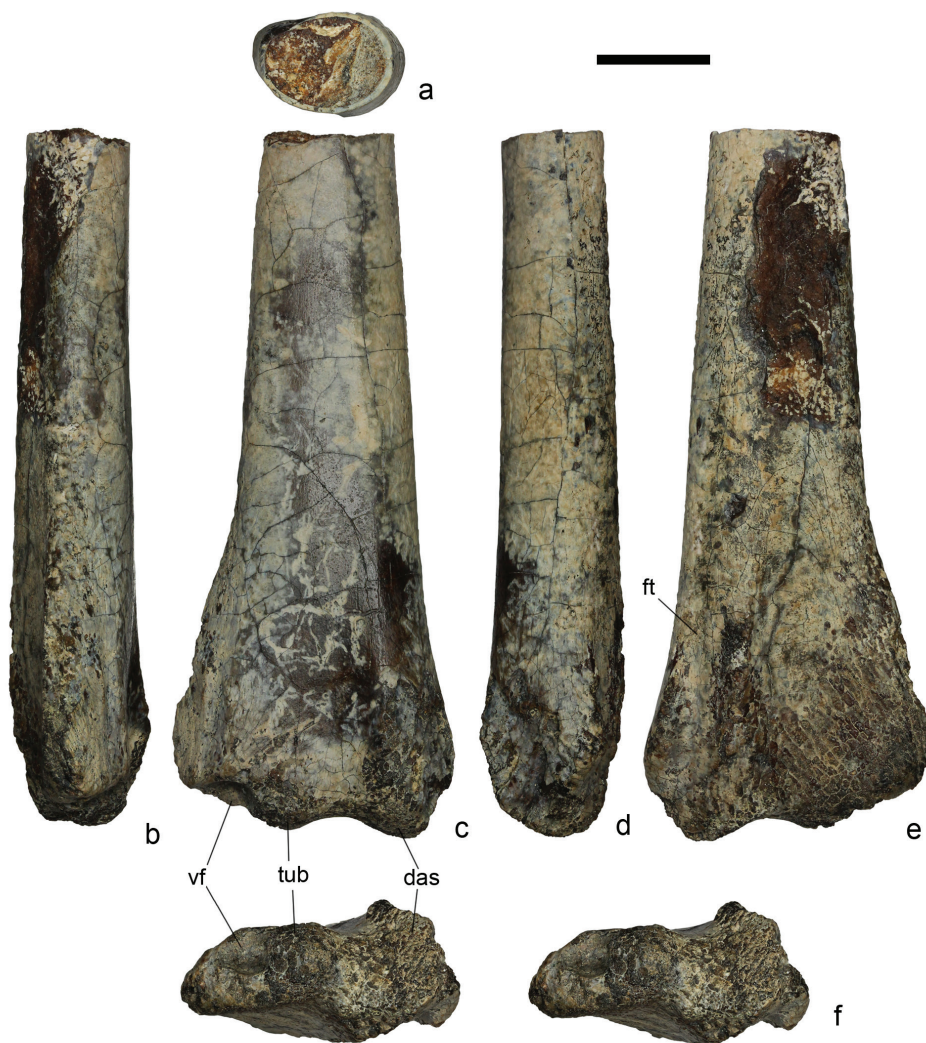


Figure 2. *Azhdarcho* sp., ZIN PH 56/43, distal fragment of a right ulna in proximal (a), ventral (b), posterior (c), dorsal (d), anterior (e), and distal (f, stereopair) views. This specimen is from the Tyulkili locality in the northeastern Aral Sea region of Kazakhstan; Zhirkindek Formation, Upper Cretaceous (upper Turonian – Coniacian). Abbreviations: das, dorsal articular surface; ft, groove for flexor tendon; tub, tuberculum; vf, ventral fovea. Scale bar is 10 mm.

half of the distal articulation surface of the bone. The tuberculum is relatively small and similar in the area to the ventral fovea. In ZIN PH 14/44 (Averianov 2010: fig. 25G, J), this tuberculum appears larger but the ventral fovea is incompletely preserved. On the posterior side of the distal end, ventral to the ventral fovea, there is a short but prominent longitudinal groove and a deeper and longer groove is also positioned on the dorsal margin of the distal end on the anterior side (Fig. 2e), pos-

sibly for a flexor tendon (Bennett 2001). Ventrally this groove is bordered by a short prominent ridge, ventral from which the anterior surface is depressed. A similar ridge is present on the opposite posterior side that connects distally with a tongue-like extension of the dorsal articulation surface. Some parts of this ridge and dorsal articulation surface are missing in ZIN PH 56/43.

The morphology of the distal part of the ulna generally shows little variation among pterodactyloid pterosaurs (see review in Wiffen and Molnar 1988). In Ornithocheiridae, the distal articulation surface of the ulna is not skewed and the ventral portion of the distal ulna is usually wider anteroposteriorly with the ventral fovea occupying only half of this width. A pneumatic foramen can often be present on the anterior side of this element close to the distal end (Wellnhofer 1985: fig. 9a, c). In ZIN PH 56/43, common to azhdarchids, this pneumatic foramen is absent and the ventral part of the distal ulna is very narrow, with a ventral fovea occupying most of its surface (Averianov 2010). In non-azhdarchid azhdarchoids, such as “*Santanadactylus spixi*” [= *Tupuxuara* sp.] (Wellnhofer 1985: fig. 25a-c) and *Tapejara wellnhoferi* (SMNK PAL 1137, pers. obs. by AA) the ventral part of the distal ulna is similarly narrow, but the distal articulation surface is less skewed. Because ZIN PH 56/43 is almost undistinguishable from the distal ulna of *A. lancicollis* from the co-eval Bissekty Formation in the nearby Kyzylkum Desert, Uzbekistan, it is tentatively assigned here to *Azhdarcho* sp.

Baibishe

The Baibishe [=Baybishe] hill locality is situated about 130 km NNW from Dzhusaly railway station (Fig. 1). The vertebrate remains from this region come from the lower and middle part of the Bostobe Formation which is exposed here above the upper Albian – Cenomanian Altykuduk Formation and Turonian Zhirkindek Formation, both of which contain plants and molluscs (Martinson et al. 1966; Shilin and Romanova 1978). The first vertebrates from the Bostobe Formation at this locality were discovered by Shilin in 1979 who collected plant remains and molluscs from the lower clay bed, a nearly complete carapace of the adocid turtle *Shachemys baibolatica* and hadrosauroid bones from the overlying yellow-grey sandstone bed (Kuznetsov and Shilin 1983; Shilin 1983). In 1982, Nesov collected a microvertebrate sample from this locality which included brackish water chondrychthians (*Polyacrodus* cf. *brabanticus*, *Polyacrodus* sp., *Hybodus kansaiensis*, *Scapanorhynchus* sp., *Ischyrrhiza* sp., *Protoplatyrhina* sp., *Ptychotrigon* sp., *Myledaphus glickmani*, *Baibishia baibishe*) and osteichthyans (Ichthyodectidae indet.), freshwater chondrosteans (Acipenseridae indet.) and holosteans (Amiidae indet.), salamanders (*Eoscapherpeton* sp.) and frogs, macrobaenids *Anatolemys maximus*, freshwater adocids *Adocus bostobensis* and *Shachemys baibolatica* and Trionychidae indet., remains of the terrestrial stem testudinoid *Lindholmemyx* sp., crocodyliforms cf. *Kansajsuchus* sp., ornithopods, sauropods, small non-avian theropods, tyrannosauroids, and birds (Mertinene and Nesov 1985; Nesov and Mertinene

1986; Nesov 1988a, 1995, 1997; Syromyatnikova and Danilov 2009; Danilov et al. 2011; Skutschas 2013). *Bishara backa*, for example, was based on an atlas vertebra from Baibishe and was first described as an albanerpetontid (Nesov 1997) and then later considered to be an unidentifiable salamander by Gardner and Averianov (1998). This element could be the oldest record of the Proteidae (Skutschas 2013). Nesov (1995) also recorded remains of a possible ceratopsid dinosaur at this site but this cannot be confirmed. A fragmentary skull roof from Baibishe referred by Nesov (1988a) to a hadrosauroid cf. *Lophorhynchon* turns out to be a giant freshwater trionychid turtle, *Khunnuchelys* n. sp. (Vitek and Danilov 2010; Danilov et al. in press). Averianov (2007b) identified bones and teeth of Tyrannosauroida indet., Therizinosauroida indet., and Dromaeosauridae indet. from Baibishe and referred CCMGE 601/12457, a femur from this site attributed by Nesov (1995) to *Tarbosaurus*, to a therizinosauroid cf. *Neimongosaurus* sp. This latter identification has been questioned by Zanno (2010).

A rich assemblage of brackish water bivalves from Baibishe was described by Martinson (1990b): *Lancedaria angustata*, *Psorula tasaranica*, *Parreysia convexa*, *Oxyntia baibishensis*, and *Rectidens asiaticus*. Nesov (1988c) also reported silicified wood at this site that contains the boring traces of insect larvae, likely jewel beetles (Buprestidae) and other coleopterans, which he considered to be ichnospecies *Rhombichnites baibishensis*.

In the microvertebrate sample from Baibishe there are also a number of indeterminant pterosaur hollow limb bone fragments (Nesov 1990; Averianov 2008). A single large specimen cf. ?Azhdarchidae was reported from this site by Nesov (1997: 111). ZIN PO 3475, a pedal ungual phalanx, is so far the only bird fossil reported from Baibishe (Nesov 1988b: 121, fig. 1(5); 1992b: 27; 1992a: 471, fig. 4K) although Bakhurina and Unwin (1995: 231) noted similarity with bones of *Dsungaripterus* and thought it instead may belong to a pterosaur.

Akkurgan

Akkurgan [=Akkurgan-Boltyk] is an isolated hill 135 km north of Dzhusaly railway station (Fig. 1) that exposes outcrops of the Bostobe Formation. This locality has become known for the plant remains collected from the light-grey clays at the bottom of the Bostobe Formation (Martinson et al. 1966; Shilin and Romanova 1978). In 1977, Shilin collected plant remains from this level and a hadrosauroid maxilla and femur fragments from the green-grey clays above. This maxilla fragment became the type specimen of *Arstanosaurus akkurganensis*, which is now considered a *nomen dubium* (Shilin and Suslov 1982; Norman and Kurzanov 1997; Horner et al. 2004). In 1982, Nesov collected bones of the freshwater chondrosteian *Acipenser shilini*, the adocids *Adocus bostobensis* and *Shachemys baibolatica*, an indeterminate trionychid, the stem testudinoid *Lindholmemys* sp., and crocodyliforms, Hadrosauroida indet. remains and the laterally compressed teeth of Tyrannosauroida indet. (Nesov and Kaznyshkin 1983; Nesov 1995, 1997; Syromyatnikova and Da-

nilov 2009; Danilov et al. 2011). Much later, Godefroit et al. (2012) described the basal hadrosauroid *Batyrosaurus rozhdestvenskyi* based on a partial skeleton from this locality.

Most recently, Naish et al. (2012) described a posterior mandible fragment from Akkurgan which they referred to the gigantic bird *Samrukia nessovi*. This specimen was subsequently considered to be a pterosaur (Buffetaut 2011), a reassignment agreed with in this paper. The *Samrukia* mandible is similar to the mandible of *Quetzalcoatlus* sp. from the Maastrichtian of Texas, USA (Kellner and Langston 1996: fig. 4) in having a peculiar posterolateral process of the lateral cotyle of the mandibular glenoid, a feature absent in ornithocheirids and pteranodontids (Wellnhofer 1985; Bennett 2001). Our view is that most likely *S. nessovi* is an azhdarchid pterosaur and thus this name is a possible synonym of *Aralazhdarcho bostobensis* known from the same formation at Shakh Shakh.

Buroinak

Buroinak [=Boroinak] is a low ridge 110–120 km NNE of Dzhusaly railway station (Fig. 1) that exposes outcrops of the Bostobe Formation. In 1982, Nesov collected the laterally compressed teeth of Tyrannosauroida indet. from this locality along with other remains of non-avian theropods and the bones of ankylosaurs, possible ceratopsians and hadrosauroids (Nesov 1995). Averianov (2007b) identified Tyrannosauroida indet. and Therizinosauroida indet. from within this sample. The other known vertebrates from this site are amiid fishes, macrobaenid, lindholmemydid, adocid, and trionychid turtles, and crocodyliforms (Nesov 1997). The adocid turtle from this locality has been recently identified as *Adocus bostobensis* (Syromyatnikova and Danilov 2009). Martinson (1990b) reported the presence of the brackish water bivalve *Sainshandia syrdarjensis* from this site and silicified wood with beetle larvae borings, *Rhombichnithes boroinakensis*, is also known to occur (Nesov 1988c).

A fragment of a possible pterosaur first wing phalanx has also been collected from the middle part of the Bostobe Formation in the northern part of the Buroinak Ridge (Glickman et al. 1987; Nesov 1990; Bakhurina and Unwin 1995; Nesov 1997; Unwin et al. 1997).

Shakh-Shakh

Shakh Shakh [=Baibolat, =Zhalmouz] was the first known and now the best sampled vertebrate locality from within the Bostobe Formation. There are two main collecting areas, Shakh Shakh I and II (Rozhdestvensky 1964), separated by about 8 km and located about 70 km north of Dzhusaly railway station (Fig. 1). The locality was discovered by geologists from the Moscow Geological Institute in 1956 (Nikiforova 1960; Rozhdestvensky 1964). In 1957 and 1961 intensive fieldwork was carried out

at this locality by teams from the Paleontological Institute of the Russian Academy of Science (Rozhdestvensky 1964, 1968) and then later (1961–1967) prospecting and excavations were made by teams from the Laboratory of Paleobiology of the Kazakh Academy of Sciences (Nurumov 1964; Bazhanov 1972; Nesov and Khisarova 1988). Nesov collected vertebrates at Shakh Shakh in 1980 and 1982. In 1995 and 2002–2007 the locality was sampled by international expeditions (Kordikova et al. 2001; Dyke and Malakhov 2004; Malakhov et al. 2009; Averianov et al. 2014). Additional specimens were also collected at this site in 2012 (Syromyatnikova and Danilov 2013).

The section of the Bostobe Formation at Shakh Shakh is composed of alternating predominantly red clays and sandstones. The main fossiliferous bed is the red clay in the middle of the section (Rozhdestvensky 1964).

The revised vertebrate fauna known from Shakh Shakh includes the euryhaline chondrychthians *Polyacrodus* cf. *brabanticus*, *Hybodus kansaiensis* and *Myledaphus glickmani*, chondrosteans (Acipenseridae indet.), holosteans (Amiidae indet.), teleosteans (Aspidorhynchiformes indet., Ichthyodectidae indet.), cryptobranchids (*Eoscaptherpeton* sp.), the possible proteid *Bishara backa*, anurans (Discoglossidae indet.), the macrobaenid *Anatolemys maximus*, the adocids *Shachemys baibolatica*, *Adocus bostobensis*, trionychids (*Aspideretoides riabinini* and “*Trionyx*” *kansaiensis*), the stem testudinoid *Lindholmemyx gravis*, squamates (Scincomorpha indet.), crocodyliforms cf. *Kansajsuchus* sp. and *Eusuchia* indet., Ankylosauridae indet., the lambeosaurine *Aralosaurus tuberiferus*, Sauropoda indet., Ornithomimidae indet., Tyrannosauroida indet., Therizinosauroida indet., Caenagnathidae (?) indet., birds and eutherian mammals (*Beleutinus orlovi* and *Zhalmouzia bazhanovi*) (Rozhdestvensky 1964; Rozhdestvensky and Khozatsky 1967; Rozhdestvensky 1968, 1970, 1973; Kuznetsov 1976, 1977; Glickman 1980; Suslov 1982; Mertinene and Nesov 1985; Nesov 1986; Kuznetsov and Chkhikvadze 1987; Efimov 1988; Nesov and Khisarova 1988; Nesov 1995; Storrs and Efimov 2000; Kordikova et al. 2001; Dyke and Malakhov 2004; Godefroit et al. 2004; Averianov 2007b; Danilov et al. 2007; Syromyatnikova and Danilov 2009; Vitek and Danilov 2010; Danilov et al. 2011; Averianov and Sues 2012; Skutschas 2013; Syromyatnikova and Danilov 2013; Averianov et al. 2014).

The first pterosaur bones reported from Shakh Shakh were collected by Rozhdestvensky but not recognized as such at the time (Averianov 2004: fig. 8). The first reported pterosaur bone from this locality is a jugal fragment (CCMGE 41/11915) collected by Nesov in 1982 (Nesov 1984: pl. 7, fig. 13, 1990, 1997: pl. 15, fig. 13; Averianov 2004: fig. 7c-e). All identifiable pterosaur specimens from Shakh Shakh likely belong to an azhdarchid which was subsequently described as *Aralazhdarcho bostobensis* (Averianov 2007a: pl. 9). Described referred specimens include an edentulous jaw fragment (ZIN PH 37/43), an anterior fragment of a mid-cervical vertebra (ZIN PH 9/43), an atlas–axis centrum (ZIN PH 44/43), a posterior dorsal vertebral centrum (ZIN PH 46/43), a distal fragment of a scapula (ZIN PH 45/43), the proximal end of a wing phalanx 2 (ZIN PH 16/43), and a proximal fragment of femur (ZIN PH 43/43). In 2007 and 2012 some additional but poorly preserved pterosaur bones were also collected by our field teams. Of these remains, the best preserved new

specimen is a proximal humerus fragment (ZIN PH 57/43) that was collected in 2012 (Fig. 3). The humeral head is incompletely preserved; it is crescentic in proximal view, with broadly concave anterior and pointed convex posterior sides (Fig. 3a). The most striking feature of this specimen is that the humeral head is not saddle-shaped, as in other azhdarchids (Averianov 2010); it is convex in anteroposterior section and almost flat in dorsoventral section as opposed to the concave shape seen in other azhdarchids (and an elevated dorsal ridge might be present on the missing dorsal part of the head) (Fig. 3a). The dorsal side of the proximal humerus extends anteriorly beyond the level of the humeral head but the base of the deltopectoral crest is missing on this specimen. This basal region should be distal to a huge pneumatic foramen on the anterior side (length 10.0 mm, width 5.5 mm; Fig. 3a, c) but only the base of the ulnar crest is preserved and directed ventrally, as in other pterodactyloids. Bennett (1989) considered the ventral (=posterior in non-flight position) orientation of the ulnar crest to be a synapomorphy for Ornithocheiroidea (Pteranodontidae + Ornithocheiridae) but this is based on comparison with the holotype of *Bennettazhia oregonensis*, where the ulnar crest is actually missing. The anterior side of this bone is deeply concave between the pneumatic foramen and the base of ulnar crest in dorsoventral section and sinusoidal anteroposteriorly. The opposite posterior side is convex in dorsoventral section and concave anteroposteriorly. The humeral neck is inclined posteriorly to the long axis of the shaft at an angle of $\sim 40^\circ$ while the articular surface of the humeral head overhangs the neck along the posterior side, so it is exposed posteriorly much more than anteriorly (Fig. 3e).

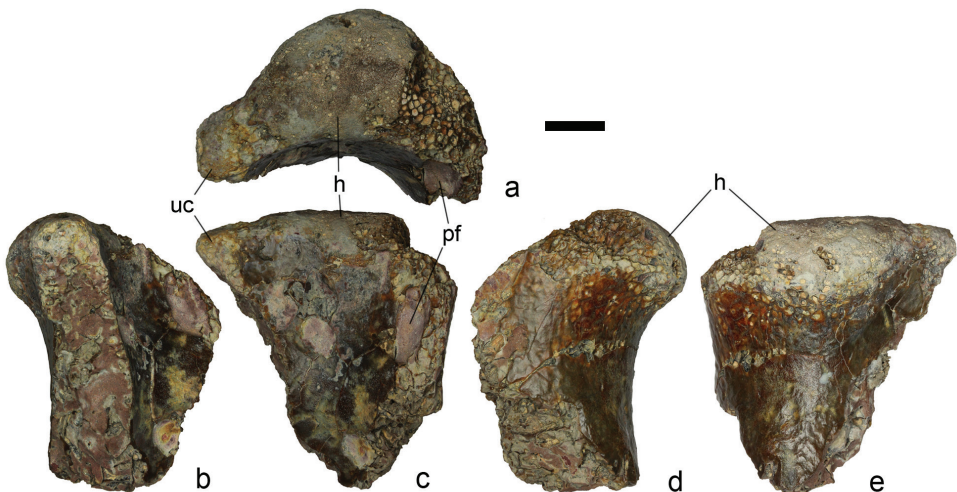


Figure 3. *Aralazhdarcho bostobensis*, ZIN PH 57/43, a proximal fragment of a left humerus in proximal (a), ventral (b), anterior (c), dorsal (d), and posterior (e) views. This specimen is from the Shakh Shakh II locality in the northeastern Aral Sea region of Kazakhstan; Bostobe Formation, Upper Cretaceous (Santonian – lower Campanian). Abbreviations: h, humeral head; pf, pneumatic foramen; uc, ulnar crest. Scale bar is 10 mm.

Paleoenvironments

The northeastern Aral Sea region, which is now in the centre of Asia, was located for most of the Late Cretaceous on the westernmost periphery of the ancient Asian landmass and was bordered by the Turgai Strait which connected Tethys to the Arctic ocean. The Turgai Sea, an infilling of the Turgai Depression north of the Aral Sea, extended north and retreated south several times following fluctuations in sea levels. In particular, the Turgai retreated during the Cenomanian regression but partially returned during the early Turonian transgression (Geology of the USSR 1970; Martinson and Nikitin 1978) (Fig. 4A). The next phase of transgression was in the Santonian to early Campanian when the Turgai Sea extended further north (Figs 4B, 5).

In paleoclimatic reconstructions, the northeastern Aral Sea region is placed at the border of tropical and subtropical climate zones in the Turonian and Santonian (Semikhatov and Chumakov 2004). Abundant remains of crocodyliforms in both the Zhirkindek and Bostobe formations are also good indicators of tropical-to-subtropical climatic conditions (Markwick 1998). Under subtropical or tropical climatic conditions in the Santonian, the western coast of the Asian landmass in this region was likely affected by strong winds, which caused significant aridization of the climate as evidenced by paleobotanical data (see below) on the one hand and steady upwelling of deep sea waters along the coast on the other. We know that the Santonian–early Campanian was a time of intensive phosphorite accumulation in the shallow waters of this region (Fig. 5), including the Aktobe phosphorite basin to the north of the Aral Sea, which occupies 25,000–30,000 km² and has resources of 700 million tons of P₂O₅ (Zhelezko 1987). Because of this high concentration of phosphorus and other minerals elevated from the sea bottom, upwelling areas are “oases of life,” places of high bioproductivity in terms of microorganisms and their consumers: primary (i.e., crustaceans and other marine invertebrates), secondary (fishes), and tertiary (i.e., marine reptiles, mammals, and sea birds). In the modern oceans, upwelling areas occupy only about 5% of total global area but produce about 25% of all fisheries (Jennings et al. 2001). There is no doubt that upwelling areas were also important in the Mesozoic. The Aktobe area produces numerous phosphatized shark teeth and fish bones (Zhelezko 1987), as well as remains of marine reptiles. Such abundant fish resources likely attracted pterosaurs that may have spent some of their time around the coast line (Fig. 5).

Localities within the Zhirkindek and Bostobe formations also contain the abundant remains of a few species of chondrichthians, amongst which the most common are hybodontiform sharks (*Hybodus kansaiensis* and *Polyacrodus* sp.) and the rhinobatoid skate *Myledaphus glickmani* (Nesov and Mertinene 1986; Nesov 1988a, 1997; Nesov and Khisarova 1988). Nesov considered this to be evidence that these accumulation basins were estuaries. Hybodontiform sharks and *Myledaphus* are common in Late Cretaceous fluvial deposits (Estes 1964; Peng et al. 2001; Neuman and Brinkman 2005) and it cannot be excluded that these taxa may have also entered freshwater rivers. Indeed, the presence of the marine lamnoid sharks *Protolamna* sp. and *Cretodus*

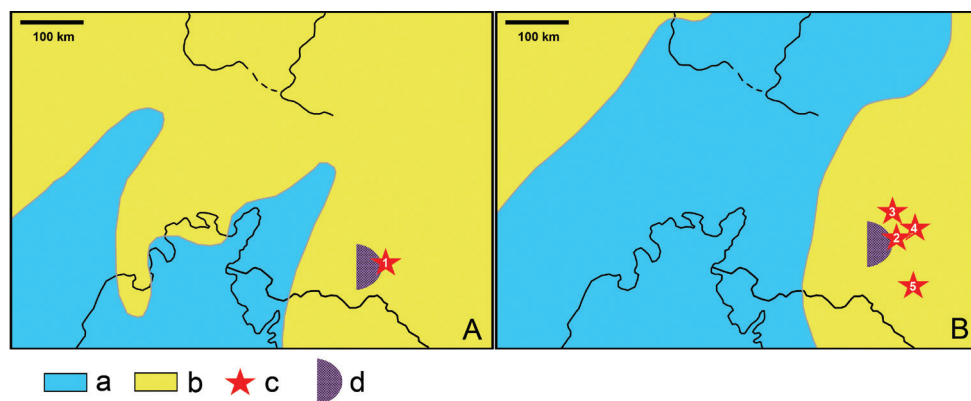


Figure 4. Relative positions of known pterosaur localities of the northeastern Aral Sea region of Kazakhstan in Turonian (**A**) and Santonian (**B**) times. These paleogeographic maps are modified from Martinson and Nikitin (1978). Legend: a, sea; b, land; c, pterosaur locality (1 Tyulkili; 2 Baibishe; 3 Akkurgan; 4 Buroinak; 5 Shakh-Shakh); d, estuarine paleoenvironment indicated by marine sharks.

longiplicatus within certain parts of the Zhirkindek Formation at the Tyulkili section clearly indicates ingress of sea waters in the basin. In the Bostobe Formation the Baibishe locality has the highest diversity of chondrychthians and includes taxa not found in other Bostobe localities (*Scapanorhynchus* sp., *Ischyrrhiza* sp., *Protoplatyrhina* sp., *Ptychotrigon* sp.). Among these taxa, the sclerorhynchid skate *Ischyrrhiza* may also occur in fluvial deposits (Estes 1964; Peng et al. 2001) and the mitsukurinid lamnoid shark *Scapanorhynchus* also occurs in the fluvial Turonian Bissekty Formation of the Kyzylkum Desert, Uzbekistan (unpublished data). Modern goblin sharks (*Mitsukurina*) are deep water (mesopelagic) species (Yano et al. 2007) yet their closest extinct relative *Scapanorhynchus* is common in near shore Late Cretaceous deposits (Arambourg 1952; Bardet et al. 2000; Kennedy et al. 2008). Our view is that the Baibishe locality likely formed in an estuarine basin while the other known Bostobe Formation vertebrate localities are of fluvial origin (Dyke and Malakhov 2004).

The mollusc fauna of the Zhirkindek and Bostobe formations consists of few unidentified gastropods along with numerous and diverse bivalves. The majority of the bivalves (19 species) belong to two orders, Unionida and Trigoniida, with a single species belonging to the order Veneroidei. Unionida are a numerous and widely distributed group well-represented in modern faunas, while the Trigoniida were more diversified and successful in the past. Just the single trigoniid genus *Neotrigonia* occurs today along with a few species of marine clams that inhabit the Australian coast from below tide level to at least 400 m water depth (Stanley 1984). The single veneroidean species, *Limnocyrena tasanica*, is from the Cyrenoididae, which is represented in the modern fauna by brackish water species, like the Florida marsh clam, *Cyrenoida floridana*, which lives in Florida Bay estuaries under salinity of 0–18‰ (Brewster-Wingari and Ishman 1999). The *Pseudohyria-Sainshandia-Limnocyrena* association found in the Zhirkindek Formation is widely distributed in north China in formations of Campanian-Maastrichtian age (Ma 1994).

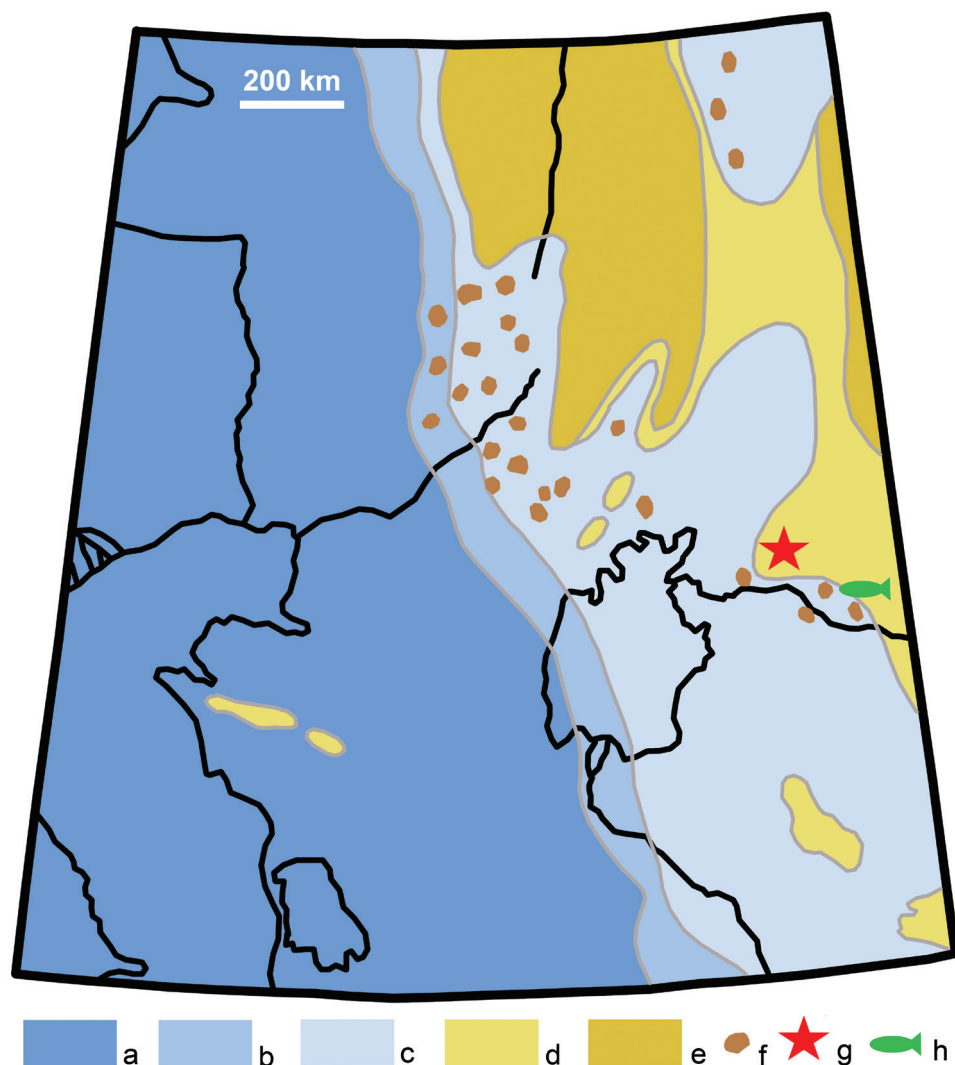


Figure 5. Paleogeographic map of western Kazakhstan in the Santonian-Campanian, modified and simplified from Sagunov and Tkachev (1975: fig. 23). Legend: a, deep water sea; b, shelf; c, shallow water sea; d, lowland coastal plain; e, elevated land; f, area of phosphate accumulation; g, pterosaur locality; h, clupeomorph locality (Taldysai).

In the paleontological literature Cretaceous trigoniid molluscs, generally referred to as Trigonioidea, are usually described as being freshwater (Martinson 1957; Tumpeesuwan et al. 2010) or non-marine in their mode-of-life (Martinson 1990a, b, 1997; Ma 1994; Chen et al. 2006; Komatsu et al. 2007; Sha 2007, 2010). This is interesting because the only living genus of the group, *Neotrigonia*, is marine (see above). Martinson (1957) thought that large, thick-shelled and sculptured *Trigonioides*

and *Sainshandia* lived in habitats transitional between freshwater and marine, most likely in lagoons. Based on its shell microstructure, Kolesnikov (1977) concluded that *Pseudohyria* (known from lower and upper Cretaceous deposits in Mongolia) lived in shallow areas of large lakes that had increased salinity and alkalinity in a warm and arid climate. However, according to Martinson (1982), fossil trigoniid molluscs were psammophilous, living in sandy ground in the highly energetic tidal zone of large lakes. Indeed, the thick and sculptured shells of trigoniid bivalves are reminiscent of marine bivalves which live in the marine tidal zone. Their massive sculptured shells may also be due to the large amounts of free calcium available in arid tropical and subtropical basins. These bivalves dominated in such energetic environments while gastropods are very rare; this latter group tend to be much more common in shallow bays that have lower energy waters (Martinson 1982, 1990a). This possible correlation might explain the rarity of fossil gastropod remains in the Zhirkindek and Bostobe formations.

The flora of the Turonian Zhirkindek Formation at the Kankazgan [=Tyulkili] locality is dominated by conifers alongside less abundant angiosperms and ferns (Shilin 1998). In contrast, the known flora at Klarakumzholy (within the same Formation) is dominated by angiosperms and a few ferns while conifers are so far absent (Shilin 2008). This association of conifers, ferns and angiosperms is characteristic of estuarine marshy environments in western Europe (Coiffard et al. 2012) but other gymnosperms are also common. An estuarine marshy paleoenvironmental interpretation for the Kankazgan locality is likely and is supported by the discovery of the marine shark *Cretodus longiplicatus*. This locality was close to the coastline in the Turonian (Fig. 4b), while Klarakumzholy, located at the eastern end of Tyulkili hills, was more inland, and its floral composition with angiosperms and ferns corresponds to Cenomanian-Santonian floodplain environments in western Europe (Coiffard et al. 2012).

According to Shilin and Romanova (1978: tab. 1) at two plant localities within the Santonian – early Campanian Bostobe Formation, Shakh Shakh and Taldysai, the flora consists only of conifers (24.2% from 227 specimens) and angiosperms (75.8%). The absence of ferns, cycads and ginkgo is striking (Shilin 1971) although both these groups were later reported in the Shakh Shakh-Taldysai floral stage (Shilin 1998). In the Cretaceous of western Europe the association of abundant conifers and angiosperms is only characteristic of Cenomanian brackish marsh environments (Coiffard et al. 2012), alongside other abundant gymnosperms. We note that Taldysai is located in the Zhezkazgan-Sarysu Depression (Fig. 5h) and has also yielded the abundant remains of trigonoiid bivalves, insects, possible euryhaline herrings referred to *Diplo-mystus* (Khisarova 1972, 1974) (best classified as *Clupeomorpha* indet.; Grande 1985), and bird feathers (Shilin and Romanova 1978: pl. 26, figs 5-7; Nesov 1992a). All this is consistent with a brackish marsh paleoenvironmental interpretation.

The known flora of the Bostobe Formation (Shakh Shakh and Taldysai) includes 8 species of ferns and 40 species of angiosperms (Shilin 1971; Shilin and Romanova 1978). Of these, the angiosperms are represented by narrow-leaved and small-leaved deciduous and subtropical trees and shrubs. The Santonian-Campanian flora of this region differs from the Turonian flora discussed above because of the absence (or

rarity) of cycads and absence of large-leaved angiosperm which might indicate more arid conditions (Shilin and Romanova 1978). Increased aridization in this region is corroborated by pollen samples from these Santonian-Campanian deposits which contain abundant xerophyllous taxa (Shilin and Romanova 1978).

Conclusions

All so far identifiable pterosaur remains from the Zhirkindek and Bostobe formations of Kazakhstan appear, based on present evidence, to belong to Azhdarchidae (although many specimens, as we have reviewed, are very incompletely preserved): *Azhdarcho* sp. is known from the Zhirkindek Formation while *Aralazhdarcho bostobensis* (and *Samrukia nessovi*) are known from the Bostobe Formation. As noted, and despite a large size difference, the possibility remains that *Samrukia nessovi* is a synonym of *Aralazhdarcho bostobensis*. Based on other palaeontological and palynological evidence, we suggest that the azhdarchid pterosaurs from the Tyulkili locality (Zhirkindek Formation) lived in a tropical-to-subtropical relatively humid climate on the shore of an estuarine basin connected to the Turgai Sea. Evidence from bivalves and the presence of marine sharks (*Cretodus* and *Protolamna*) supports the argument that this basin was subject to periodic influxes of sea water and at times reached normal marine salinity. The flora is dominated by thermophilous conifers and less abundant ferns and angiosperms which indicate an estuary marsh paleoenvironment. The azhdarchids from the Bostobe Formation lived on the coastal fluvial plain along the Turgai Sea. Most localities (Akkurgan, Buroinak, and Shakh Shakh) were formed in a floodplain environment but the sediments at the Baibishe locality were formed in a brackish-water estuary as indicated by a greater diversity of chondrichthians and brackish-water bivalves. The shallow waters near this coastal flood plain were a place of intensive phosphate accumulation due to upwelling conditions caused by strong winds from the ancient Asian landmass. These winds were also the reason for significant aridization during the Santonian and early Campanian, which is evident from paleobotanical data. We speculate that pterosaurs may have been attracted to this area by an abundance of resources in the highly bioproductive estuaries and nearshore upwelling waters.

Acknowledgements

AA thanks Jiang Shunxing (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China), John Scanella (Museum of the Rockies, Bozeman, USA), Eberhard Frey (Staatliches Museum für Naturkunde, Karlsruhe, Germany), and Hans-Dieter Sues (United States National Museum, Smithsonian Institution, Washington, USA) for access to pterosaur specimens. AA is also grateful to Philipp Trikolidi (A.P. Karpinsky Russian Geological Research Institute, Saint Petersburg, Russia) for help with geological literature. We thank S. Christopher Bennett (Department of Biologi-

cal Sciences, Fort Hays State University, Hays, USA) for reading an earlier version of the paper and comments. We thank Junchang Lü (Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China) for reviewing the paper. This work was supported by the Russian Scientific Fund project 14-14-00015, University College Dublin and Chris and Clare Leonard (Dublin, Ireland).

References

- Arambourg C (1952) Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). Notes et Mémoires du Service Géologique du Maroc 92: 1–372.
- Averianov AO (2004) New data on Cretaceous flying reptiles (Pterosauria) from Russia, Kazakhstan, and Kyrgyzstan. *Paleontological Journal* 38: 426–436.
- Averianov AO (2007a) New records of azhdarchids (Pterosauria, Azhdarchidae) from the Late Cretaceous of Russia, Kazakhstan, and Central Asia. *Paleontological Journal* 41: 189–197. doi: 10.1134/S0031030107020098
- Averianov AO (2007b) Theropod dinosaurs from the Late Cretaceous of North-East Aral Sea area, Kazakhstan. *Cretaceous Research* 28: 532–544. doi: 10.1016/j.cretres.2006.08.008
- Averianov AO (2008) [Superorder Pterosauria]. In: Ivakhnenko MF, Kurochkin EN (Eds) *Fossil Vertebrates of Russia and Adjacent Territories Fossil Reptiles and Birds Part 1*. GEOS, Moscow, 319–342.
- Averianov AO (2009) [Ankylosaur (Ornithischia, Ankylosauridae) humerus from the Late Cretaceous of Kazakhstan]. In: Shishkin MA, Tverdokhlebov VP (Eds) [Researches on paleontology and biostratigraphy of ancient continental deposits (Memories of Professor Vitalii G Ochev)]. Nauchnaya Kniga Publishers, Saratov, 78–80.
- Averianov AO (2010) The osteology of *Azhdarcho lancicollis* Nessov, 1984 (Pterosauria, Azhdarchidae) from the Late Cretaceous of Uzbekistan. *Proceedings of the Zoological Institute RAS* 314: 264–317. http://www.zin.ru/journals/trudyzin/doc/vol_314_3/TZ_314_3_Averyanov.pdf
- Averianov AO, Archibald JD, Dyke GJ (2014) A new eutherian mammal from the Late Cretaceous of Kazakhstan. *Acta Palaeontologica Polonica* 59: 537–542. doi: 10.4202/app.2011.0143
- Averianov AO, Sues H-D (2009) First record of a basal neoceratopsian dinosaur from the Late Cretaceous of Kazakhstan. *Acta Palaeontologica Polonica* 54: 553–556. doi: 10.4202/app.2008.0079
- Averianov AO, Sues H-D (2012) Correlation of Late Cretaceous continental vertebrate assemblages in Middle and Central Asia. *Journal of Stratigraphy* 36: 462–485.
- Bakhurina NN, Unwin DM (1995) A survey of pterosaurs from the Jurassic and Cretaceous of the former Soviet Union and Mongolia. *Historical Biology* 10: 197–245. doi: 10.1080/10292389509380522
- Bardet N, Cappetta H, Pereda Suberbiola X, Mouty M, Al Maleh AK, Ahmad AM, Khrata O, Gannoum N (2000) The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. *Geological Magazine* 137: 269–290. doi: 10.1017/S0016756800003988

- Bazhanov VS (1972) [First Mesozoic Mammalia (*Beleutinus orlovi* Bashanov) from the USSR]. *Teriologiya*, 74–80.
- Bennett SC (1989) A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology* 63: 669–677.
- Bennett SC (2001) The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon*. Part I. General description and osteology. *Palaeontographica, Abteilung A: Paläozoologie, Stratigraphie* 260: 1–112.
- Brewster-Wingari GL, Ishman SE (1999) Historical trends in salinity and substrate in Central Florida Bay: A paleoecological reconstruction using modern analogue data. *Estuaries* 22: 369–383. doi: 10.2307/1353205
- Buffetaut E (2011) *Samrukia nessovi*, from the Late Cretaceous of Kazakhstan: A large pterosaur, not a giant bird. *Annales de Paleontologie* 97: 133–138. doi: 10.1016/j.anpal.2011.10.001
- Chen J-H, Komatsu T, Cao M-Z, Stiller F (2006) *Kumamotoa*, an early Late Cretaceous non-marine bivalve, from Fujian, south China. *Journal of Asian Earth Sciences* 27: 943–951. doi: 10.1016/j.jseas.2005.10.002
- Coiffard C, Gomez B, Daviero-Gomez V, Dilcher DL (2012) Rise to dominance of angiosperm pioneers in European Cretaceous environments. *Proceedings of the National Academy of Sciences USA* 109: 20955–20959. doi: 10.1073/pnas.1218633110
- Danilov IG, Sukhanov VB, Syromyatnikova EV (2011) New Asiatic materials on turtles of the family Adocidae with review of the adocid record in Asia. *Proceedings of the Zoological Institute RAS* 315: 101–132.
- Danilov IG, Syromyatnikova EV, Sukhanov VB (2007) [Turtles of the genus *Shachemys* from the Upper Cretaceous of Asia]. In: Rozanov AY, Lopatin AV, Parkhaev PY (Eds) [Modern Paleontology: Classical and Newest Methods]. Paleontological Institute of the Russian Academy of Sciences, Moscow, 59–72.
- Danilov IG, Vitek NS, Averianov AO, Glinskiy VN (in press) A new softshelled trionychid turtle of the genus *Khunnuchelys* from the Upper Cretaceous Bostobe Formation of Kazakhstan. *Acta Palaeontologica Polonica*. doi: 10.4202/app.2013.0045
- Dyke GJ, Malakhov DV (2004) Abundance and taphonomy of dinosaur teeth and other vertebrate remains from the Bostobynskaya Formation, north-east Aral Sea region, Republic of Kazakhstan. *Cretaceous Research* 25: 669–674. doi: 10.1016/j.cretres.2004.06.004
- Efimov MB (1988) [Fossil crocodiles and champsosaurs of Mongolia and USSR]. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* 36: 1–108.
- Estes RD (1964) Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. *University of California Publications in Geological Sciences* 49: 1–180.
- Gardner JD, Averianov AO (1998) Albanerpetontid amphibians from the Upper Cretaceous of Middle Asia. *Acta Palaeontologica Polonica* 43: 453–467.
- Geology of the USSR (1970) West Kazakhstan (Part 1) – Geological Description (Book 1). Nedra, Moscow, 879 pp.
- Glickman LS (1980) [Evolution of Cretaceous and Cenozoic Lamnoid Sharks]. Nauka, Moscow, 248 pp.

- Glickman LS, Mertinene RA, Nesov LA, Rozhdestvensky AK, Khosatzky LI, Yakovlev VN (1987) [Vertebrates]. In: Moskvina MM (Ed.) [Stratigraphy of the USSR Cretaceous System Semivolume 2], 255–262.
- Godefroit P, Alifanov VR, Bolotsky YL (2004) A re-appraisal of *Aralosaurus tuberiferus* (Dinosauria, Hadrosauria) from the Late Cretaceous of Kazakhstan. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 74(supplement): 139–154.
- Godefroit P, Escuillié F, Bolotsky YL, Lauters P (2012) A new basal hadrosauroid dinosaur from the Upper Cretaceous of Kazakhstan. In: Godefroit P (Ed.) Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, 335–358.
- Grande L (1985) Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181: 231–372.
- Horner JR, Weishampel DB, Forster CA (2004) Hadrosauridae. In: Weishampel DB, Dodson P, Osmolska H (Eds) The Dinosauria Second Edition. University of California Press, Berkeley, Los Angeles, London, 438–463. doi: 10.1525/california/9780520242098.003.0023
- Jennings S, Kaiser MJ, Reynolds JD (2001) Marine Fisheries Ecology. Blackwell Science, Oxford, 432 pp.
- Kellner AWA, Langston W Jr. (1996) Cranial remains of *Quetzalcoatlus* (Pterosauria, Azhdarchidae) from Late Cretaceous sediments of Big Bend National Park, Texas. Journal of Vertebrate Paleontology 16: 222–231. doi: 10.1080/02724634.1996.10011310
- Kennedy WJ, King C, Ward DJ (2008) The upper Albion and lower Cenomanian succession at Kolbay, eastern Mangyshlak (southwest Kazakhstan). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 78: 117–147.
- Khisarova GD (1972) [Clupeiformes from the Late Cretaceous deposits of Kazakhstan]. [Session Devoted to the 100 years Anniversary of Academician AA Borissiak]. Paleontological Institute, USSR Academy of Sciences, Moscow, 67–68.
- Khisarova GD (1974) [New species of Cretaceous fishes from Taldysai]. Materialy po Istории Fauny i Flory Kazakhstana 6: 11–14.
- Kolesnikov TM (1977) [Taxonomic specificity of shell microstructure in bivalve mollusks of the genus *Pseudohyria* from the Cretaceous deposits of Mongolia]. Trudy Sovmestnoi Sovetskogo-Mongol'skoi Paleontologicheskoi Ekspeditsii 4: 97–104.
- Komatsu T, Jinhua C, Ugai H, Hirose K (2007) Notes on non-marine bivalve *Trigonioides* (*Trigonioides*?) from the mid-Cretaceous Goshoura Group, Kyushu, Japan. Journal of Asian Earth Sciences 29: 795–802. doi: 10.1016/j.jseas.2006.06.001
- Kordikova EG, Polly DP, Alifanov VR, Rocek Z, Gunnell GF, Averianov AO (2001) Small vertebrates from the Late Cretaceous and Early Tertiary of the northeastern Aral Sea Region, Kazakhstan. Journal of Paleontology 75: 390–400. doi: 10.1666/0022-3360(2001)075<0390:SVFTLC>2.0.CO;2
- Kuznetsov VV (1976) [A fresh-water turtle from the Senonian deposits of North-East Aral Sea area]. Paleontologicheskii Zhurnal 4: 125–127.
- Kuznetsov VV (1977) [Finding of the turtle genus *Basilemys* in the Late Cretaceous of the USSR]. [Questions of Herpetology Abstracts of the Fourth All-Union Herpetological Conference]. Nauka, Leningrad, 124–125.

- Kuznetsov VV, Chkhikvadze VM (1987) [The Late Cretaceous trionychids from Shakh-Shakh locality in Kazakhstan]. *Materialy po Istorii Fauny i Flory Kazakhstana* 9: 33–39.
- Kuznetsov VV, Shilin PV (1983) [Late Cretaceous turtle from Baibishe (North-East Aral Sea region)]. *Izvestiya Akademii Nauk Kazakhskoi SSR, Seriya biologicheskaya* 6: 41–44.
- Ma Q (1994) Nonmarine Cretaceous bivalve assemblages in China. *Cretaceous Research* 15: 271–284. doi: 10.1006/cres.1994.1017
- Malakhov DV, Dyke GJ, King C (2009) Remote sensing applied to paleontology: exploration of Upper Cretaceous sediments in Kazakhstan for potential fossil sites. *Palaeontologia Electronica* 12: 1–10.
- Markwick PJ (1998) Fossil crocodylians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate. *Palaeogeography, Palaeoclimatology, Palaeoecology* 137: 205–271.
- Martinson GG (1957) [Mesozoic freshwater mollusks of several regions of Eastern and Central Asia]. *Trudy Baikal'skoi Limnologicheskoi Stantsii* 15: 262–336.
- Martinson GG (1982) [Late Cretaceous mollusks of Mongolia]. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* 17: 1–84.
- Martinson GG (1990a) [Non-marine malacofauna and its significance for stratigraphy and correlation of Cretaceous deposits]. In: Krasilov VA (Ed.) *Continental Cretaceous of the USSR. Dal'nevostochnoe Otdelenie AN SSSR, Vladivostok*, 8–11.
- Martinson GG (1990b) [Non marine bivalvian mollusks from the Cretaceous deposits of Aral Sea area and Turgai flexure]. *Paleontologicheskii Zhurnal*, 17–24.
- Martinson GG (1997) [Some new species of Cretaceous non-marine mollusks from the continental deposits of Aral Sea region]. *Paleontologicheskii Zhurnal*, 10–13.
- Martinson GG, Nikitin VG (1978) [Stratigraphic position of mollusks from continental deposits of northern and eastern Aral Sea Area]. *Izvestiya Akademii Nauk SSSR, Seriya Geologicheskaya*, 139–142.
- Martinson GG, Nikitin VG, Teplova LS, Vasiliev IV (1966) [Stratigraphy and correlation of Cretaceous continental deposits of Aral Sea area]. *Sovetskaya Geologiya*, 92–103.
- Mertinene RA, Nesov LA (1985) [Hybodont sharks from the Cretaceous of Middle Asia]. *Doklady Akademii Nauk Tadzhikskoi SSR* 28: 588–592.
- Naish D, Dyke GJ, Cau A, Escuillié F, Godefroit P (2012) A gigantic bird from the Upper Cretaceous of Central Asia. *Biology Letters* 8: 97–100. doi: 10.1098/rsbl.2011.0683
- Nesov LA (1984) [Pterosaurs and birds from the Late Cretaceous of Middle Asia]. *Paleontologicheskii Zhurnal*, 47–57.
- Nesov LA (1986) Some late Mesozoic and Paleocene turtles of Soviet Middle Asia. *Studia Geologica Salamanticensia, Studia Palaeocheloniologica* 2: 7–22.
- Nesov LA (1988a) [Assemblages of late Mesozoic and Paleocene vertebrates of Middle Asia]. In: Bogdanova TN, Oshurkova MV (Eds) [Formation and Evolution of the Continental Biotas]. *Izdatelstvo Nauka, Leningrad*, 93–101.
- Nesov LA (1988b) [New Cretaceous and Paleogene birds of Soviet Middle Asia and Kazakhstan and environments]. *Trudy Zoologicheskogo Instituta AN SSSR* 182: 116–123.
- Nesov LA (1988c) [Traces of vital functions of organisms of the Late Mesozoic - Paleocene of Middle Asia and Kazakhstan as indicators of the ancient vertebrates biotops]. In: Bogda-

- nova TN, Khozatsky LI, Ishchenko AA (Eds) [Fossil Traces of Vital Activity and Dynamics of the Environment in Ancient Biotopes]. Naukova Dumka, Kiev, 76–90.
- Nesov LA (1990) [Flying reptiles of the Jurassic and Cretaceous of the USSR and significance of their remains for the paleogeographic environmental reconstruction]. Vestnik Leningradskogo Universiteta, Seriya 7: Geologiya, Geografiya 4(28): 3–10.
- Nesov LA (1992a) Mesozoic and Paleogene birds of the USSR and their paleoenvironments. In: Campbell KE Jr (Ed.) Papers in Avian Paleontology Honoring Pierce Brodkorb. Los Angeles County Museum, Los Angeles, 465–478.
- Nesov LA (1992b) [Review of localities and remains of Mesozoic and Paleogene birds of the USSR and the description of new findings]. Russkii Ornitologicheskii Zhurnal 1: 7–50.
- Nesov LA (1993) [New Mesozoic mammals of Middle Asia and Kazakhstan and comments about evolution of theriofaunas of Cretaceous coastal plains of Asia]. Trudy Zoologicheskogo Instituta RAN 249: 105–133.
- Nesov LA (1995) [Dinosaurs of Northern Eurasia: New Data about Assemblages, Ecology and Paleobiogeography]. Izdatel'stvo Sankt-Peterburgskogo Universiteta, Saint Petersburg, 156 pp.
- Nesov LA (1997) [Cretaceous Nonmarine Vertebrates of Northern Eurasia] (Posthumous edition by LB Golovneva and AO Averianov). Izdatel'stvo Sankt-Peterburgskogo Universiteta, Saint Petersburg, 218 pp.
- Nesov LA, Kaznyshkin MN (1983) [New sturgeons of the Cretaceous and Paleogene of the USSR]. [Problems of Modern Paleichthyology]. Moscow, 68–76.
- Nesov LA, Khisarova GD (1988) [New data about Upper Cretaceous vertebrates from Shakh-Shakh and Baibolat localities (North-Eastern Aral area)]. Materialy po Istorii Fauny i Flory Kazakhstana 10: 5–14.
- Nesov LA, Mertinene RA (1986) [Remains of chondrichthyan fishes from the Cretaceous of Middle Asia and Kazakhstan as a source of information on the age and origin of the deposits]. In: Krymgoltz GY, Belenkova VS (Eds) Paleontology and Detailed Stratigraphic Correlation. Izdatel'stvo Nauka, Leningrad, 35–41.
- Neuman AG, Brinkman DB (2005) Fishes of the fluvial beds. In: Currie PJ, Koppelhus EB (Eds) Pterosaurs Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed. Indiana University Press, Bloomington, Indianapolis, 167–185.
- Nikiforova KV (1960) [Cenozoic of Golodnaya Steppe of Central Kazakhstan]. Trudy Geologicheskogo Instituta AN SSSR 45: 1–254.
- Norman DB, Kurzanov SM (1997) On Asian ornithopods (Dinosauria: Ornithischia). 2. *Arstanosaurus akkurganensis* Shilin and Suslov, 1982. Proceedings of the Geologists' Association 108: 191–199. doi: 10.1016/S0016-7878(97)80027-2
- Nurumov TN (1964) [On findings of dinosaur remains in Kazakhstan]. In: Terentiev PV (Ed.) [Questions of Herpetology Materials of Herpetological Conference]. Izdatel'stvo Leningradskogo Universiteta, Leningrad, 49–50.
- Peng J-H, Russell AP, Brinkman DB (2001) Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Carnian) of southeastern Alberta: an illustrated guide. Provincial Museum of Alberta, Natural History Occasional Paper 25: 1–54.
- Riabini AN (1948) [Note on a flying reptile from the Jurassic of the Kara-Tau]. Trudy Paleontologicheskogo Instituta AN SSSR 15: 86–93.

- Rozhdestvensky AK (1964) [New data on the localities of dinosaurs on the territory of Kazakhstan and Middle Asia]. Nauchnye Trudy Tashkentskogo Gosudarstvennogo Universiteta Imeni VI Lenina, Seriya Geologiya 234: 227–241.
- Rozhdestvensky AK (1968) [Hadrosaurs of Kazakhstan]. [Upper Paleozoic and Mesozoic Amphibians and Reptiles of the USSR]. Nauka, Moscow, 97–141.
- Rozhdestvensky AK (1970) [About giant ungual phalanges of enigmatic Mesozoic vertebrates]. Paleontologicheskii Zhurnal, 131–141.
- Rozhdestvensky AK (1973) [Study of Cretaceous reptiles in Russia]. Paleontologicheskii Zhurnal, 90–99.
- Rozhdestvensky AK, Khozatsky LI (1967) [Late Mesozoic terrestrial vertebrates of Asiatic part of the USSR]. In: Martinson GG (Ed.) [Stratigraphy and Paleontology of Mesozoic and Paleogene-Neogene Continental Deposits of Asiatic Part of the USSR]. Nauka, Leningrad, 82–92.
- Sagunov VG, Tkachev VR (1975) [Phosphorite bearing deposits of West Kazakhstan]. Nauka, Alma-Ata, 143 pp.
- Semikhatov MA, Chumakov NM (2004) [Climate in the Epochs of Major Biospheric Transformations]. Trudy Geologicheskogo Instituta RAN 550: 1–299.
- Sha J (2007) Cretaceous trigoniodid (non-marine Bivalvia) assemblages and biostratigraphy in Asia with special remarks on the classification of Trigoniodacea. Journal of Asian Earth Sciences 29: 62–83. doi: 10.1016/j.jseaes.2006.01.003
- Sha J (2010) Historical distribution patterns of trigoniodids (non-marine Cretaceous bivalves) in Asia and their palaeogeographic significance. Proceedings of the Royal Society B: Biological Sciences 277: 277–283. doi: 10.1098/rspb.2009.0936
- Sharov AG (1971) [New flying reptiles from the Mesozoic of Kazakhstan and Kirghizia]. Trudy Paleontologicheskogo Instituta AN SSSR 130: 104–113.
- Shilin PV (1971) [Flora from the Senonian deposits of North-East Aral Sea region and South of Central Kazakhstan]. Materialy po Istorii Fauny i Flory Kazakhstana 5: 86–96.
- Shilin PV (1982) [Characteristic of Turonian and Senonian floras of Lower Syr-Dar'ya Uplift (Southern Kazakhstan)]. Materialy po Istorii Fauny i Flory Kazakhstana 8: 113–121.
- Shilin PV (1983) [Late Cretaceous floras of Lower Syr-Darya Uplift]. Paleontologicheskii Zhurnal, 105–112.
- Shilin PV (1986) [Late Cretaceous floras of Kazakhstan]. Nauka, Alma-Ata, 176 pp.
- Shilin PV (1998) Cretaceous flora of Tyulikili, Northeastern Priaralye, Kazakhstan. In: Lucas SG, Kirkland JI, Estep JW (Eds) Lower and Middle Cretaceous Terrestrial Ecosystems. New Mexico Museum of Natural History and Science Bulletin 14: 95–103.
- Shilin PV (2008) Upper Cretaceous flora of Karakumzholy, Northeastern Aral Region. Paleontological Journal 42: 1405–1409. doi: 10.1134/S0031030108120046
- Shilin PV, Romanova EV (1978) [Senonian floras of Kazakhstan]. Nauka, Alma-Ata, 177 pp.
- Shilin PV, Suslov YV (1982) [Hadrosaur from North-Eastern Aral Sea area]. Paleontologicheskii Zhurnal, 131–135.
- Skutschas PP (2013) Mesozoic salamanders and albanerpetontids of Middle Asia, Kazakhstan, and Siberia. Palaeobiodiversity and Palaeoenvironments 93: 441–457. doi: 10.1007/s12549-013-0126-8
- Sokolov MI (1978) [Shark teeth as guide fossils for zonal partition of the Cretaceous deposits of Turan Platform]. Nedra, Moscow, 60 pp.

- Stanley SM (1984) *Neotrigonia*, the sole surviving genus of the Trigoniidae (Bivalvia, Mollusca). In: Eldredge N, Stanley SM (Eds) Living Fossils. Springer, New York, Berlin, Heidelberg, Tokyo, 243–246. doi: 10.1007/978-1-4613-8271-3_30
- Storrs GW, Efimov MB (2000) Mesozoic crocodyliforms of north-central Eurasia. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN (Eds) The Age of Dinosaurs in Russia and Mongolia. Cambridge University Press, Cambridge, 402–419.
- Suslov YV (1982) [Ungual phalanges of dromaeosaurid from the Late Cretaceous deposits of Kzyl-Orda Province]. Materialy po Istorii Fauny i Flory Kazakhstana 8: 5–16.
- Syromyatnikova EV, Danilov IG (2009) New material and a revision of turtles of the genus *Adocus* (Adocidae) from the Late Cretaceous of Middle Asia and Kazakhstan. Proceedings of the Zoological Institute of the Russian Academy of Sciences 313: 74–94.
- Syromyatnikova EV, Danilov IG (2013) New material and phylogenetic position of *Adocus bostobensis*, a poorly known adocid turtle from the Late Cretaceous of Kazakhstan. Proceedings of the Zoological Institute RAS 317: 195–201.
- Tumpeesuwan S, Sato Y, Nakhapadungrat S (2010) A new species of *Pseudohyria* (*Matsumotoina*) (Bivalvia: Trigonioidoidea) from the Early Cretaceous Sao Khua Formation, Khorat Group, Northeastern Thailand. Tropical Natural History 10: 93–106.
- Underwood CJ, Goswami A, Prasad GVR, Verma O, Flynn JJ (2011) Marine vertebrates from the ‘middle’ Cretaceous (early Cenomanian) of South India. Journal of Vertebrate Paleontology 31. doi: 10.1080/02724634.2011.574518
- Unwin DM, Bakhurina NN (1994) *Sordes pilosus* and the nature of the pterosaur flight apparatus. Nature 371: 62–64. doi: 10.1038/371062a0
- Unwin DM, Bakhurina NN, Lockley MG, Manabe M, Lü J (1997) Pterosaurs from Asia. Paleontological Society of Korea Special Publication 2: 43–65.
- Vitek NS, Danilov IG (2010) New material and a reassessment of soft-shelled turtles (Trionychidae) from the Late Cretaceous of Middle Asia and Kazakhstan. Journal of Vertebrate Paleontology 30: 383–393. doi: 10.1080/02724631003617548
- Wellnhofer P (1985) Neue Pterosaurier aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien. Palaeontographica, Abteilung A: Palaeozoologie, Stratigraphie 187: 105–182.
- Werner C (1989) Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. Palaeo Ichthyologica 5: 1–112.
- Wiffen J, Molnar RE (1988) First pterosaur from New Zealand. Alcheringa 12: 53–59. doi: 10.1080/03115518808618996
- Yano K, Miya M, Aizawa M, Noichi T (2007) Some aspects of the biology of the goblin shark, *Mitsukurina owstoni*, collected from the Tokyo Submarine Canyon and adjacent waters, Japan. Ichthyological Research 54: 388–398. doi: 10.1007/s10228-007-0414-2
- Zanno LE (2010) A taxonomic and phylogenetic re-evaluation of Therizinosauria (Dinosauria: Maniraptora). Journal of Systematic Palaeontology 8: 503–543. doi: 10.1080/14772019.2010.488045
- Zhelezko VI (1987) [Aktyubinsk Phosphorite Basin]. Institut Geologii i Geokhimii, Ural'skii Nauchnyi Tsentr AN SSSR, Sverdlovsk, 51 pp.

Two new species of *Zospeum* Bourguignat, 1856 from the Basque-Cantabrian Mountains, Northern Spain (Eupulmonata, Ellobioidea, Carychiidae)

Adrienne Jochum¹, Anton J. de Winter², Alexander M. Weigand³,
Benjamín Gómez⁴, Carlos Prieto⁵

1 Naturhistorisches Museum der Burgergemeinde Bern, CH-3005 Bern, Switzerland; Institute of Ecology and Evolution, University of Bern, CH-3012 Bern, Switzerland **2** Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands **3** Department of Animal Ecology, Evolution and Biodiversity, Ruhr University Bochum, 44801 Bochum, Germany **4** Department of Zoology, University of the Basque Country (UPV/EHU), 01006-Vitoria, Spain **5** Department of Zoology and Animal Cell Biology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), 48080-Bilbao, Spain

Corresponding author: Adrienne Jochum (Adrienne.jochum@gmail.com)

Academic editor: Eike Neubert | Received 20 December 2014 | Accepted 10 February 2015 | Published 23 February 2015

<http://zoobank.org/71AA2566-F9F6-4368-B35F-D90986BAF643>

Citation: Jochum A, de Winter AJ, Weigand AM, Gómez B, Prieto C (2015) Two new species of *Zospeum* Bourguignat, 1856 from the Basque-Cantabrian Mountains, Northern Spain (Eupulmonata, Ellobioidea, Carychiidae). ZooKeys 483: 81–96. doi: 10.3897/zookeys.483.9167

Abstract

Two new species of the genus *Zospeum* Bourguignat, 1856 are described from caves in the Sierra de Aitzgorri (Gipuzkoa) and the Sierra Salvada (Burgos) in Northern Spain. The taxa *Z. vasconicum* **sp. n.** and *Z. zaldivarae* **sp. n.** have recently, without a formal name, been included in a molecular study of worldwide members of the Carychiidae. In the present paper, the shell morphology and variation of these species is described and illustrated.

Keywords

Cave-dwelling species, subterranean snail, microgastropoda, pseudo-cryptic species, shell variability, ecology, conservation

Introduction

The subterranean genus *Zospeum* Bourguignat, 1856 (Ellobioidea, Carychiidae) encompasses a Palearctic radiation of terrestrial snails. These unpigmented, blind gastropods are amongst the smallest terrestrial gastropods known, with some species barely reaching 1 mm in shell size and inhabiting caves at depths as deep as 950 m (Weigand 2013). *Zospeum* species inhabit moist, muddy cave walls, rock crevices, speleothems and ceilings in the deep recesses of karst caves, far from the entrance zone. Stable environmental conditions such as minimal fluctuations in temperature, humidity, airflow, water levels and the constant influx of organic matter are characteristic for caves harbouring *Zospeum* populations throughout their known Cantabrian, Pyrenean, Southern Alpine and Dinaric distributions. The greatest species diversity is recorded from caves located in the vast karst regions of south-central and south-eastern Europe (see Bole 1974, Pezzoli 1992). The past four decades have witnessed a number of species discoveries in northern Spain, viz., *Zospeum bellesi* Gittenberger, 1973, *Zospeum suarezi* Gittenberger, 1980, *Zospeum biscaiense* Gómez & Prieto, 1983 and Jochum et al. 2012, whereby the oldest Iberian record dates back to the mid 19th century (*Zospeum schaufussi*, von Frauenfeld, 1862). This latter description was long overlooked until first quoted by Giusti (1975). A faunistic overview of the land snails of northern Spain (Altonaga et al. 1994) indicated the existence of four more species (*Zospeum* sp. n. 1–4). So far, these taxa have not been described.

Additional collecting in northern Spain by various workers has yielded extensive new *Zospeum* material, revealing the existence of yet still more taxa. This study is ongoing. In many cases, the considerable variability observed between and within different cave systems precludes easy delimitation of species using shell morphology alone.

In a recent paper, Weigand et al. (2013) addressed the evolution of the worldwide members of the entire family Carychiidae, including a number of Iberian *Zospeum* species. Two of these remain unnamed, yet proved to be molecularly distinct from all Iberian (and other) taxa studied thus far. In order to augment our knowledge of biodiversity in general, and specifically here for Spain, as well as to deposit their DNA sequences in public databases such as GenBank, these taxa will be described and their shell morphology compared to Iberian taxa already known. This concerns the two molecularly flagged, but so far unnamed lineages Z17 and Z18 (morphospecies *Zospeum* sp. 1 and *Zospeum* sp. 2) in Weigand et al. (2013).

Material and methods

Shells were measured as indicated in Figure 1. The number of whorls of each shell was counted according to the method described in Kerney and Cameron (1979). For the species descriptions, shell measurements are expressed as ratios such as SH:SD, HLW:SH, PH:SH, PH:PD, W:*ln*H (coiling tightness, Emberton 2001). Measurements were taken from images obtained by either a Leica DFC420 digital camera

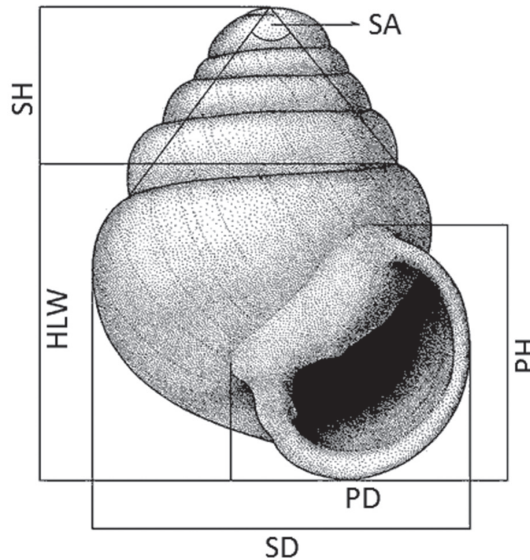


Figure 1. Measurement on *Zospeum* shells in frontal view. Abbreviations: **HLW** height of last whorl **PH** peristome height **PD** peristome diameter **SA** spire angle **SD** shell diameter **SH** shell height.

attached to a Leica M165c stereo microscope, using Leica LAS V4.4 software; or with a Nikon digital camera attached to a Nikon SMZ1500 stereo microscope, using the Nikon DS-L1 analysis image system software for measurements.

We also address a number of qualitative aspects of shell morphology: peristome shape; whorl profile (whorl convexity); regularity of the protoconch; teleoconch sculpture; development of apertural barriers visible in frontal view, including the presence/absence of a deeply immersed denticle/lamella on the parieto-columellar region of the aperture; development of the columellar lamella as discernable in very fresh, transparent shells, or by perforating the body whorl of the adult shell.

Material is housed in the following collections:

- | | |
|----------------------|--|
| AJC | Adrienne Jochum Collection: formerly Institute of Ecology, Evolution & Diversity, Phylogeny & Systematics Collection, Goethe-Universität, Frankfurt am Main, Germany |
| MCBI CSR SASA | Malacological collection of the Biological Institute of the Centre for Scientific Research of the Slovenian Academy of Sciences and Arts in Ljubljana, Slovenia |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid, Spain |
| NMBE | Naturhistorisches Museum der Burgergemeinde Bern, Bern, Switzerland |
| RMNH | Naturalis Biodiversity Center (formerly RijksMuseum van Natuurlijke Historie), Leiden, The Netherlands |

SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany
UPV/EHU-FC	Colección de Fauna Cavernícola (Departamento de Zoología) de la Universidad del País Vasco-Euskal Herriko Unibertsitatea, Bilbao, Spain

Taxonomy

Family Carychiidae Jeffreys, 1830

Genus *Zospeum* Bourguignat, 1856

Zospeum vasconicum Prieto, De Winter, Weigand, Gómez & Jochum, sp. n.

<http://zoobank.org/90EF1F13-9D16-4F08-9398-DCF7CFDE17AA>

Figures 3–5

Zospeum sp. n. 1, Altonaga et al. 1994: 72 (in part).

Zospeum sp. n. 1, Jochum et al. 2012: 402, Fig. 3 A.

Zospeum sp. n. 1, Weigand et al. 2013: 8, Fig. 2.

Material. *Type material.* Holotype (MNCN15.05/60147H): Spain, Prov. Gipuzkoa, Oñate, Valle de Araotz, Cueva de la Ermita de Sandaili, UTM 30TWN4580260906, N42.999442, E-2.438076, alt. c. 400 m, moist, muddy walls in karst cave, 15.11.1984, leg. C. Prieto, B. Gómez & K. Altonaga.

Paratypes: locus typicus: 53 shells (UPV/EHU-FC: 74) and 4 dried snails (UPV/EHU-FC: 75), data as the holotype; 41 shells (UPV/EHU-FC: 549), 18.06.2011, leg. C. Prieto, A. Jochum, A. Weigand, R. Slapnik & J. Valentinčič; 6 shells (MNCN15.05/60147P, ex UPV/EHU-FC: 549), *ibid.*; 6 shells (SMF 341634, *ibid.*), *ibid.*; 6 shells (RMNH.5003914, *ibid.*), *ibid.*; 6 shells (NMBE 529864/6, *ibid.*), *ibid.*; 19 shells (AJC/1864), *ibid.*

Other material. (Fig. 2): Prov. Bizkaia: Yurre, Urkizu, Cueva de Otxas, UTM 30TWN2050081208, N43.183362, E-2.747741, alt. c. 500 m, 18.01.1981, leg. B. Gómez, R. Martín, K. Altonaga, 23 shells (UPV/EHU-FC:24); same locality, 19.06.2011, leg. C. Prieto, A. Jochum, A. Weigand, R. Slapnik & J. Valentinčič, 30 shells (MCBI CSR SASA 40115), *ibid.*, 20 shells (AJC/1867), *ibid.* 11 shells (RMNH.5003916); Mañaria, Cueva de Silibranka-2, UTM 30TWN2741175235, N 43.129357 E -2.662995, alt. 220m, 20.06.2011, leg. C. Prieto, A. Jochum, A. Weigand, R. Slapnik & J. Valentinčič, 80 shells (UPV/EHU-FC:557), *ibid.*, 5 shells (MCBI CSR SASA 40090), *ibid.*, 18 shells (AJC/1851), *ibid.* 10 shells (RMNH.5003915); Dima, Indusi, Cueva del Cráneo, UTM 30TWN2157275145, N43.128736, E-2.734786, alt. c. 400 m, 20.06.2011, leg. C. Prieto, A. Jochum, A. Weigand, R. Slapnik & J. Valentinčič, 13 shells (UPV/EHU-FC:556), *ibid.*, 13 shells (AJC/1853).

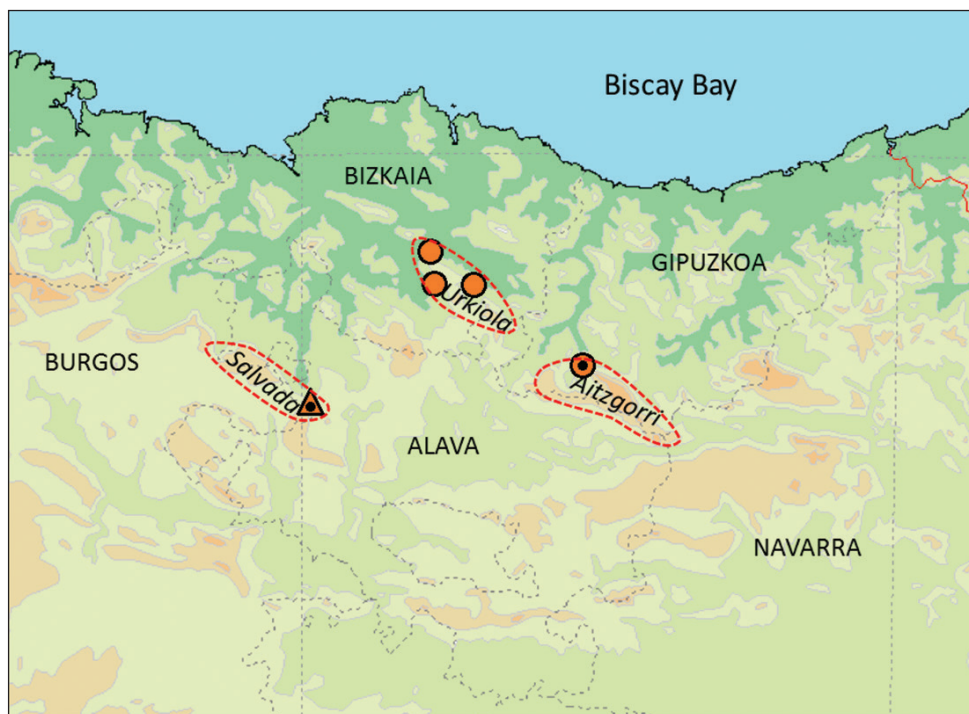


Figure 2. Map indicating geographic position of massifs and caves with *Zospeum* species. Dot in Triangle, *Z. zaldivarae* sp. n.: Cueva de Las Paúles (locus typicus); Dot in circle, *Z. vasconicum* sp. n.: Cueva de la Ermita de Sandaili (locus typicus); Simple orange circles, *Z. vasconicum* sp. n. localities: Cueva de Otxas; Cueva Silibranka-2; Cueva del Cranéo.

Diagnosis. Shell *ca.* 1.2 mm, transparent, elongate or elongate-conical with an entire, roundish and more or less thickened peristome, lacking obvious apertural barriers, but often with an obsolete lamella (denticle) in the parieto-columellar corner; columella with a single, low annular lamella.

Description (material from type locality). Measurements of holotype and paratypes are provided in Table 1.

Shell minute, rather variable in height (on average *ca.* 1.2 mm), conical to elongate-conical with about 5 whorls, regularly coiled, suture deep, whorls convex, more or less strongly shouldered, especially in the more conical shells; teleoconch sculpture of fine, occasionally almost rib-like, axial striae; weak axial ribbing immediately behind the palatal-basal lip, occurring for a short distance; aperture more or less circular; peristome closely adhering to spire, reflected, moderately thickened, roundish, but often somewhat higher than wide or wider than high, taking up *ca.* 40% of shell height; umbilicus closed, umbilical depression deep, with fine or coarser, sometimes almost rib-like, axial striae; apertural barriers absent apart from a rather low lamella (appearing as a tiny denticle) on the parietal-columellar corner, discernable only in oblique

Table 1. Holotype dimensions, and mean, maximum (max), minimum (min), and standard deviation (sd) of shell measurements (see Figure 1) of four populations of *Zospeum vasconicum* sp. n.: Cueva de la Ermita de Sandaili, N=20; Cueva de Otxas, N=11; Cueva Silibranka-2, N=10; Cueva del Cranéo, N=11. SH – shell height, SW – shell width, HLW – height of last whorl, PH – peristome height, PD – peristome diameter, SA – spire angle, W – number of whorls, CT– coiling tightness. SA in degrees, other measurements in mm.

Sandaili	SH	SW	HLW	PH	PD	SA	W	H/D	HLW/H	PH/H	CT	PH/PW
holotype	1.20	0.83	0.77	0.43	0.43	59	4.7	1.45	0.64	0.36	25.78	1.0
mean	1.23	0.84	0.76	0.46	0.46	58	4.95	1.47	0.62	0.37	25.59	1.0
max	1.45	0.92	0.85	0.51	0.53	65	5.5	1.58	0.65	0.41	42.35	1.11
min	1.12	0.77	0.67	0.4	0.4	52	4.6	1.34	0.55	0.34	14.80	0.87
sd	0.07	0.046	0.041	0.035	0.030	3.68	0.228	0.072	0.027	0.023	6.31	0.068
Silibranka												
mean	1.29	0.81	0.73	0.45	0.43	56.3	5.55	1.59	0.57	0.35	22.42	1.04
max	1.38	0.86	0.76	0.51	0.46	60	6	1.71	0.58	0.38	27.10	1.13
min	1.23	0.75	0.67	0.41	0.40	49	5.25	1.52	0.54	0.33	18.71	0.99
sd	0.048	0.033	0.029	0.029	0.018	3.335	0.194	0.054	0.016	0.016	3.068	0.044
Otxas												
mean	1.29	0.80	0.74	0.44	0.45	58.5	5.29	1.61	0.58	0.34	21.04	0.98
max	1.36	0.85	0.82	0.48	0.49	65	5.6	1.70	0.60	0.37	24.44	1.05
min	1.24	0.74	0.68	0.40	0.42	54	5	1.46	0.54	0.32	17.44	0.933
sd	0.046	0.037	0.038	0.025	0.024	3.725	0.194	0.078	0.024	0.017	2.608	0.032
Cranéo												
mean	1.24	0.87	0.80	0.52	0.50	63.1	4.97	1.41	0.64	0.42	23.59	1.05
max	1.28	0.9	0.88	0.62	0.55	68	5	1.48	0.69	0.48	26.23	1.15
min	1.21	0.84	0.75	0.44	0.46	61	4.85	1.38	0.61	0.35	20.25	0.90
sd	0.021	0.018	0.039	0.049	0.027	2.514	0.063	0.032	0.024	0.038	1.742	0.087

apertural view; columella with a single, low annular lamella, only visible in body whorl at some distance from aperture.

Differential diagnosis. Differs from *Z. biscaiense* by the smaller, more elongate shell and the absence of major apertural barriers; from *Z. schaufussi* (*sensu* Gittenberger 1980) by the roundish peristome; *Z. suarezi* is generally smaller, and has a more elaborate, two-tiered arrangement of lamellae on the columella; in *Z. bellesi*, apertural barriers and columellar ornamentation are completely absent.

Etymology. The new species is named after the pre-Roman Era Vascones Tribe (from Latin *gens Vasconum*), which at the arrival of the Romans during the 1st century, inhabited a territory spanning the region between the upper course of the Ebro River and the southern basin of the western Pyrenees. This tribe is considered (disputed) the ancestor of the Basque People.

Distribution. Sierra de Aitzgorri and the adjacent Sierra de Aramotz-Anboto in the Provinces of Gipuzkoa and Bizkaia, Spain (Fig. 2). Both massifs are formed in Lower Cretaceous (Urgonian) limestone bedrock and separated by the valley excavated by the Deba River.

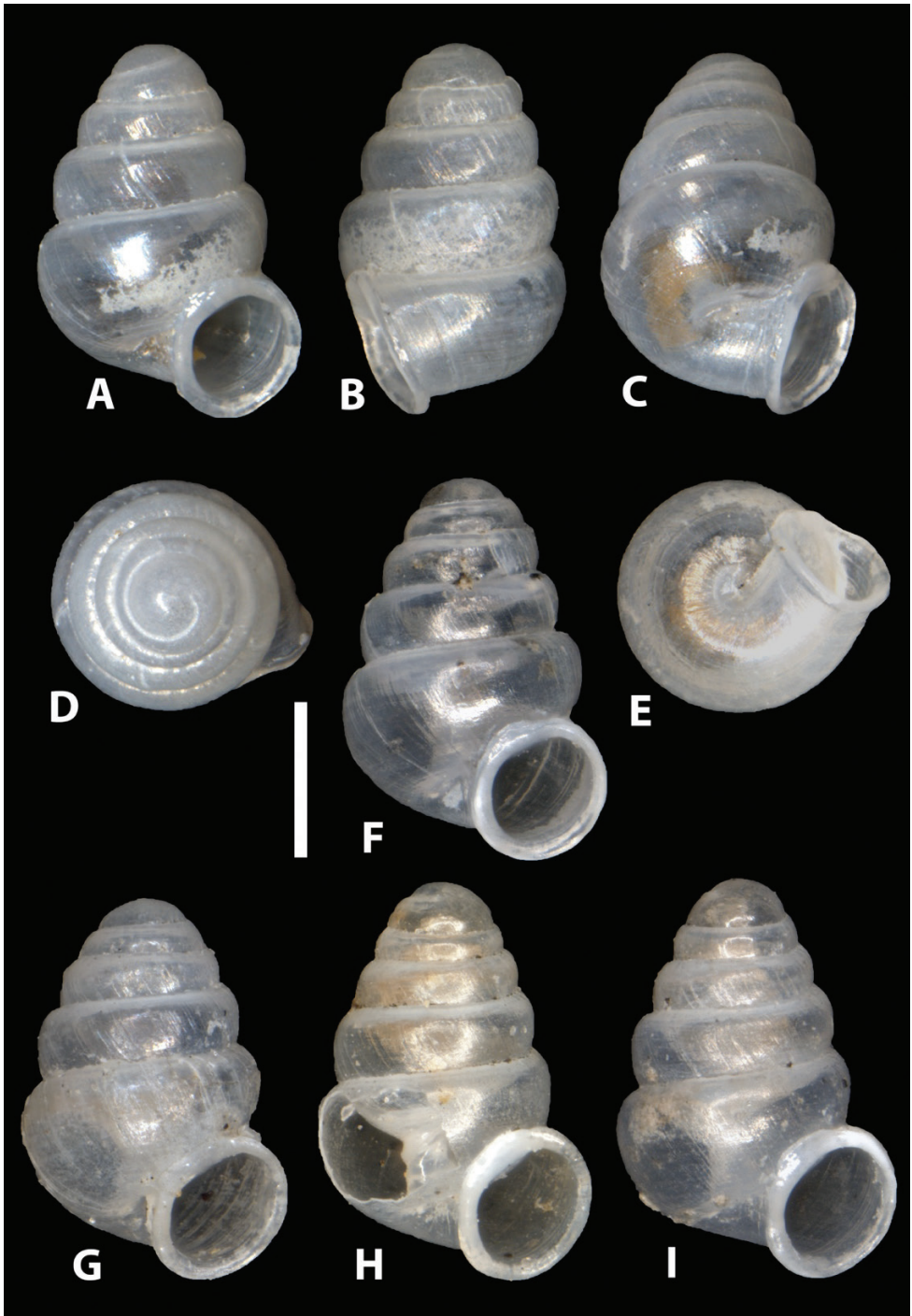


Figure 3. *Zospeum vasconicum* sp. n., **A–E** different views of holotype (MNCN 15.05/60147H) **F–I** paratype shells (MNCN 15.05/60147P) **H** paratype shell with window cut in body whorl exposing columella. Scale bar 0.5 mm.

Ecology. Live *Z. vasconicum* were found in Cueva Arrikutz on densely perforated mats of fine mud lining the walls of the upper level of the cave. In the immediate vicinity of this colony, numerous translucent *Zospeum* shells were found embedded in a thick, uniform layer of mud, superficially interspersed with yellow, clumped strands of fungal aggregations (Fig. 8A–B). Only single live individuals of *Z. vasconicum* were found on the walls of Cueva de la Ermita de Sandaili. No bats or bat guano were seen in the vicinity of the collection site.

Conservation. In the caves where this species occurs (see above), fresh empty shells were found in relative abundance at various spots within these caves, suggesting that the species commonly occurs there, and that these populations are not immediately threatened. Still, on a global scale, its distribution is likely limited to less than 5 caves within a radius of less than 20 km². In conjunction with the categories for the IUCN Red List (IUCN Standards and Petitions Subcommittee 2014), it is considered a vulnerable, narrow range endemic (Vu, D2). Habitat disturbance by unrestricted tourism may pose the largest threat. The cave entrance of Cueva de la Ermita de Sandaili contains a chapel, is openly accessible and is not protected as an entity within a natural park. Neighbouring Cueva Arrikutz belongs to the Natural Park of Aizkorri-Araotz and opened for tourism in June 2007.

Remarks. Although the populations studied in this paper were collected from currently non-contiguous caves, which are geologically part of two adjacent limestone complexes i.e. Otxas, Cráneo and Silibranka-2 of the Aramotz-Anboto massif and Sandaili of the Aizkorri massif, these populations were found to be very closely related, sharing identical or very similar CO1, 16S and H3 sequences (Weigand et al. 2013). However, morphologically, significant differences exist between these populations. Although shell dimensions are quite variable, even within populations, populations differ more or less in shell size and shape (see Table 1). Shells from the type locality and from Cueva del Cráneo, are on average, smaller, significantly less slender, have less whorls and a proportionately larger body whorl than those from Cueva Silibranka-2 and Cueva de Otxas, but the range of some characters overlap. These populations are not different in spire angle and coiling tightness. Shells from Cueva del Cráneo seem to have larger peristomes than specimens from the other caves. Observed are additional qualitative differences between the populations such as in sculptural texture (coarseness of rib-striation; ribbing behind palatal lip present in type locality and Cueva del Cráneo, indistinct or absent in Silibranka-2 and Otxas); whorl profile (topotypic shells have more convex and more strongly shouldered whorls than e.g. the Silibranka-2 population), as well as in the expression of the parieto-columellar denticle (obsolete or absent in Silibranka-2 but generally present in shells from the other caves). In some Cueva de Otxas shells, the peristome is slightly detached from the spire (Fig. 5C). We restrict the type material to (selected) shells from the Cueva de la Ermita de Sandaili. However, material documented by Jochum et al. (2012) from the neighbouring Cueva Arrikutz within the Natural Park of Aizkorri-Araotz, Oñate (N42.997222, W2.428076), is likely also to be *Z. vasconicum*. The nearest passage of the Arrikutz-Gesaltza cave system is less than 150 m from the Cueva de la Ermita de Sandaili on the other side of the river. However, the Arrikutz material was not molecularly assessed by Weigand et al. (2013).

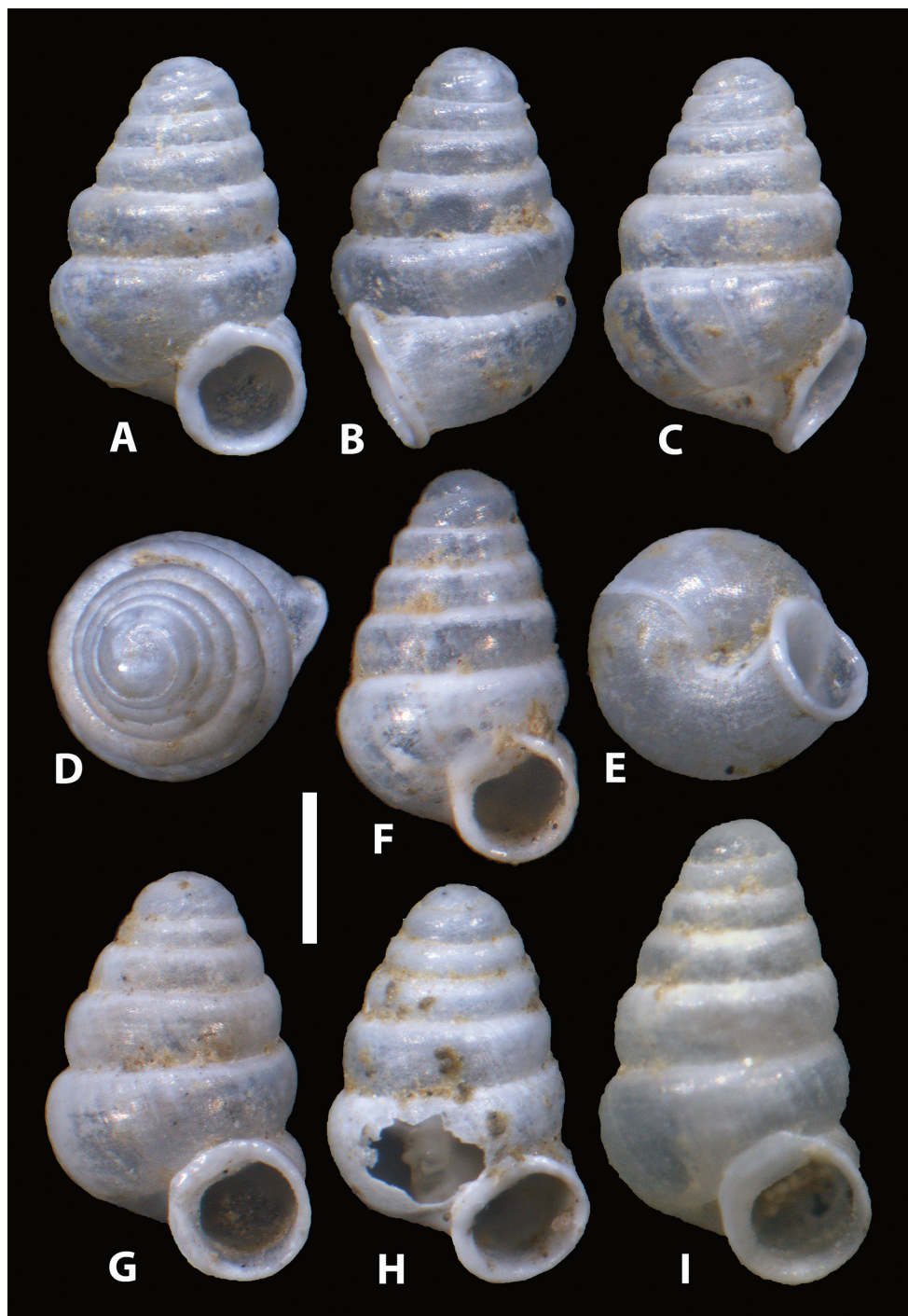


Figure 4. *Zospeum vasconicum* sp. n., **A, F-I** shells from Cueva Silibranka-2 in frontal view (RMNH.5003915) **B-E** different views of specimen **A**; **H** shell with window cut in body whorl exposing columella. Scale bar 0.5 mm.

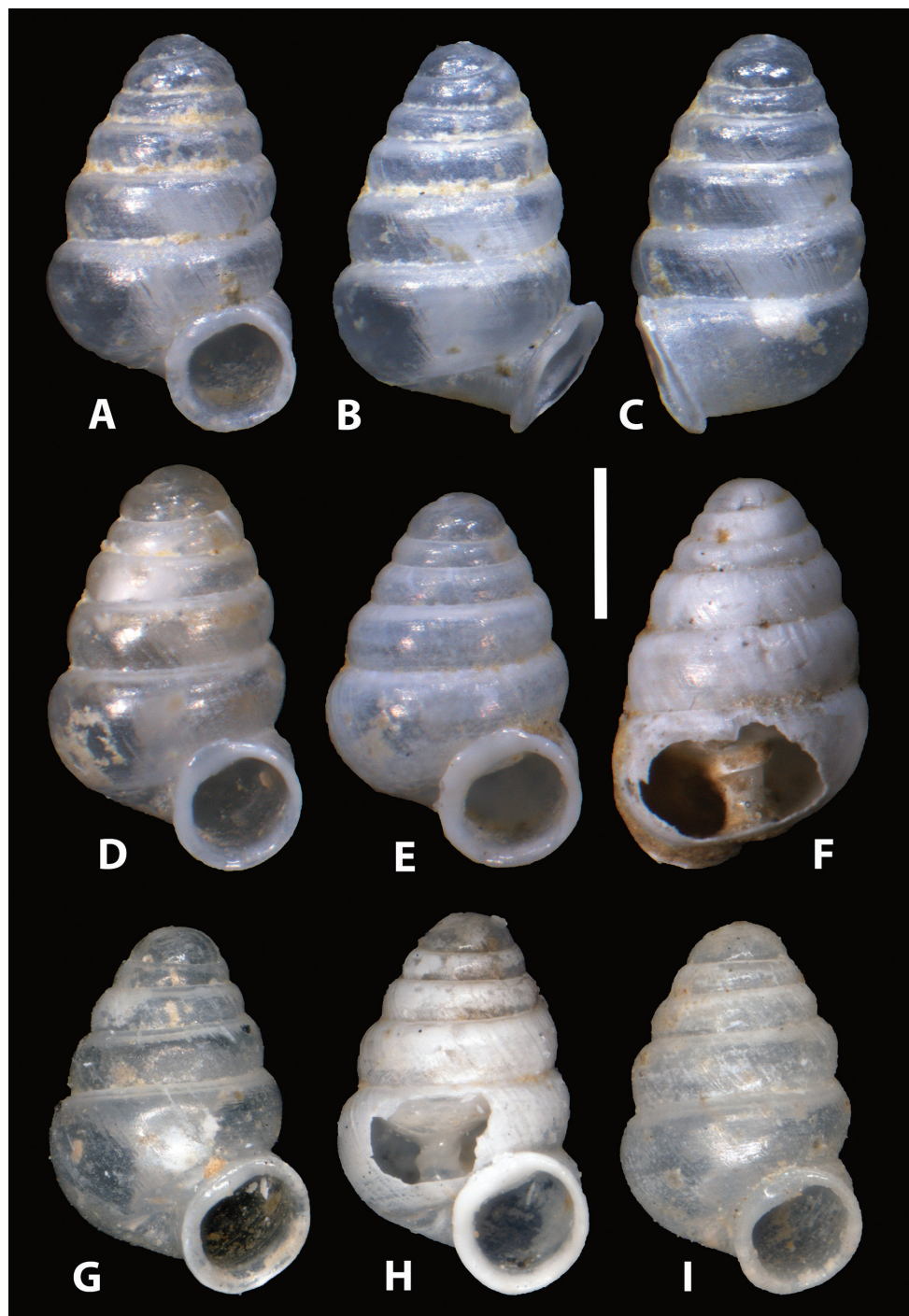


Figure 5. *Zospeum vasconicum* sp. n., Shells from Cueva de Otxas (**A–F** RMNH.5003916); and Cueva del Cranéo (**G–I** UPV/EHU-FC: 556). **B–C** different views of **A**; **F**, **H** shells with window cut in body whorl exposing columella. Scale bar 0.5 mm.

***Zospeum zaldivarae* Prieto, De Winter, Weigand, Gómez & Jochum, sp. n.**

<http://zoobank.org/8C10D84B-0558-443A-87C7-20E499A3963D>

Figures 6–7

Zospeum sp., Prieto and Gómez 1985: 145, Fig. 3 A–B.

Zospeum sp. n. 3, Altonaga et al. 1994: 73 (in part).

Zospeum sp. n. 3, Jochum et al. 2012: 402, Fig. 3 B.

Zospeum sp. 2, Weigand et al. 2013: 8, Fig. 2.

Material. *Type material.* Holotype (MNCN15.05/60148H): Spain, Prov. Burgos, Berberana, Monte de Santiago, Cueva de Las Paúles, UTM 30TWN0062054680, N43.1282, E-2.73618, alt. c. 840 m, moist, muddy walls in karst cave, 09.11.2013, leg. C. Prieto.

Paratypes: locus typicus: 8 specimens (MNCN15.05/60148P ex UPV/EHU-FC:1608) and 2 shells (NMBE 529904/2), 2 shells (SMF 341635) and 2 shells (RMNH.5003943), data as the holotype. 1 shell (UPV/EHU-FC:64), 12.02.1984, leg. P. Zaldívar. 2 shells (MNCN 15.05/60149, ex UPV/EHU-FC:70) and 3 shells (UPV/EHU-FC:72), 11.11.1984, leg. C. Prieto, B. Gómez & P. Zaldívar, 9 specimens (UPV/EHU-FC:559), 21.06.2011, leg. C. Prieto, A. Jochum, A. Weigand, R. Slapnik & J. Valentinčič. 7 specimens + 5 shells (UPV/EHU-FC:560), *ibid.*, 3 specimens molecularly processed (Weigand et al. 2013), 7 shells (4 broken) (AJC/1877), *ibid.*, 5 shells (broken) (MCBI CSR SASA 40598), 11.11.1984, leg. C. Prieto & B. Gómez, 3 shells (RMNH.234152).

Diagnosis. Shell turbate-conical with approximately 5 ½ regularly coiled, convex, rounded whorls, transparent, comparatively large; columellar and palatal-basal lip narrowly reflected; umbilicus closed, umbilical depression deep.

Description. Measurements are provided in Table 2.

Shell minute, turbate-conical, with approximately 5 ½ regularly coiled, convex, rounded whorls; shell transparent when fresh, chalky white with age, comparatively large, rather variable in shape; teleoconch sculpture of irregular axial striae or blunt growth lines, often crossed by an equally superficial spiral element, some distinct axial ribbing may be present for a short distance immediately behind palatal-basal lip; last whorl large and tumid, encompassing *ca.* 2/3 of shell height; aperture lunate; peristome somewhat higher than wide, closely adhering to spire, taking up about half of the shell height, angular, with a thin, straight parietal callus; apertural dentition usually consisting of a small, short lamella on the parietal wall and a tooth on the parietal-columellar corner of the peristome (barely conspicuous in frontal view (Fig. 6A), best discernable in a slightly oblique, apertural view (Fig. 6D)); apertural barriers can however, be entirely absent (Fig. 7D); columella with a single, low, lamella-like dilatation (Fig. 7G), only visible in body whorl at some distance from the aperture.

Differential diagnosis. Though comparatively large amongst Iberian species, the *Z. zaldivarae* shell is minute (shell height *ca.* 1.5 mm) and turbate-conical in form. It is however, larger, wider (*ca.* 1.2 mm) and less elongate than other known Iberian

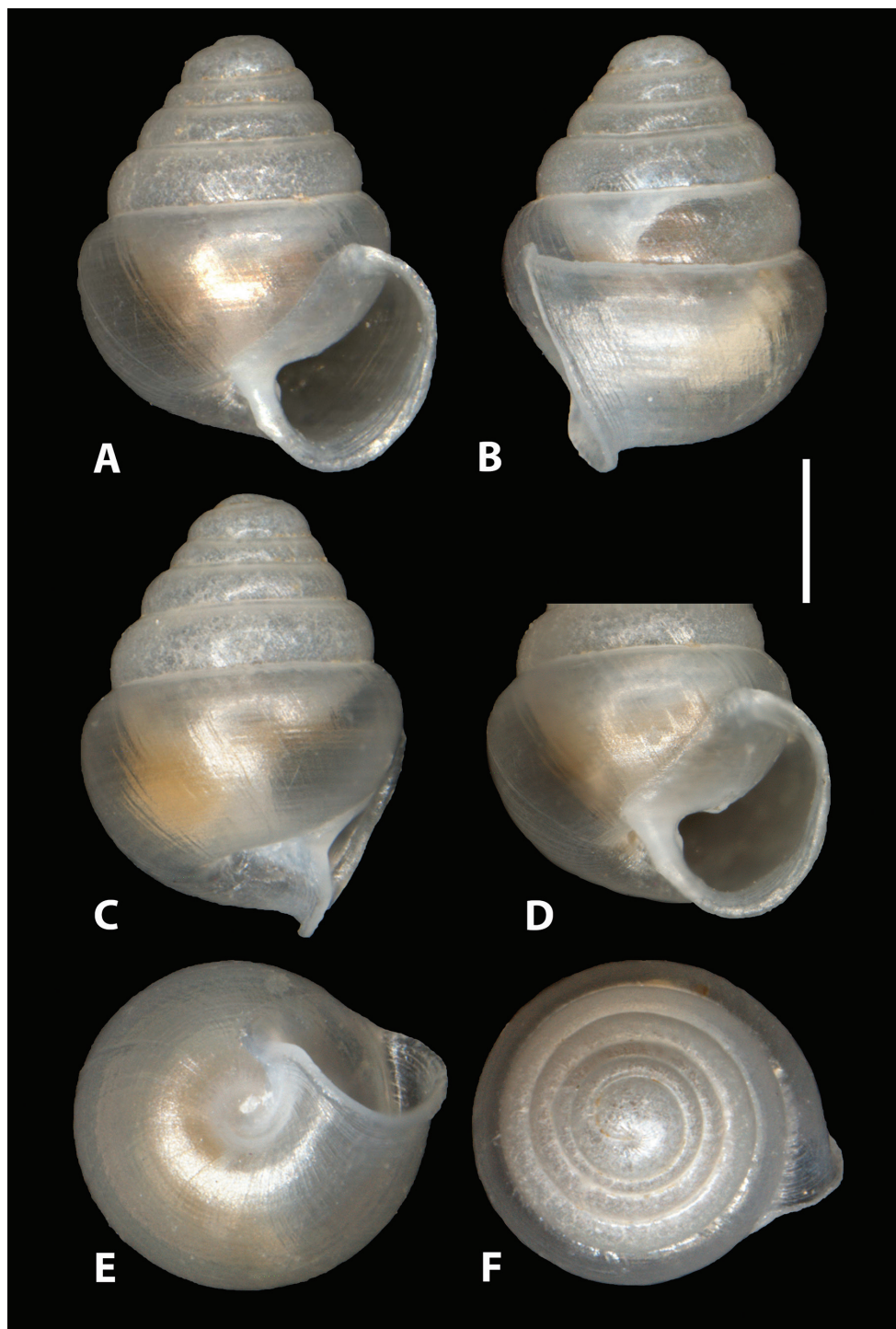


Figure 6. *Zospeum zaldivarae* sp. n., **A, E–F** different views of holotype shell (MNCN 15.05/60148H) **D** aperture in slightly oblique view showing apertural barriers.

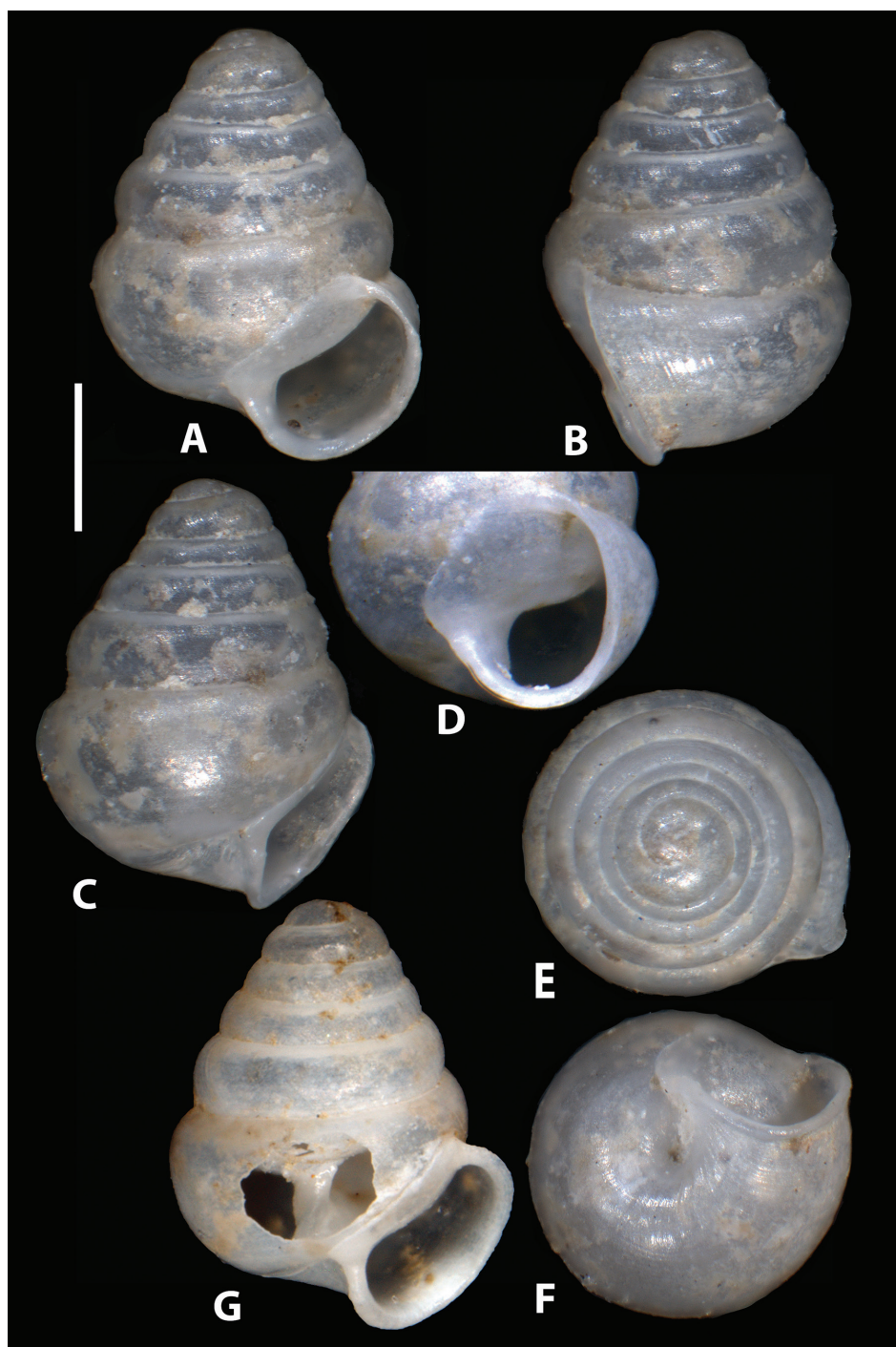


Figure 7. *Zospeum zaldivarae* sp. n., **A–F** different views of edentate paratype shell (RMNH.234152) **D** aperture in oblique view **G** paratype shell (UPV/EHU-FC: 72) with window in body whorl exposing columella.

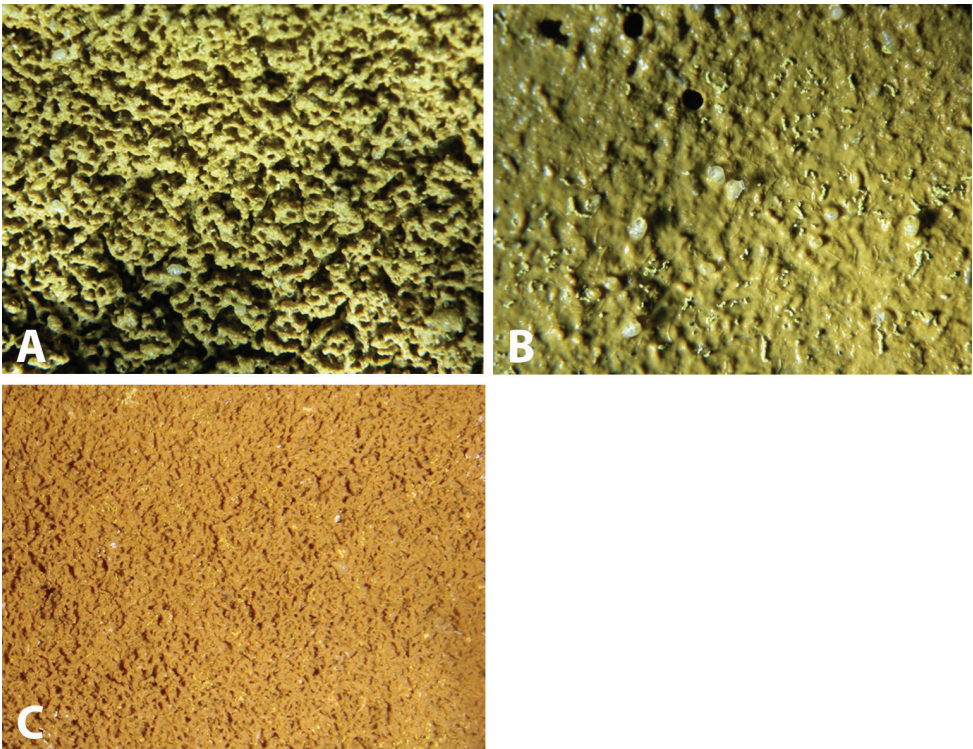


Figure 8. Habitat of *Zospeum* species. **A–B** Moist muddy layer with *Zospeum vasconicum* sp. n. in Cueva Arrikruz; Prov. Gipuzkoa, Natural Park of Aizkorri-Araotz, Oñate **C** Muddy sediment matrix of *Zospeum zaldivarae* sp. n. habitat in Cueva de Las Paúles (locus typicus) with congener (*Z. suarezi*) in view.

Table 2. Holotype dimensions and summary of shell measurements (mean, maximum (max), minimum (min), and standard deviation (sd)) of type material of *Zospeum zaldivarae* sp. n.: SH – shell height, SW – shell width, HLW – height of last whorl, PH – peristome height, PD – peristome diameter, SA – spire angle, W – number of whorls, CT– coiling tightness. SA in degrees, other measurements in mm.

	SH	SW	HLW	PH	PW	SA	W	SH/ SW	HLW/ SH	PH/ SH	CT	PH/ PW
holotype	1.52	1.25	0.96	0.78	0.73	70	5.4	1.22	0.63	0.51	12.9	1.07
mean	1.50	1.16	0.94	0.73	0.69	66.60	5.53	1.29	0.63	0.49	13.90	1.06
max	1.66	1.25	1.02	0.80	0.78	75.00	6.20	1.42	0.67	0.52	16.70	1.17
min	1.39	1.06	0.83	0.68	0.60	60.00	5.15	1.21	0.58	0.46	11.81	1.00
sd	0.070	0.063	0.056	0.041	0.051	3.888	0.268	0.072	0.025	0.020	1.397	0.048

Zospeum species except *Z. biscaiense*. *Zospeum biscaiense* has a more tightly coiled shell with palatal-basal apertural barriers.

Etymology. The new species is named after M^a Pilar Zaldivar, a biologist and speleologist from the *Niphargus* Speleological Team, who discovered the species in the 1980’s.

Distribution. Only known from the type locality.

Ecology. *Zospeum zaldivarae* was found sparingly in a muddy sediment matrix of somewhat coarse, vermiform texture interspersed by clumped aggregations of yellow- and white-coloured fungi (Fig. 8C) (Jochum et al. 2012 fig. A–B). No bats or bat guano were seen in the vicinity of the collection site. The species was found syntopically with *Z. suarezi*.

Conservation. *Zospeum zaldivarae* is only known from the Cueva de Las Paúles. Consequently, and in conjunction with the Guidelines for the IUCN Red List (IUCN Standards and Petitions Subcommittee 2014) it is a vulnerable, narrow range endemic (Vu D2) and as such, warrants immediate conservation priority. Although this cave belongs to the Natural Monument of Monte Santiago, it is nonetheless relatively easily accessible to the public.

Remarks. *Zospeum zaldivarae* appears to be polymorphic in the presence/absence of apertural barriers. These barriers were not noticed in the material sequenced by Weigand et al. (2013), but their presence cannot be excluded. However, we have little doubt that the dentate and edentate specimens co-occurring at the type locality are conspecific.

Zospeum zaldivarae is conchologically quite different from most other Iberian *Zospeum* species hitherto described. In shape, it best resembles *Z. biscaiense*. These two species share a wide shell with a reniform aperture and an angular, not roundish, peristome with a straight palatal-columellar callus. Also, phylogenetically, this species is distinct (Weigand et al. 2013) and possibly more closely related to *Z. biscaiense*.

Acknowledgements

We wish to thank the personnel at Cueva Arrikutz for their generous cooperation and interest in our work. A special thank you goes to Benedikt Hartmann for his help in sorting the AJC Spanish topotypic material. We also thank the editor, Eike Neubert and the two reviewers, Barna Páll-Gergely and Edmund Gittenberger, for their constructive input and improvement of the manuscript. This work was partially funded by the Basque Government through the Research group on “Systematics, Biogeography and Population Dynamics” (GIC10/76; IT575/13).

References

- Altonaga K, Gómez BJ, Martin R, Prieto CE, Puente AI, Rallo A (1994) Estudio faunístico y biogeográfico de los Moluscos terrestres del norte de la Península Ibérica. Eusko Legebiltzarra – Parlamento Vasco (Premio Xabier María de Munibe), Vitoria, 505 pp.
- Bole J (1974) Rod *Zospeum* Bourguignat 1856 (Gastropoda, Ellobiidae) v Jugoslaviji. Slovenska Akademija Znanosti in Umetnosti. Razprave 17(5): 1–43.
- Bourguignat JR (1856) Aménités malacologiques. § LI. Du genre *Zospeum*. Revue et Magasin de Zoologie pure et appliquée (2) 8: 499–516.

- Emberton KC (2001) Dentate *Gulella* of Madagascar (Pulmonata: Streptaxidae). American Malacological Bulletin 16: 71–129. <http://www.biodiversitylibrary.org/item/173085#page/81/mode/1up>
- Frauenfeld G von (1862) Ueber ein neues Höhlen-*Carychium* (*Zospeum* Brg.) und zwei neue fossile Paludinen. Verhandlungen der Zoologisch-botanischen Gesellschaft in Wien 12: 969–972. <http://www.biodiversitylibrary.org/item/95692#page/487/mode/1up>
- Gittenberger E (1973) Eine *Zospeum*-Art aus den Pyrenäen, *Zospeum bellesi* spec. n. Basteria 37(5–6): 137–140.
- Gittenberger E (1980) Three notes on Iberian terrestrial gastropods. Zoologische Mededelingen (Leiden) 55: 201–213.
- Giusti F (1975) Notulae Malacologicae XXI. Prime indagini anatomiche sul genere *Zospeum* (Pulmonata, Basommatophora). Conchiglie 11: 53–64.
- Gómez BJ, Prieto CE (1983) *Zospeum biscaiense* n. sp. (Gastropoda, Ellobiidae) otro molusco troglobio para la Península Ibérica. Speleon 26–27: 7–10.
- IUCN (2014) Guidelines for Using the IUCN Red List Categories and Criteria. Version 11. Prepared by the Standards and Petitions Subcommittee 11: 16–59. <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>
- Jeffreys JG (1830) A synopsis on the testaceous pneumonobrancheous Mollusca of Great Britain. Transactions of the Linnean Society of London 16(2): 324, 362.
- Jochum A, Weigand AM, Slapnik R, Valentinčič J, Prieto CE (2012) The microscopic ellobioid, *Zospeum* Bourguignat, 1856 (Pulmonata, Ellobioidea, Carychiidae) makes a big debut in Basque Country and the province of Burgos (Spain). MalaCo 8: 400–403. http://www.bik-f.de/files/publications/jochum_malaco_2012.pdf
- Pezzoli E (1992) Il Genere *Zospeum* Bourguignat, 1856 in Italia (Gastropoda Pulmonata Basommatophora) Censimento Delle Stazioni as Oggi Segnalate. Natura Bresciana (Atti del Museo Civico di Storia Naturale di Brescia) 27: 123–169.
- Prieto CE, Gómez BJ (1985) Primeros datos de *Zospeum* (Mollusca, Gastropoda, Ellobiidae) para la provincia de Burgos. Actas de II Simposium Regional de Espeleología de la Federación Castellana Norte de Espeleología, Burgos, 12–14 de octubre de 1984, 143–147.
- Weigand AM, Jochum A, Slapnik R, Schnitzler J, Zarza E, Klusmann-Kolb A (2013) Evolution of microgastropods (Ellobioidea, Carychiidae): Integrating taxonomic, phylogenetic and evolutionary hypotheses. BMC Evolutionary Biology 13(1): 1–18. doi: 10.1186/1471-2148-13-18
- Weigand AM (2013) New *Zospeum* species (Gastropoda, Ellobioidea, Carychiidae) from 980 m depth in the Lukina Jama – Trojama cave system (Velebit Mts., Croatia). Subterranean Biology 11: 45–53. doi: 10.3897/subtbiol.11.5966

A revision of the Nearctic species of *Liancalus* Loew (Diptera, Dolichopodidae)

Justin B. Runyon^{1,2}, Richard L. Hurley³

1 Rocky Mountain Research Station, USDA Forest Service, 1648 S. 7th Avenue, Bozeman, Montana 59717, USA **2** Montana Entomology Collection, Montana State University, Room 50 Marsh Laboratory, Bozeman, Montana 59717, USA **3** Deceased, formerly, Montana Entomology Collection, Montana State University, Room 50 Marsh Laboratory, Bozeman, Montana 59717, USA

Corresponding author: Justin B. Runyon (jrunyon@montana.edu)

Academic editor: M. Ivković | Received 7 January 2015 | Accepted 9 February 2015 | Published 23 February 2015

<http://zoobank.org/AA541FB5-5148-492A-8A57-F62764812F44>

Citation: Runyon JB, Hurley RL (2015) A Revision of the Nearctic species of *Liancalus* Loew (Diptera, Dolichopodidae). ZooKeys 483: 97–147. doi: 10.3897/zookeys.483.9222

Abstract

The genus *Liancalus* Loew is revised for the Nearctic Region. Seven species are documented from this region including two new species: *Liancalus genualis* Loew, *L. hydrophilus* Aldrich, *L. limbatus* Van Duzee, *L. pterodactyl* **sp. n.**, *L. querulus* Osten Sacken, *L. similis* Aldrich, and *L. sonorus* **sp. n.** Lectotypes are designated for the following species: *L. genualis*, *L. hydrophilus*, *L. querulus*, and *L. similis*. The species are illustrated, a key to males and females is provided, and their distributions mapped. Adults of *Liancalus* are some of the largest species of Dolichopodidae and commonly occur on waterfalls and vertical seeps.

Keywords

Nearctic, long-legged flies, Dolichopodidae, Hydrophorinae, wings, new species, courtship display

Introduction

Liancalus Loew, is a genus of long-legged flies in the subfamily Hydrophorinae containing 21 described species from all zoogeographical regions except Australasia and Oceania. Six species are known from the Palearctic Region, seven from the Nearctic Region, five from the Afrotropical Region, and three from the Oriental Region (Yang

et al. 2006). Adults have a diagnostic finger-like projection on the proepimeron near base of coxa I (Fig. 1). *Liancalus* includes some of the largest species of Dolichopodidae (body length approaches 12 mm in some species) and are commonly found in madicolous habitats, especially on or near waterfalls and seeps.

Males are readily identified to species using secondary sexual structures such as length of the cerci (Fig. 2), relative length of the first two segments of the fore tarsi (Fig. 3), and most easily, by their modified wings (Figs 4–6). The modified wings of males likely serve a signaling function in courtship. Males of several species have been observed standing in front of females and fanning their wings, e.g., the Palearctic *L. virens* (Scopoli) (Crossley 1988). We have also observed similar behavior in *L. pterodactyl* sp. n. and *L. similis* Aldrich). The wing tips of males of many *Liancalus* species, including all seven Nearctic species, have darkened areas often enclosing a white spot (Figs 4–5, 7), which would increase the signal contrast during fanning (see Fig. 2 in Zimmer et al. 2003). Males of some species also have lobes and long hairs near their wing tips (Figs 4, 7) that could signal females via sounds produced during fanning, similar to what has been proposed for species of *Erebomyia* Runyon & Hurley (Runyon and Hurley 2004, Hurley and Runyon 2009). The modified fore tarsi in males may also play a role in courtship (see Remarks for *L. limbatus* Van Duzee).

Like most Dolichopodidae, little is known about their biology. Adults and larvae are predators and adults have been documented feeding on arthropods, especially larvae of nematoceros Diptera (Masunaga 2001, Ulrich 2004). Adult females of *L. similis* have been observed feeding on nematoceros larvae in Montana (Suppl. material 1). Larvae of *L. similis* were found within algal mats below waterfalls and described by Corpus (1986); larvae of the Palearctic *L. virens* (Vaillant 1948) and the Oriental *L. zhenzhuristi* (Masunaga 2001) have also been described. Mouthparts of adults (Cregan 1941) and larvae (Sinclair 1992) have been described and illustrated for several Nearctic species.

In 1945, Harmston and Knowlton stated, "Possessing long, graceful bodies, delicately tinted with brilliant hues of bronze and purple against a green background, few Diptera are more beautiful than the species of *Liancalus*". Here, we revise these beautiful flies occurring in the Nearctic, illustrate the species, map their distributions, and provide a key to species.

Notes on nomenclature

Loew (1857: 22) originally used the name *Liancalus* stating: "Will man diese Gruppe zu einer Gattung erheben, so ist der mir von Herrn Haliday brieflich vorgeschlagene Name *Liancalus* ein ganz passender. Herr Rondani hat den bereits früher an eine Käfergattung vergebenen Namen *Anoplomerus* dafür vorgeschlagen, der verworfen werden muss". ["If one wants to raise this group to a genus, then the name *Liancalus* suggested by Mr. Haliday in a letter is completely suitable. Mr. Rondani has already proposed the name *Anoplomerus* for this, which has previously been given to a beetle genus and

which must be rejected"]. Most subsequent workers have interpreted Loew's use of the name *Liancalus* to be a replacement name for *Anoplomerus* (e.g., Pollet et al. 2004; Yang et al. 2006), but Coquillett (1910) obviously considered it a new genus-group when he designated a type species. Loew clearly stated that this group already had a name – *Anoplomerus* – but that this name had to be rejected and that *Liancalus* is a suitable name for the group. This would indicate that Loew intended *Liancalus* as a replacement name.

Following this logic, i.e. *Liancalus* is a replacement name for *Anoplomerus*, would cause significant nomenclatural instability and confusion. This is because Rondani (1856), in the unpaginated last page of his work, changed the type species of *Anoplomerus* from "*Hydrophorus Regius* Fabr." [now treated as a *Liancalus* Loew, 1857] to "*Hydrophorus Notatus* Meig." [now treated as a *Scellus* Loew, 1857] (discussed in Hurley 1995 and O'Hara et al. 2011). As a replacement name, *Liancalus* Loew would automatically take the type species of the name replaced, *Hydrophorus notatus* Meigen, making *Liancalus* a synonym of *Scellus*, and leaving the species currently in *Liancalus* without a generic name, thus threatening current usage of both *Liancalus* and *Scellus*, names and concepts that have been frequently and widely used. Therefore, an application has been submitted to the International Commission on Zoological Nomenclature (Runyon et al. submitted) to invoke its Plenary Powers under Article 78 (ICZN 1999) to conserve both generic concepts as presently used. Under Article 82.1, we are therefore required to maintain prevailing usage.

Materials and methods

This study was made possible by examination of more than two thousand specimens from the following collections, listed below with codens in parentheses; codens follow "The Insect and Spider Collections of the World" website (Evenhuis 2014): American Museum of Natural History, New York, USA (AMNH); Brigham Young University, Provo, USA (BYU); California Academy of Sciences, San Francisco, USA (CAS); Carnegie Museum of Natural History, Pittsburgh, USA (CMNH); Canadian National Collection of Insects, Ottawa, Canada (CNC); California State Collection of Arthropods, Sacramento, USA (CSCA); Colorado State University, Ft. Collins, USA (CSUC); Cornell University Insect Collection, Ithaca, USA (CUIC); University of Guelph Insect Collection, Guelph, Canada (DEBU); Essig Museum of Entomology, University of California, Berkeley, USA (EMEC); Utah State University Insect Collection, Logan, USA (EMUS); Florida State Collection of Arthropods, Gainesville, USA (FSCA); Illinois Natural History Survey, Champaign, USA (INHS); Iowa State University Insect Collection, Ames, USA (ISUI); Los Angeles County Museum of Natural History, Los Angeles, USA (LACM); Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ); Michigan State University, East Lansing, USA (MSUC); Montana Entomology Collection, Bozeman, USA (MTEC); New York State Museum, Albany, USA (NYSM); Oregon Department of Agriculture In-

sect Museum, Salem, USA (ODAC); Oregon State Arthropod Collection, Corvallis, USA (OSAC); Ohio State University, Columbus, USA (OSU); Snow Entomological Collections, University of Kansas, Lawrence, USA (SEMC); University of Arizona Insect Collection, Tucson, USA (UAIC); Spencer Entomological Museum, University of British Columbia, Vancouver, Canada (UBCZ); R.M. Bohart Museum of Entomology, University of California, Davis, USA (UCD); University of California, Riverside, USA (UCR); University of Georgia Collection of Arthropods, Athens, USA (UGCA); University of Minnesota, St. Paul, USA (UMSP); United States National Museum of Natural History, Washington, District of Columbia, USA (USNM); W.F. Barr Entomological Collection, Pullman, USA (WSU); University of Idaho, Moscow, USA (WFBM); University of Michigan, Ann Arbor, USA (UMMZ); James Entomological Collection, Washington State University, Pullman, USA (WSU).

Descriptions of structural terminology follow McAlpine (1981), except for genitalia which follow Sinclair and Cumming (2006). Illustrations of male genitalia are shown approximately as they appear on intact specimens (rotated approximately 180° and lateroflexed to the right), but in descriptions "dorsal" and "ventral" refer to the morphological positions before rotation and lateroflexion (e.g., top of page in Figs 10–12 is ventral), with the top of the page ventral and the bottom of the page dorsal. Genitalia were cleared first using 10% KOH and then 85% lactic acid then mounted in glycerin for examination and illustration. Body length was measured from the base of antenna to tip of the abdomen. Wing length was measured from the humeral cross-vein to the wing apex. Density of pollen is characterized as in Runyon and Hurley (2003), Runyon (2008), and Hurley and Runyon (2009).

The following abbreviations and terms are used: *ad* = anterodorsal(ly); *av* = anteroventral(ly); *pd* = posterodorsal(ly); *pv* = posteroventral(ly); T1, T2, etc. = abdominal tergite one, abdominal tergite two, etc.; S1, S2, etc. = abdominal sternite one, abdominal sternite two, etc. Legs are designated by roman numerals, tarsomeres by bracketed Arabic numerals (e.g., Tarsus III(4) = 4th tarsomere of hindleg).

Label data for type specimens are cited verbatim in quotation marks. Lines on a label are separated by a slash (/); labels on a pin are separated by semicolons; additional information is included in square brackets ([]). The repository of each type is given in parentheses. Label data for other specimens are summarized using a standardized format. For U.S. states, each county is only given once followed by localities from that county which are separated by commas; counties are separated by semicolons. The following abbreviations are used in the "material examined" sections: Crk – Creek; Co – County; Cpgd – Campground; Cyn – Canyon; E – east; Hwy – Highway; mi. – miles; Mt/Mts – Mountain/Mountains; N – north; NF – National Forest; NP – National Park; nr – near; PK – Park; PP – Provincial Park; R – River; S – south; SP – State Park; Spr/Sprs – spring/springs; Tr – Trail; W – west. The following abbreviations for frequent collectors are used: ALM – A.L. Melander; DDW – D.D. Wilder; PHA – P.H. Arnaud Jr.; JBR – J.B. Runyon; RLH – R.L. Hurley; WJT – W.J. Turner; FCH – F.C. Harmston; JRV – J.R. Vockeroth; JMA – J. M. Aldrich; KJG – K.J. Goeden.

Taxonomy

Genus *Liancalus* Loew, 1857

Anoplomerus Rondani, 1856: Rondani 1856: 141. Type species: *Dolichopus regius* Fabricius, 1805 treated as type species, awaiting ruling by the International Commission on Zoological Nomenclature. Preoccupied by *Anoplomerus* Guérin-Méneville, 1844.

Anoplopus Rondani, 1857: Rondani 1857: 14. Replacement name for *Anoplomerus* Rondani 1856 [Not Guérin-Méneville 1844]. Type species taken as that of replaced name under ICZN Art. 67.8: *Dolichopus regius* Fabricius (pending ICZN ruling). Preoccupied by *Anoplopus* Wagler, 1830.

Liancalus Loew, 1857: Loew 1857: 22. Replacement name for *Anoplomerus* Rondani, 1856 [Not Guérin-Méneville 1844]. Type species taken as that of replaced name under ICZN Art. 67.8: *Dolichopus regius* Fabricius. Bigot 1859: 230; Loew 1861: 69–70; Loew 1864: 198–200; Osten Sacken 1877: 318; Gobert 1887: 33; Bigot 1890: 277; Aldrich 1893: 569; Becker et al. 1903: 343–344; Aldrich 1904: 271; Aldrich 1905: 298; Coquillett 1910: 561; Lundbeck 1912: 22, 352–356; Wahlgren 1912: 5, 48; Frey 1915: 74; Van Duzee 1917: 126; Becker 1917–1918: 160, 193; Becker 1922a: 117–119; Becker 1922b: 41; Curran 1926: 406–407; Parent 1932: 121–122; Curran 1934: 217; Parent 1938: 19, 268, 306; Parent 1939: 276; Harmston and Knowlton 1945: 55–56; Robinson 1964: 118, 182; Dyte 1967: 123; Cole 1969: 272, 282; Robinson 1970a: 59, 62; Robinson 1970b: 57; Dyte 1975: 241–242; D’Assis Fonseca 1978: 41; Negrobov 1978: 416–417; Negrobov 1979: 928; Robinson and Vockeroth 1981: 633, 635, 637; Hurley 1985: 3; Negrobov et al. 1987: 157–158; Negrobov 1991: 41; Wei and Liu 1995: 35; Yang 1998: 153; Masunaga 2001: 109, 117–118; Pollet et al. 2004: 52; Yang et al. 2006: 19, 246; Bickel 2009: 683; Evenhuis and Bickel 2011: 4–5; O’Hara et al. 2011: 30; Yang et al. 2011: 363; Kahanpää 2014: 203.

Notes. The type species of *Liancalus* is involved in a convoluted nomenclatural issue resulting from an unpaginated correction page at the end of Rondani (1856) and interpretation of Loew’s (1857) creation of the name. If a straightforward use of the ICZN rules were to be followed, the genus here and previously considered *Liancalus* Loew would lack a valid generic name. However, the purpose of the ICZN is to “Promote stability and universality” (ICZN Preamble), and when strict application of the Code would act contrary to this purpose, the International Commission on Zoological Commission is empowered to set aside the rules using their Plenary Powers (ICZN Art. 78.1). Therefore, a petition has been prepared for the ICZN (Runyon et al. submitted) asking that they use their Plenary Powers to preserve prevailing usage of *Liancalus* by setting aside the type species under the Rules, and replace it with a type species that retains established and universal usage. In the meantime, under ICZN Art. 82.1, prevailing use is to be maintained until such time as the



Figure 1. Lateral view of head and thorax of the holotype of *Liancalus pterodactyl* sp. n. The finger-like projection on the proepimeron is indicated with an arrow; this lobe is diagnostic for the genus *Liancalus*. Scale bar = 1 mm.

Commission's ruling is published. Therefore, *Liancalus* will be treated herein as if its type species is *Dolichopus regius* Fabricius, 1805.

Diagnosis. Large flies of rather uniform general color and appearance (Figs 8–9) whose males and females can be recognized by the finger-like projection ventrally from proepimeron near base of coxa I (Fig. 1).

Description. Male. Body length 6.5–12.0 mm, wing length 6.0–8.5 mm.

Head: Face and frons broadly separated with distinct frontoclypeal suture near mid-face (Fig. 1). Eyes with short hairs between facets. Vertical setae on small elevation; ocellar tubercle prominent with 2 large setae, without hairs; with 2 postocellar setae. Gena absent. Proboscis somewhat sclerotized, slightly enlarged, covered with sparse gray-brown pollen; each labellar lobe with 6 geminately sclerotized pseudotracheae. Antenna of rather uniform shape, size, and color (Figs 1, 8–9); black, scape without dorsal setae; pedicel with apical ring of setae/setulae, longest setae dorsally and ventrally; first flagellomere about as long as wide, broadly pointed apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum metallic green to green-blue with silver-gray pollen and bronze-red stripes; 0–14 acrostichal setae in a single row; usually 6 dorsocentral setae (6–10

in *L. pterodactyl*), 2 notopleural setae; 1–3 strong, black postpronotal setae (often with some smaller white hairs), usually 2 presutural intra-alar setae (1 in *L. genualis*), 1 presutural seta, 2 postsutural supra-alar setae, and 1 postalar seta per side; scutellum usually with 6 large marginal setae (8–9 in *L. pterodactyl*), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic bronze-green, covered with dense silver-gray pollen, without setae or hairs (Fig. 1).

Legs: Legs very long, slender, dark metallic green (Figs 8–9). Coxa I uniformly covered with white hairs on anterior surface; coxa II with white hairs on anterior surface and black *ad* seta near middle; coxa III with a black dorsal seta near middle (Fig. 1). Femur II and III with a slender preapical *ad* seta near 3/4. Tarsus I either with tarsomere 1 long and tarsomere 2 short (Figs 3A–E), or with tarsomere 1 short and tarsomere 2 long (Figs 3F–G).

Wing: Modified with dark brown markings and spots, sometimes enclosing a white apical spot and sometimes with lobes and setae (Figs 4–7). Calypter yellow with a fan of long, pale yellow setae. Halter pale yellow.

Abdomen: Cylindrical, elongate, and slightly broadened at apex (Fig. 2). T5 prolonged ventrally into two lateral flap-like projections that form a hood or pocket for the apex of the hypopygium. Hypopygium (Figs 10–12) nearly round, capping apex of abdomen. Phallus arched to rather sharply bent dorsally just before apex, with apical margin minutely serrate. Hypandrium rather broad, thin, arched anteriorly near apex with lateral lobe bearing setulae and a larger seta at or near apex. Epandrium with large, apical, thin, nearly transparent lobe that is hinged and can be raised or lowered dorsoventrally; at rest, this lobe sits against and covers the surstylus and base of cerci. Surstylus somewhat pointed, strongly sclerotized, directed medially, with large spatulate seta near apex. Cerci broad basally, with either very short (Figs 2E–F, 12) or very long filaments that project anteriorly below abdomen (Figs 2A–D, 8).

Female. Body length 5.0–9.0 mm, wing length 5.5–7.5 mm. Lacking typical male secondary sexual characters and similar to male except: face broader, nearly parallel-sided; palpi larger; fore tarsi unmodified; wings unmodified, but with diagnostic dark brown spots in most specimens (Fig. 16); abdomen shorter and somewhat flattened dorsoventrally.

Immatures. Larvae twelve segmented, cylindrical, truncate posteriorly and tapered anteriorly, opalescent with transparent cuticle; antenna with basal ring bearing sensilla; mouthparts dark brown to black, labrum large with pointed tip (sometimes hooked and/or with tooth-like projections), mandibular hook well developed; metacephalic rods enlarged at caudal tips, longer than tentorial arm. Pupa with prothoracic respiratory horns about 2 mm long, sharply pointed at tips; frontofacial sutures distinct, brown; abdominal segments 2–7 with rows of posteriorly-directed spines. Cocoon elliptical, externally composed of sand grains and sometimes moss and mud, inner surface smooth; respiratory horn tips exposed. See Vaillant (1948), Corpus (1986) and Masunaga (2001) for illustrations and photographs of immature stages.

Remarks. Cerci of male specimens sometimes shrivel upon drying. In teneral specimens, the spots on the wings can be very faint which can render them, particularly females, difficult to identify.

Key to Nearctic species of *Liancalus* Loew

- 1 Male **2**
- Female **8**
- 2 Cerci very short (Fig. 2E–F); foretarsus with tarsomere 1 short and tarsomere 2 long (Fig. 3F–G) **3**
- Cerci very long (Figs 2A–D, 8); foretarsus with tarsomere 1 long and tarsomere 2 very short (Fig. 3A–E) **4**
- 3 Wing with brown clouding on most of apical half and a small black speck near center of cell m (Fig. 6B) ***similis* Aldrich**
- Wing with semicircular brown cloud near apex, without black speck in cell m (Fig. 6A) ***querulus* Osten Sacken**
- 4 Wing with outstanding setae on posteroapical margin (Figs 4, 7) **5**
- Wing without obvious setae on posteroapical margin (Fig. 5) **6**
- 5 Wing margin with proximal setae arising from apex of long, slender, finger-like lobe (Figs 4A, 7); cerci with long setae confined to apical half (Fig. 2D) ***pterodactyl* sp. n.**
- Wing margin with proximal setae arising from short, rounded lobe (Fig. 4B); cerci with long, pale setae along full-length (Fig. 8) ***hydrophilus* Aldrich**
- 6 Crossvein dm-cu nearly straight (Fig. 5C) ***limbatus* Van Duzee**
- Crossvein dm-cu strongly arched (Fig. 5A–B) **7**
- 7 Wing margin excavated posterior to vein M_1 (Fig. 5A); intra-alar seta at transverse suture missing (eastern North America) ***genualis* Loew**
- Wing margin without or with very small excavation posterior to vein M_1 (Fig. 5B); intra-alar seta at transverse suture present (Arizona, Mexico) ***sonorus* sp. n.**
- 8 Intra-alar seta at transverse suture absent; wing as in Fig. 16B (eastern North America) ***genualis* Loew**
- Intra-alar seta at transverse suture present (western North America) **9**
- 9 Postcranial hairs (beard) with dorsal one-quarter or more brown to black; femur I with long (subequal to width of femur), white hairs ventrally to *pv*; wing as in Fig. 16A ***pterodactyl* sp. n.**
- Postcranial hairs (beard) white or yellow, at most with a few black hairs dorsally; femur I with much shorter white hairs ventrally to *pv* **10**
- 10 Wing with small brown cloud on or near M_1 beyond crossvein dm-cu (this brown clouding sometimes faint) (Fig. 16B, D–G) **11**
- Wing without small brown cloud on or near M_1 beyond crossvein dm-cu (Fig. 16C) ***hydrophilus* Aldrich**
- 11 Brown clouding in cell r_{4+5} more or less continuous with clouding in cell bm+dm (often joined by light brown clouding) (Fig. 16B, D, F) **13**
- Brown cloud in cell r_{4+5} separated from cloud in cell bm+dm by distinct clear space (Fig. 16E, G) **12**
- 12 Wing with crossvein dm-cu meeting M_1 at approximately 90° angle; brown cloud in cell bm+dm intersecting crossvein dm-cu (Fig. 16E) ***similis* Aldrich**

- Wing with crossvein dm-cu meeting M_1 at nearly 45° angle; brown cloud in cell bm+dm not reaching crossvein dm-cu (Fig. 16G)..... ***querulus* Osten Sacken**
- 13 Acrostichal setae stout, long (two-thirds to three-quarters size of dorsocentral setae); 3rd costal sector (at apex of cell r_{2+3}) about 1.5 times length of 4th costal sector (at apex of cell r_{4+5}) (Fig. 16D)..... ***limbatus* Van Duzee**
- Acrostichal setae absent, or short and hair-like (less than one-half size of dorsocentral setae); 3rd costal sector about 2 times length of 4th costal sector (Fig. 16B, F) **14**
- 14 Acrostichal setae short, with at least one seta posterior to anterior-most dorsocentral seta (Arizona, Mexico)..... ***sonorus* sp. n.**
- Acrostichal setae absent, or minute and confined to anterior slope of scutum (eastern North America) ***genualis* Loew**

***Liancalus genualis* Loew, 1861**

Figs 2A, 3C, 5A, 10A, 13, 16B

Diagnosis. Males and females are distinguished by the absence of acrostichal setae and having only 1 presutural intra-alar seta. Males are further distinguished by having tarsus I with tarsomere 2 very short (Fig. 3C), cerci long (Fig. 2A), and wing as in Fig. 5A. This species is most similar to *L. sonorus* sp. n. but easily separated by the number of intra-alar seta (*L. sonorus* have 2), the male wings (Fig. 5A–B), and distribution (Fig. 13).

Redescription. Male. Body length 7.0–9.0 mm, wing length 6.5–7.5 mm. **Head:** Face narrowed below antenna, slightly widening toward palpus, green or blue with silver-gray pollen that is most dense along eyes and below frontoclypeal suture. Ommatidia near face slightly larger than remaining ommatidia. Vertex covered with silver pollen that is sparse medially revealing metallic green or blue ground color. Vertical setae on very small elevation; ocellar tubercle prominent with 2 large setae (slightly larger than vertical setae); with 2 postocellar setae which are two-thirds length ocellar setae; postocular setae approximately one-third size of vertical setae with about dorsal one-half black (approximately 12 black setae), ventral half (approximately 15 setae) white and more slender and slightly longer than black postocular setae. Ventral postcranial hairs (beard) rather sparse, wholly white. Palpus black, covered with moderately dense silver pollen and long, dense, dark brown to black setae on basal half. Antenna black, first flagellomere about as long as wide, broadly pointed apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum green to green-blue with moderately dense silver-gray pollen, with large red-bronze stripes between dorsocentral setae, and along intra-alar setae; medial stripe metallic pink; posterior slope of scutum bronze with lateral blue-green spots; scutellum bronze, with sparse silver pollen; notopleuron and postpronotum covered with silver pollen, often with some blue-green reflections; scutum with acrostichal setae absent (sometimes with a few small hairs on anterior slope of scutum); 6 dorsocentral setae, 2 notopleural setae, 1–2 strong, black postpronotal setae (often a few smaller white hairs), 1 presutural intra-alar seta (the posterior-most seta near transverse



Figure 2. Lateral view (unless otherwise noted) of abdomens and postabdomens of males, **A** *Liancalus genualis* Loew **B** *L. sonorus* sp. n. **C** *L. limbatus* Van Duzee (dorsolateral view) **D** *L. pterodactyl* sp. n. **E** *L. similis* Aldrich, and **F** *L. querulus* Osten Sacken. Scale bars = 1 mm. See Figure 8 for *L. hydrophilus*.

suture missing but with remnant dark spot where this seta inserted in other *Liancalus* – similar to small darkened area surrounding insertion of other setae on dorsum), 1 presutural seta, 2 postsutural supra-alar setae, and 1 postalar seta per side; scutellum with 6 large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic bronze-green, covered with dense silver-gray pollen, without setae or hairs.

Legs: Legs concolorous with pleura, but with distinctly less silver-gray pollen, femoral ‘knees’ orange (Fig. 2A). Coxa I uniformly covered with white hairs on anterior

surface (length of hairs subequal to width of coxa I), with a few black, slender setae at apex. Coxa II with a few white hairs anteriorly, a few white setae near apex, and a black *ad* seta just beyond 1/2. Coxa III with a few short, white hairs on anterior surface and a black dorsal seta near 1/2. Femur I with sparse, short, white hairs *av* to *pv* on basal half (length < half width of femur). Femur II with row of short (\leq width of femur) posterior to *pv* setae on distal half, those near to just beyond middle of femur white, longest and becoming black and shorter apically. Femur III with some white hairs (length \leq width of femur) on dorsal and posterior surface at base. Tarsus I(1) long, as long as remaining tarsomeres combined (Fig. 3C). Tarsus I(2) very short, about as long as wide, with ventral row of setae/setulae (Fig. 3C). Ratios of tibia:tarsomeres for leg I: 18-9-1-4-3-2; for leg II: 28-25-11-4-2-2; for leg III: 35-18-19-5-2-2.

Wing (Fig. 5A): Hyaline, with a longitudinal spurious vein between R_{4+5} and M_1 that is arched on apical third of wing and terminates near midpoint of a circular, translucent, apical spot that is white in certain lights; this spot enclosed within a brown, apical cloud that extends anteriorly along costa to R_1 ; some light clouding also evident narrowly along R_{4+5} on apical one-quarter of wing. Wing margin excavated posterior to M_1 ; with short, broad lobe between M_1 and CuA_1 . Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate, rather blunt at apex (Fig. 2A); T1 metallic green with dense silver pollen laterally becoming less dense dorsally, with bronze along posterior edge and occasionally with a diffuse bronze stripe dorsally. T2-T4 blue-green with dense silver pollen on basal one-half to two-thirds, with apical one-third to one-half bronze. T5 dark bronze with metallic green reflections and sparse silver pollen. T6 dark bronze with blue-green reflections and with dense silver pollen. T1-T3 with yellowish hair laterally, longest on T1 and T2, without black hairs or setae. Sternites bronze with dense silver-gray pollen. S1 bare except for lateral small tuft of yellow hairs at extreme base. S2 and S3 with sparse yellow hairs. S4 mostly bare. Hypopygium (Fig. 10A): cercus very long, slender, cylindrical, with long pale yellow dorsal and ventral setae (Fig. 2A).

Female. Body length 6.0–7.5 mm, wing length 6.0–7.0 mm. Similar to male except for face wider, dark violet-green covered with moderate to dense brown pollen; palpus black with silver pollen apically, dense golden-brown pollen basally, and black setae. Femur II posteriorly to *pv* with row of short (< half width of femur) hairs on apical half, those near middle white and becoming black apically. Wing (Fig. 16B) hyaline, with three diffuse brown clouds: largest one in cells r_{4+5} and $bm+dm$ and crossing M_1 near midpoint of wing, one on M_1 beyond crossvein $dm-cu$, and smallest one on R_{4+5} at apex of wing.

Remarks. Loew reported types from "Middle States"; a hand-written label on one of the paralectotypes collected by Loew appears to be "KY". Adults of this species have been frequently found in caves, e.g., in Arkansas (Barnes et al. 2009), Indiana (Banta 1907), Georgia (Reeves et al. 2000), Kentucky and Minnesota (see material examined).

Distribution. This is the only species of *Liancalus* known to occur in eastern North America (Fig. 13).

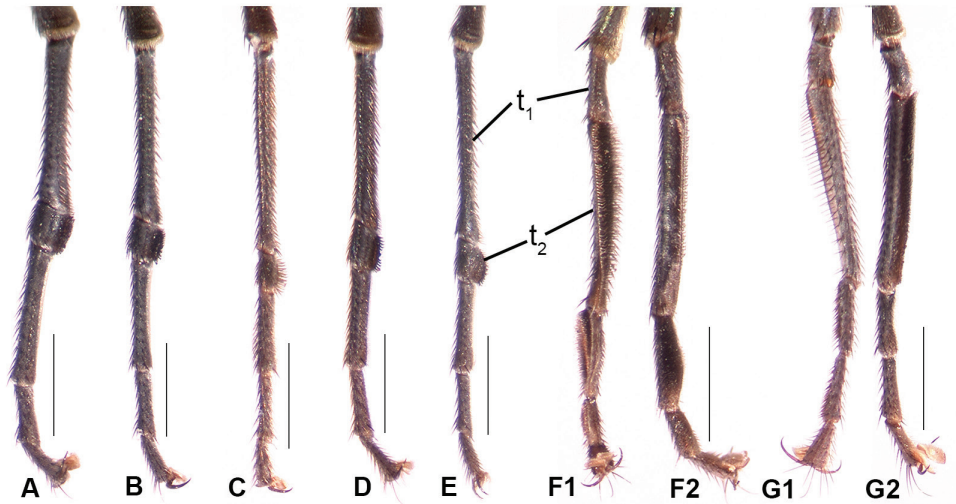


Figure 3. Front tarsi of males, **A** *Liancalus pterodactyl* sp. n., medial view **B** *L. hydrophilus* Aldrich, medial view **C** *L. genualis* Loew, medial view **D** *L. limbatus* Van Duzee, medial view **E** *L. sonorus* sp. n., medial view **F1** *L. querulus* Osten Sacken, ventral view **F2** *L. querulus*, medial view **G1** *L. similis* Aldrich, ventral view **G2** *L. similis*, medial view. Scale bars = 0.5 mm. t_1 = tarsomere 1, t_2 = tarsomere 2.

Type material examined. LECTOTYPE (designated here to fix identity of the species) ♂, labelled: "Loew/ Coll."; "Type 12944" [red label]; "Jan.-Jul. 2007/ MCZ Image/ Database" [with image of a camera]; "MCZ-ENT/ 00012944" [with barcode]; "LECTOTYPE/ ♂ *Liancalus/ genualis* Loew/ des. Runyon & Hurley" [red label] (MCZ). **PARALECTOTYPES:** Same data as lectotype, but without MCZ Image Database label, MCZ-ENT 00302768 (1 ♂, MCZ). Same data as previous, MCZ-ENT 00302769 (1 ♀, MCZ). Same data as previous, MCZ-ENT 00302770 (1 ♀, MCZ). Same data as previous, "KY" [?]; "*L. genualis*" [hand-written]; MCZ-ENT 00302767 (1 ♂, MCZ).

Additional material examined. CANADA. New Brunswick: St. Andrews, littoral rocks, 19.v.1978, S.A. Marshall (1 ♀, CNC). **Nova Scotia:** Truro, 5.vii.1913, R. Matheson (1 ♀, CUI). **Ontario:** Ottawa, 1.viii.1926, C.H. Curran (1 ♀, CNC), Ottawa, 12.viii.1924, F.P. Ide (1 ♀, CNC), Ottawa, 22-30.ix.1956, JRV (5 ♂, 19 ♀, CNC), same as previous, at seepage on limestone cliff, 1-7.viii.1987, JRV (18 ♂, 7 ♀, CNC), same as previous, 2.viii.1988 (6 ♂, 6 ♀, CNC), same as previous, 15-21.vii.1956 (7 ♀, CNC), same as previous, 15-16.viii.1956 (1 ♂, 2 ♀, CNC), Niagara Falls, 6.viii.1929, ALM (1 ♀, USNM), Owen Sound, 18.viii.1976, J.M. Cumming (1 ♂, DEBU), Elora, 15.v.1977, K. Barber (2 ♀, DEBU, Inglis Falls, seepage spring, 11.vii.1985, B. Sinclair (1 ♀, DEBU), same as previous, madicolous zone, 25.vii.1985 (1 ♀, DEBU), Algonquin Park, 10.viii.1940, J.S. Rogers (1 ♂, UMMZ). **Quebec:** Gatineau Pk., Luskville Falls, 14.vii.1972, F. Brodo (2 ♂, CNC), Duncan L, nr.

Rupert, 1.viii.1969, J.F. McAlpine (1 ♂, 1 ♀, CNC), Gaspé Bay, 18.vii.1931, JMA (2 ♀, USNM), Gatineau Pk., Lusk Falls, 26.vi.1991, JRV (1 ♂, 1 ♀, CNC), Wakefield, 1.viii.1959, JRV (1 ♀, CNC), Lac Mondor, Ste. Flore, 6.v.1951, E.G. Munroe (1 ♀, CNC), Meach L, Old Chelsea, 16.iv.1973, D.M. Wood (2 ♀, CNC), Old Chelsea, 20.ix.1955, JRV (1 ♀, CNC), same as previous, 9.x.1955 (1 ♀, CNC), same as previous, 16.v.1958 (1 ♀, CNC), Gaspé, 24.viii.1937, C.P. Alexander (1 ♂, EMUS), Kingsmere, 16.v.1958, J.G. Chillcott (1 ♀, CNC), Vinton, 5-12.vi.1900 (2 ♂, OSU), Kazubazua, 16.viii.1927, F.P. Ide (1 ♀, CNC). **USA. Arkansas:** Springdale, viii.1933 (1 ♀, MCZ); Logan Co., Magazine Mt, Ozark For., 2800', 11.vi.1948, S.S. Roback (10 ♂, 11 ♀, INHS); Marion Co., Buffalo R, 670-800', 30.vii.1974, G.W. Byers & C.W. Young (7 ♂, 6 ♀, SEMC); Pope Co., Ozark Nat. For., Falling Water Falls, 22.v.1991, J.E. Swann (1 ♀, DEBU); Stone Co., Ozark Nat. For., Hwy 5, roadcut seepage, 21.v.1991, B.J. Sinclair (2 ♂, 2 ♀, CNC); Washington Co., Devil's Den St. Park, 1400 ft, 27.v.1977, Byers, May & Young (1 ♂, 1 ♀, SEMC); Yell Co., Mt. Nebo St. Pk., ex. Gum Sprg. Tr., 22.v.1991, B.J. Sinclair (1 ♂, CNC). **Kentucky:** Whitley Co., Cumberland Falls St. Pk., ex. roadcut seeps, 17-18.vi.1990, B.J. Sinclair (1 ♂, CNC). **Georgia:** Neels Gap, 5.vi.1946, P.W. Fattig (1 ♂, 1 ♀, USNM); Bartow Co., Yarborough Cave (Adairsville), ix.1998, W. Reeves (1 ♂, MTEC); Dade Co., Cloudland Canyon S.P., ex. limestone seep, 15.v.1986, B.J. Sinclair (1 ♂, 1 ♀, DEBU). **Illinois:** Giant City, 28.vii.1930, Knight & Ross (4 ♂, 4 ♀, INHS); Jackson Co., Makanda, 26.vi.1909, sweeping (5 ♂, 2 ♀, EMUS, INHS), same as previous, 4.vi.1919 (2 ♀, INHS); Lake Co., Lake Forest, 12.v.1904, J.G.N. (1 ♂, 6 ♀, CUIC); Pope Co., Herod, 9.viii.1905 (7 ♂, 5 ♀, INHS). **Indiana:** Jefferson Co., Hanover, Crowe Ravine, 11.vi.1921, C.P. Alexander (1 ♂, USNM), Clifty Falls St. Pk., interior of old tunnel, 5.ix.1950, T.H. Hubbell (1 ♂, UMMZ); Marion Co., vic. Indianapolis, 1.viii.1943, FCH (9 ♂, 9 ♀, CMNH, CNC, EMUS, FSCA, MTEC), same as previous, 8.viii.1943 (2 ♂, 2 ♀, CAS, FSCA), same as previous, 22.viii.1943 (2 ♂, 2 ♀, CAS, MTEC), same as previous, 4.vi.1944 (8 ♂, 5 ♀, CAS, CNC, EMUS, FSCA, LACM, OSAC), same as previous, 11.vi.1944 (2 ♂, 2 ♀, CNC, INHS); Vigo Co., Terre Haute, 6.viii.1944, FCH (15 ♂, 15 ♀, CUIC, EMUS, FSCA, INHS, ISUI, MTEC, NYSM), Nr. Ft. Harrison, 11.vii.1943, FCH (4 ♂, 5 ♀, CMNH, EMUS, FSCA, MTEC). **Maine:** Acadia Nat. Pk., 3.viii.1972, FCH (2 ♂, 6 ♀, CAS, EMUS, FSCA); Waldo Co., Belfast, 2.viii.1972, FCH (1 ♂, MTEC). **Michigan:** Iron Co., T43N-R35W-Sec. 24, 27.vii.1971, DDW (4 ♂, 6 ♀, MSUC, USNM). **Minnesota:** Hennepin Co., Minneapolis, O.W. Oestlund (1 ♀, UMSP), Fort Snelling, in sandstone cave, 9.i.1935, D.G. Denning (2 ♀, UMSP); Lake Co., Encampment R, 6.viii.1939, R.H. Daggy (3 ♀, UMSP), 5.viii.1939, H.T. Peters (1 ♂, UMSP); Ramsey Co., 20.v.1936, D. Denning (1 ♀, UMSP). **Mississippi:** Lafayette Co., Spring 1943, F.M. Hull (2 ♂, 6 ♀, CNC). **Missouri:** Saint Louis, 6.vii.1972, FCH (4 ♂, 1 ♀, CAS, EMUS, FSCA); Carter Co., Big Spring Park, 16.vii.1953, G.W. Byers (3 ♂, UMMZ); Sainte Genevieve Co., vi.1951, W. Downes (2 ♀, MTEC). **New Jersey:** Bergen Co., Palisades, 4.vii.1920, J. Bequaert (3 ♂, 1 ♀, MCZ, WSU). **New York:** J. Brown's Well, Fulton Ck, 13.viii.1905, N.Y.S.

Coll. (1 ♂, 4 ♀, CUIC); Albany Co., Meadowdale, 2.viii.1904, N.Y.S. Coll., D.B. Young (2 ♂, 9 ♀, CNC, NYSM); Dutchess Co., Po'k'psie, N.Y.S. Coll., 17.vi.1904 (2 ♂, 6 ♀, NYSM); Erie Co., Spring Brook, 25.vi.1911, M.C. Van Duzee (3 ♀, CAS), S. Wales, 9.vii.1911, M.C. Van Duzee (1 ♀, CAS), Colden, 3.viii.1913, M.C. Van Duzee (1 ♂, 1 ♀, CAS, NYSM), same as previous, 2.viii.1914 (1 ♀, CAS), same as previous, 9.viii.1914 (1 ♀, CAS), same as previous, 9.vii.1922 (2 ♂, 2 ♀, CAS); Essex Co., Keene Valley, around and on wet cliff face, 1200', 20.vii.1962, JRV (1 ♂, 8 ♀, CNC), Keen Valley (Beede's), 3.viii.1886, N.Y.S. Coll. (1 ♂, 8 ♀, NYSM, USNM), same as previous, 5.viii.1886 (1 ♀, NYSM), same as previous, 7.viii.1889 (1 ♂, 6 ♀, NYSM, USNM), same as previous, 12.viii.1889 (2 ♂, NYSM), same as previous, 16.vii.1890 (1 ♀, NYSM), same as previous, 12.viii.1890 (1 ♂, NYSM, USNM), Elizabethtown, 22.viii.1937 (6 ♂, 5 ♀, MTEC); Fulton Co., Gloversville, 19.vi.1910, Alexander (1 ♀, CUIC); Greene Co., Prattsville, 3.viii.1974, FCH (1 ♀, INHS); Hamilton Co., 6 mi. E Indian L, 43°45'30", 74°10'14", 15.v.1977, 1820', T.L. McCabe (1 ♀, NYSM); Montgomery Co., Canajoharie, 8.vii.1934, H.K. Townes (2 ♀, AMNH); Niagara Co., Niagara Falls, 31.vii.1910, M.C. Van Duzee (6 ♂, 9 ♀, CAS, CNC, CUIC, OSU), same as previous, 4.viii.1912 (1 ♂, 1 ♀, CAS, OSU), same as previous, 6.x.1912 (1 ♂, CAS), same as previous, 19.v.1918 (2 ♀, CAS, NYSM), same as previous, 17.vii.1921 (2 ♂, 1 ♀, CAS); Tompkins Co., Ithaca, 5.viii.1947 (1 ♂, INHS), Ithaca, Buttermilk, 18.vii.1920 (2 ♂, 6 ♀, CUIC), Ludlowville, 4.vii.1965, L.L. Pechuman (1 ♀, CUIC), same as previous, 7.vii.1966 (1 ♀, CUIC), same as previous, 4.viii.1966 (1 ♂, CUIC), same as previous, 6.vii.1967 (1 ♀, CUIC), same as previous, 29.viii.1970 (1 ♀, CUIC), same as previous, 26-27.vi.1973 (2 ♀, CUIC), same as previous, 6-13.vii.1963 (3 ♀, CUIC, USNM), same as previous, waterfall, 13.vi.1979 (3 ♀, CUIC), Ithaca, 25.iii.1917, R.C. Shannon (2 ♀, USNM), Ithaca, 15.viii.1928, ALM (3 ♂, 2 ♀, USNM), Ithaca, 26.iii.1991 (2 ♀, USNM), Ithaca, 2.viii.1887, JMA (1 ♂, USNM), Ithaca, 26.iii.1891, JMA (3 ♀, USNM), Ithaca, 13.vii.1893, JMA (1 ♂, USNM), Ithaca, 24.vii.1894, JMA (1 ♂, USNM), Ithaca, vii.1901, JMA (2 ♂, 1 ♀, USNM), Ithaca, Sixmile Crk, 29.vii.1958, H.E. Evans (2 ♀, CUIC), same as previous, 9.viii.1961, J.L. Laffoon (2 ♂, 5 ♀, ISUI), Ithaca, Cornell U. campus, 2.iii.1972, G. & K. Eickwort (1 ♀, CUIC), Taughanick, Ithaca, 21.iv.1917, Shannon (3 ♀, CUIC), Taughannock Falls, 21.iv.1917, S.H. Emerson (1 ♀, CUIC), same as previous, E.G. Anderson (2 ♀, UMSP), Ithaca, 31.iii.1917, S.H. Emerson (1 ♀, UMSP), Ithaca, Coy Glen, 9.viii.1961, J.L. Laffoon (1 ♂, 1 ♀, ISUI), Ithaca, 4.iv.1924, C.H. Curran (1 ♀, AMNH), Ithaca, 22-25.iii.1917, E.G. Anderson (9 ♀, UMSP), same as previous, 18.iv.1917 (3 ♀, CUIC, UMSP), Ithaca, 25.iii.1915, R.C. Shannon (2 ♀, CUIC), same as previous, 25.iii.1917 (9 ♀, CUIC); Tompkins Co., Ludlowville, 4.vii.1965, L.L. Pechuman (1 ♀, CUIC), same as previous, 7.vii.1966 (1 ♀, CUIC), same as previous, 4.viii.1966 (1 ♂, CUIC), same as previous, 6.vii.1967 (1 ♀, CUIC), same as previous, 29.viii.1970 (1 ♀, CUIC), same as previous, 26-27.vi.1973 (2 ♀, CUIC), same as previous, 6-13.vii.1963 (3 ♀, CUIC, USNM), same as previous, waterfall, 13.vi.1979 (3 ♀, CUIC), Ithaca, Buttermilk, 18.vii.1920 (2 ♂, 6 ♀, CUIC), Ithaca, Coy Glen, 9.

viii.1961, J.L. Laffoon (1 ♂, 1 ♀, ISUI), Ithaca, Sixmile Crk, 29.vii.1958, H.E. Evans (2 ♀, CUIC), same as previous, 9.viii.1961, J.L. Laffoon (2 ♂, 5 ♀, ISUI), Ithaca, Cornell U. campus, 2.iii.1972, G. & K. Eickwort (1 ♀, CUIC), Taughanick, Ithaca, 21.iv.1917, Shannon (3 ♀, CUIC), Taughannock Falls, 21.iv.1917, S.H. Emerson (1 ♀, CUIC), same as previous, E.G. Anderson (2 ♀, UMSP), Ithaca, 2.viii.1887, JMA (1 ♂, USNM), same as previous, 26.iii.1891 (3 ♀, USNM), same as previous, 13.vii.1893 (1 ♂, USNM), same as previous, 24.vii.1894 (1 ♂, USNM), same as previous, vii.1901 (2 ♂, 1 ♀, USNM), same as previous, 25.iii.1915, R.C. Shannon (2 ♀, CUIC), same as previous, 25.iii.1917 (11 ♀, CUIC), same as previous, 22-25.iii.1917, E.G. Anderson (9 ♀, UMSP), same as previous, 18.iv.1917 (3 ♀, CUIC, UMSP), same as previous, 31.iii.1917, S.H. Emerson (1 ♀, UMSP), same as previous, 4.iv.1924, C.H. Curran (1 ♀, AMNH), same as previous, 15.viii.1928, ALM (3 ♂, 2 ♀, USNM), same as previous, 5.viii.1947 (1 ♂, INHS), same as previous, 26.iii.1991 (2 ♀, USNM); Yates Co., Penn Yan, 30.vii.1972, FCH (1 ♂, 1 ♀, CAS).

North Carolina: Mt. Pisgah, 4-5000 ft, 8.vii.1959, H.V. Weems Jr. (3♂, 5 ♀, FSCA); Haywood Co., Wagon Tree Gap, Blue Ridge Pkwy, 30.v.1965, J.G. Chillecott (1 ♂, 1 ♀, CNC), 19 mi. S Canton, 2.viii.1988, RLH (2 ♀, MTEC); Macon Co., Highlands, 17.vi.1957, JRV (1 ♀, CNC); Swain Co., GtSmokies NP, Clingmans Dome, 21.vi.1941, ALM (1 ♂, 2 ♀, USNM), Nantahala Gorge, 2000 ft, 27.viii.1930, N. Banks (1 ♀, MCZ); Transylvania Co., Near L Toxaway, 3000 ft, 28.viii.1930, Carpenter (1 ♀, MCZ), "Tennessee Ridge" Mts, Owen's Gap, 4000 ft, 28.viii.1930, N. Banks (1 ♀, MCZ); Yancey Co., Black Mts, Mt Mitchell, 5000-6711 ft, ix.1930, N. Banks (1 ♂, MCZ). **Pennsylvania:** Allegheny Co., Carn. Mus., on window, 5.x.1903, H. Kahl (1 ♂, CMNH); Lycoming Co., 3 mi. S Ralston, 4.vi.1983, RLH (1 ♀, MTEC), 27.vii.1972, DDW (2 ♀, CAS); Mifflin Co., 0.4 mi. W Laurel Crk Rsvr, 1240 ft, 28.viii.2003, JBR (1 ♂, 1 ♀, MTEC); Philadelphia Co., West Park, Phila, 21.viii.1894, JMA (2 ♀, USNM), same as previous, C.W. Johnson (1 ♂, EMUS), same as previous, Philadelphia (3 ♀, MCZ). **South Carolina:** Pickens Co., Table Rock State Park, 35°2'N, 82°32'W, 1500', 6.vii.1958, J. Laffoon (6 ♂, 8 ♀, ISUI). **Tennessee:** Smoky Mts, 5800 ft, 6.vi.1939, C.P. Alexander (1 ♂, EMUS). **Virginia:** Botetourt Co., North Crk Area, 21.ix.1983, Kondratieff (1 ♂, 2 ♀, CSUC), near Arcadia, 21.ix.1983, S. Bullington (3 ♂, CSCA); Dickenson Co., Ramey Fork, 3 mi. N Clintwood, 1400 ft, 15.viii.2008, JBR (3 ♂, 1 ♀, MTEC), Pound R, N37°11.58', W82°26.63', 4.vi.2008, JBR (3 ♂, 2 ♀, MTEC), Mill Crk, 0.5 mi. NW Blowing Rock, 1900 ft, N37°1.929', W82°25.514', 16.vi.2008, JBR (1 ♂, MTEC); Grayson Co., Mt Rogers S slope, 13.vii.1969, J.B. Karren (1 ♀, EMUS); Montgomery Co., Cedar Run – RR tracks, 13.vii.1979, P. Firth (1 ♀, CSUC); Patrick Co., Pinnacles of Dan, 15.iv.1978, B. Kondratieff (1 ♀, CSUC). **West Virginia:** Boone Co., Hwy 3 at Lincoln Co. line, 3.viii.1992, RLH (1 ♂, MTEC); Braxton Co., 1.5 km NW Falls Mill, Little Kanawha R, seep, 14.xi.2003, D.R. Jones & N.L. Smith (4 ♀, MTEC); Logan Co., 2 mi. SE Blair, 3.viii.1992, RLH (2 ♂, 1 ♀, MTEC); Nicholas Co., Gauley R, Summerville Dam, 1400 ft, 11.v.2004, JBR (1 ♂, 3 ♀, MTEC); Wyoming Co., under bridge over creek, 14.vii.1982, Kondratieff (1 ♂, CSUC).

***Liancalus hydrophilus* Aldrich, 1893**

Figs 3B, 4B, 8, 11B, 14A, 16C

Diagnosis. This is one of two Nearctic species in which males have setae on the wing margin (Fig. 4). Males can be distinguished by the relatively short, rounded lobe between wing veins M_1 and CuA_1 (Fig. 4B), and by the long cerci with evenly spaced, long setae along their full-length (Fig. 8).

Redescription. Male. Body length 8.0–10.5 mm, wing length 6.5–8.0 mm. Habitus (Fig. 8). **Head:** Face rather broad, widening toward palpus, metallic green above frontoclypeal suture, covered with dense silver pollen below suture. Vertex covered with silver pollen that is often sparser medially revealing metallic green-blue ground color. Vertical setae on very small elevation; ocellar tubercle prominent with 2 large setae (slightly larger than vertical setae); with 2 postocellar setae which are two-thirds length ocellar setae; postocular setae approximately one-half size of vertical setae with about dorsal one-half of postocular setae black (approximately 15 black setae), ventral half (approximately 10 setae) white and more slender and slightly longer than black postocular setae. Ventral postcranial hairs (beard) rather sparse, usually wholly white (sometimes dorsal-most 1–3 hairs brown to black). Palpus black, covered with moderately dense silver pollen apically, golden brown pollen at base, with long, black setae on basal two-thirds. Antenna black, first flagellomere about as long as wide, slightly pointed apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum green to green-blue with moderately dense silver-gray pollen, with red-bronze stripes between acrostichal and dorsocentral setae, and along intra-alar setae; posterior slope of scutum blue-green with medial bronze stripe; notopleuron and postpronotum (humerus) covered with dense silver pollen, often with some blue-green reflections; 6 dorsocentral setae; 3–8 acrostichal setae (usually < 6), in a single row; 2 notopleural setae; postpronotum with 1–3 strong, black setae and often a few smaller white hairs; 2 presutural intra-alar seta (one near suture); 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum mostly bronze, with some green-blue color at base, covered with sparse silver pollen, with 6 large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic bronze-green, covered with dense silver-gray pollen, without setae or hairs.

Legs: Legs concolorous with pleura, but with slightly less silver-gray pollen, femoral ‘knees’ very narrowly orange. Coxa I uniformly covered with white hairs on anterior surface (length of hairs subequal to width of coxa I), with a couple to few black, slender setae at apex. Coxa II with scattered white hairs anteriorly, a few white and black setae near apex, and a black *ad* seta just beyond 1/2. Coxa III with a few short, white hairs on anterior surface and a black dorsal seta near 1/2. Femur I with row of black, *pd* setae on apical half (length \leq half width of femur). Femur II with row of posterior setae on distal half (length \leq width of femur), those near to just beyond middle of femur longest, white, and becoming black and shorter apically. Femur III with scattered white hairs (length \leq width of femur) dorsally at base. Tarsus I(2) very short, about as long

as wide, with ventral row of setae/setulae (Fig. 3B). Ratios of tibia:tarsomeres for leg I: 17-7-2-5-3-2; for leg II: 24-20-8-4-2-2; for leg III: 35-17-13-4-2-2.

Wing (Fig. 4B): Hyaline, with a longitudinal spurious vein immediately above M_1 that ends near junction of M_1 with dm-cu and usually two small brown clouds just beyond junction of dm-cu and CuA_1 (these spots sometimes faint); apical portion of membrane between R_{4+5} and M_1 with a small, narrow, translucent, area that is white in certain lights and enclosed within a small, brown cloud. Fourth costal sector (between R_{4+5} and M_1) flattened with a cluster of 3–6 black setae at apex of M_1 that are usually fused apically; wing margin between M_1 and CuA_1 with a rather short (length subequal to width), broad lobe bearing several black setae at apex that are usually fused apically. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate, rather blunt at apex (Fig. 8); T1 metallic green with dense silver pollen laterally becoming less dense dorsally, with bronze along posterior edge and occasionally with a diffuse bronze stripe dorsally. T2–T4 green-blue with dense silver pollen on basal one-half to two-thirds, with apical one-third to one-half bronze; T2 usually bronze dorsally at base. T5 dark bronze with metallic green reflections and sparse silver pollen. T6 dark bronze with blue-green reflections and dense silver pollen. T1–T3 with wholly to nearly wholly yellowish hair laterally, longest on T1 and T2. Sternites bronze with dense silver-gray pollen. S1 bare except for lateral small tuft of yellow hairs at extreme base. S2 and S3 with sparse yellow hairs. S4 mostly bare. Hypopygium (Fig. 11B): cercus very long, as long or longer than abdomen, slender, cylindrical, with very long, evenly-spaced, pale yellow setae along full-length ventrally (Fig. 8), with some hairs crinkly on apical half.

Female. Body length 6.0–8.0 mm, wing length 6.0–7.0 mm. Similar to male except for face wider, dark metallic green to violet covered with sparse to moderately dense brown pollen; palpus black with silver pollen along margins and dense brown pollen basally, and black setae. Femur I with *pd* row of black setae on apical half (longest subequal to width of femur) and very sparse, very short white hairs on posterior and ventral surface. Femur II posteriorly to *pd* with row of short (length \leq width of femur) hairs which are white on basal half and black on apical half. Wing (Fig. 16C) hyaline, with a rather large, diffuse, faint brown cloud in cells r_{4+5} and $bm+dm$ and crossing M_1 just beyond midpoint of wing; usually with some indistinct brown clouding along wing margin between R_1 and M_1 .

Remarks. Aldrich (1893) described the habits of this species at the type locality near Custer, SD. On page 570, Aldrich writes, "From several seams in the rock there is a gentle flow of almost ice-cold water, which covers a considerable area of vertical rock in a thin sheet. Standing in this icy water were my flies!" Similarly, Van Duzee (1917: 127) wrote, "I took a single male...resting on rocks over which water was trickling in South Cheyenne Canon [sic]".

Distribution. This species is confined to interior western North America (Fig. 14A).

Type material examined. **LECTOTYPE** (designated here to fix identity of the species) ♂, labelled: "Custer/ SD"; "JM Aldrich/ Coll"; "COTYPE/ No. 50276/ U.S.N.M." [red label]; "Liancalus/ hydrophilus/ Ald." [hand-written]; "LECTOTYPE/



Figure 4. Wings of male **A** *Liancalus pterodactyl* sp. n., and **B** *L. hydrophilus* Aldrich. Scale bars = 1 mm.

♂ *Liancalus/ hydrophilus* Aldrich/ des. Runyon & Hurley" [red label] (USNM). **PARALECTOTYPE:** ♂, labelled: "Cotype" [hand-written]; "Custer SD"; "det. Aldrich"; "Type 13503" [red label]; "PARALECTOTYPE/ ♂ *Liancalus/ hydrophilus* Aldrich/ des. Runyon & Hurley" [red label] (MCZ).

Additional material examined. USA. Arizona: Cochise Co., 18–28.vi.1916, V.W. Owen (4 ♂, 6 ♀, CAS), Portal, S.W. Res. Sta. AMNH, 23.vi.1968, V.D. Roth & FCH (1 ♂, MTEC), Rustler Park, 9.vi.1972, W.W. Wirth (1 ♂, 1 ♀, USNM), same as previous, 5.vii.1940, R.H. Beamer (1 ♀, SEMC), Ramsey Cyn, Huachuca Mts, 5500 ft, 23.iv.2002, RLH & JBR (3 ♀, MTEC), Cave Crk at Herb Martyr Campgrd (Dam), 5800 ft, N31°52.35', W109°14.09', 6.iv.2011, JBR (1 ♂, 1 ♀, MTEC), Chiricahua Mts, Rustlers Pk., 5.vii.1940, D.E. Hardy (1 ♀, SEMC); Coconino Co., Oak Crk Cyn, 24 mi. S Flagstaff, 25.vii.1959, Samuelson & Radford (1 ♀, UAIC), Oak Crk Cyn, 3500', G.C. Eickwort (2 ♀, MSUC); Graham Co., Wet Cyn, Pinaleno Mts, 5900 ft, 26.iv.2001, RLH & JBR (1 ♂, 1 ♀, MTEC); Pima Co., Catalina Mts, Marshall Gulch near Summerhaven, 28.v.1986, J. Jenkins (15 ♂, 15 ♀, MTEC), Mt Lemmon, Catalina Mts, 14.vi.1979, M. Hetz (1 ♂, UAIC), Cat-

alina Mts, HkHy mi22, 9.vi.1958, Nutting & Butler (1 ♀, UAIC); Santa Cruz Co., Coronado National Forest, Santa Rita Mts, Madera Cyn, 3–4.vi.1991, B.J. Sinclair (2 ♂, 1 ♀, CNC), same as previous, 27.iv.1979, K.N. Barber (1 ♂, 1 ♀, DEBU), same as previous, 5700 ft, N31°42.59', W110°52.18', 4.iv.2011, JBR (1 ♀, MTEC). **Colorado:** Green Mt Falls, 12.viii.1943, H.H. Ross (1 ♀, INHS); Boulder Co., Boulder (1 ♂, 1 ♀, CUIC), same as previous, JMA (2 ♂, 2 ♀, USNM), same as previous, C.W. Johnson (3 ♂, 1 ♀, MCZ); Cameron Pass, 13.viii.1964, FCH (2 ♂, 2 ♀, FSCA), Cameron Pass, Campbell L, 12.viii.1947, H.H. Ross (2 ♂, INHS); Garfield Co., Rifle, 18.vii.1947, FCH (2 ♂, 3 ♀, CAS, MTEC, ODAC), Glenwood Cyn, off I-70 rest stop, 19.ix.1986, M.K. Kroening (1 ♂, 1 ♀, CSUC); Larimer Co., Lory St. Park, 15.iv.1984, P. Opler (2 ♀, CSUC), Buckhorn Crk, 12.ix.1996, B. Kondratieff (1 ♂, CSUC); Mesa Co., Big Crk at jct. with Plateau, Rt. 330, 19.ix.1986, M.K. Kroening (1 ♂, CSUC); Mineral Co., Hwy 160, Treasure Falls, 15.viii.1983, PHA (4 ♀, CAS); Moffat Co., 11.vii.1986, Yampa R, B. Kondratieff (1 ♂, CSUC); Montezuma Co., Dolores, 9.vi.1960, FCH (1 ♂, 1 ♀ FSCA); Ouray Co., 5 km S of Ouray, on Uncompahgre R, 2697 m, 14.viii.1973, PHA (1 ♂, CAS); Park Co., Fairplay, 13.vi.1961, FCH (1 ♂, 2 ♀, FSCA, MTEC). **Nevada:** Elko Co., Lamoille Crk, 25 mi. SE Elko, 8800 ft, 11.viii.2005, JBR & RLH (1 ♂, 3 ♀, MTEC), Ruby Mts, W of Terrace Cmpgrd, 16.viii.1989, RLH (1 ♂, 1 ♀, MTEC). **New Mexico:** Catron Co., Luna, 25.vi.1968, FCH (4 ♂, 5 ♀, CAS, EMUS, FSCA), Reserve, 25.vi.1968, FCH (1 ♂, 1 ♀, CAS, FSCA); Grant Co., Silver City, 25.vi.1968, FCH (1 ♀, MTEC); Socorro Co., Magdalena Mts, viii.1894, H. Kahl (2 ♂, 1 ♀, CMNH), Magdalena, W.M. Wheeler (2 ♂, 2 ♀, AMNH, CAS). **South Dakota:** Custer Co., Custer (5 ♂, 8 ♀, LACM, UMSP, USNM), French Crk, Black Hills, A. Borkent, 25.iv.1981 (2 ♀, CNC); Lawrence Co., Bridal Veil Falls, 6 mi. S Spearfish, 4250 ft, 19.viii.2003, JBR (2 ♂, 2 ♀, MTEC). **Utah:** Boulder Mt, 26.viii.1978, FCH (14 ♂, 7 ♀, CAS, EMUS, FSCA, MTEC), Zion Pk, 29.vi.1940, ALM (1 ♂, USNM); Cache Co., Logan Meadows, 15.x.1939, G.F. Knowlton & FCH (2 ♂, 2 ♀, CAS, CNC), Logan Cyn, 28.viii.1939, FCH (3 ♂, 2 ♀, CAS, EMUS, OSU), same as previous, 15–18.viii.1940 (2 ♂, 5 ♀, EMUS), same as previous, 24.x.1969, R. Kirkland (1 ♂, BYU), Willow Park, 23.viii.1986, B.C. Giwod (1 ♂, EMUS), Logan, 3–11.1934, C.F. Smith (1 ♀, AMNH), same as previous, T.O. Thatcher (1 ♀, AMNH); Daggett Co., Linwood, 6.ix.1939, G.F. Knowlton & FCH (1 ♂, 1 ♀, CNC), Dowd Springs, 17.viii.1978, FCH (1 ♂, 8 ♀, MTEC); Duchesne Co., Uinta Canyon, Wandin Park 18.vii.1950, FCH (1 ♀, CNC), Pole Crk, Uinta Mts, 19.vii.1950, FCH (1 ♂, FSCA); Garfield Co., Death Hollow jct., Boulder Mail Trail, 37°50'37N, 111°30'52W, 11.vii.2000, E.C. Green, W.N. Mendel, M. Moody, C.R. Nelson (1 ♀, BYU), Grand Staircase-Escalante Natl. Monument, spring off Hwy 12, 7.5 mi. E Henrieville, N 37°36'46", W 111°53'48", 6578 ft, malaise trap, 2–17.viii.2000, W.N. Mendel, E.C. Green, M. Moody (2 ♂, BYU, MTEC), Calf Crk between upper and lower falls, off Hwy 12, 37°51'18N, 111°27'07W, E.C. Green, W.N. Mendel, C.R. Nelson (2 ♂, 1 ♀, BYU); Grand Co., Moab, 4.vi.1940, G.F. Knowlton & FCH (3 ♂, 3 ♀, FSCA, MTEC), same as previous, 18.v.1939 (1♂, 4 ♀, CAS, EMUS), La Sal Mts, Warner Cp.,

9500', 21.vii.1968, Malaise trap, W.J. Hanson (1 ♀, EMUS), Westwater, 26.ix.1939, G.F. Knowlton & FCH (1 ♀, INHS); Kane Co., Sheep Crk jct., Skutumpah Rd, 37°29'43N, 112°03'59W, 5531 ft, 29.ix.1999, R.W. Baumann, K.T. Huntzinger, C.R. Nelson (1 ♂, MTEC), Snake Crk above jct. Paria R, 37°20'44N, 112°00'29W, 3-4.viii.2000, E.C. Green, W.N. Mendel, M. Moody, C.R. Nelson (1 ♂, BYU); San Juan Co., La Sal, 27.vi.1951, FCH (3 ♂, 6 ♀, CAS, EMUS, FSCA, CUIC); Utah Co., Mt Timpanogos, 4.viii.1946, FCH (3 ♂, 1 ♀, CNC, LACM), same as previous, 12.vii.1941, FCH & G.F. Knowlton (1 ♂, 1 ♀, EMUS), American Fork, 6.vii.1939, G.F. Knowlton (1 ♂, EMUS), St. George, 20.iv.1939, G.F. Knowlton & FCH (1 ♀, EMUS), Battle Crk, nr. Pleasant Grove, 31.vii.1984, C.R. Nelson (1 ♀, BYU), 12 mi. E Thistle, Hwy 6, 14.viii.1984, Nelson & Allred (2 ♂, 1 ♀, BYU); Washington Co., Zion Nat'l Park, Birch Crk, 27.vii.1975, W.J. Hanson (2 ♂, 5 ♀, EMUS), Zion Nat'l Park, narrows, 21.vi.1981, C.R. Nelson (1 ♂, 2 ♀, BYU). **Wyoming:** Albany Co., Laramie, 15.viii.1950, N. Davis (1 ♀, ISUI); Park Co., Yellowstone Nat'l Park, Rustic Falls, 7200 ft, 44°56.03' N, 110°43.55'W, 28.viii.2009, JBR (1 ♀, MTEC), Yellowstone Park, falls, 23.vii.1923, ALM (2 ♀, USNM).

Liancalus limbatus Van Duzee, 1917

Figs 2C, 3D, 5C, 10C, 14B, 16D

Diagnosis. Males of this species have long cerci, wing without marginal setae but with a distinct marginal lobe between veins M_1 and CuA_1 , and with crossvein dm-cu relatively straight (Fig. 5C). Female wing as in Fig. 16D.

Redescription. Male. Body length 8.0–9.0 mm, wing length 6.5–7.5 mm. **Head:** Face narrow, slightly widening toward palpus, metallic green to bronze with sparse to moderately dense silver pollen. Vertex covered with silver pollen mostly hiding metallic green to blue ground color. Vertical setae on very small elevation; ocellar tubercle prominent with 2 large setae (subequal in size to vertical setae); with 2 postocellar setae which are one-half to two-thirds size of ocellar setae; postocular setae approximately one-half size of vertical setae with about dorsal one-half of postocular setae black (approximately 15 black setae), ventral half (approximately 10 setae) white and more slender and slightly longer than black postocular setae. Ventral postcranial hairs (beard) rather sparse, usually wholly white but rarely with 1–3 brown to black setae. Palpus relatively small, black, covered with sparse silver pollen and scattered yellow to yellow-brown hairs. Antenna black, first flagellomere about as long as wide, rounded apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum green to green-blue with moderately dense silver-gray pollen, with bronze to bronze-green stripes between acrostichal and dorsocentral setae and along intra-alar setae; posterior slope of scutum and scutellum blue-green with some silver pollen; notopleuron and postpronotum (humerus) covered with dense silver pollen, usually with some blue-green or bronze reflections; 6 dorsocentral setae; 6–9 large acrostichal setae (largest two-thirds size of dorsocentral setae), in a single row; 2 noto-

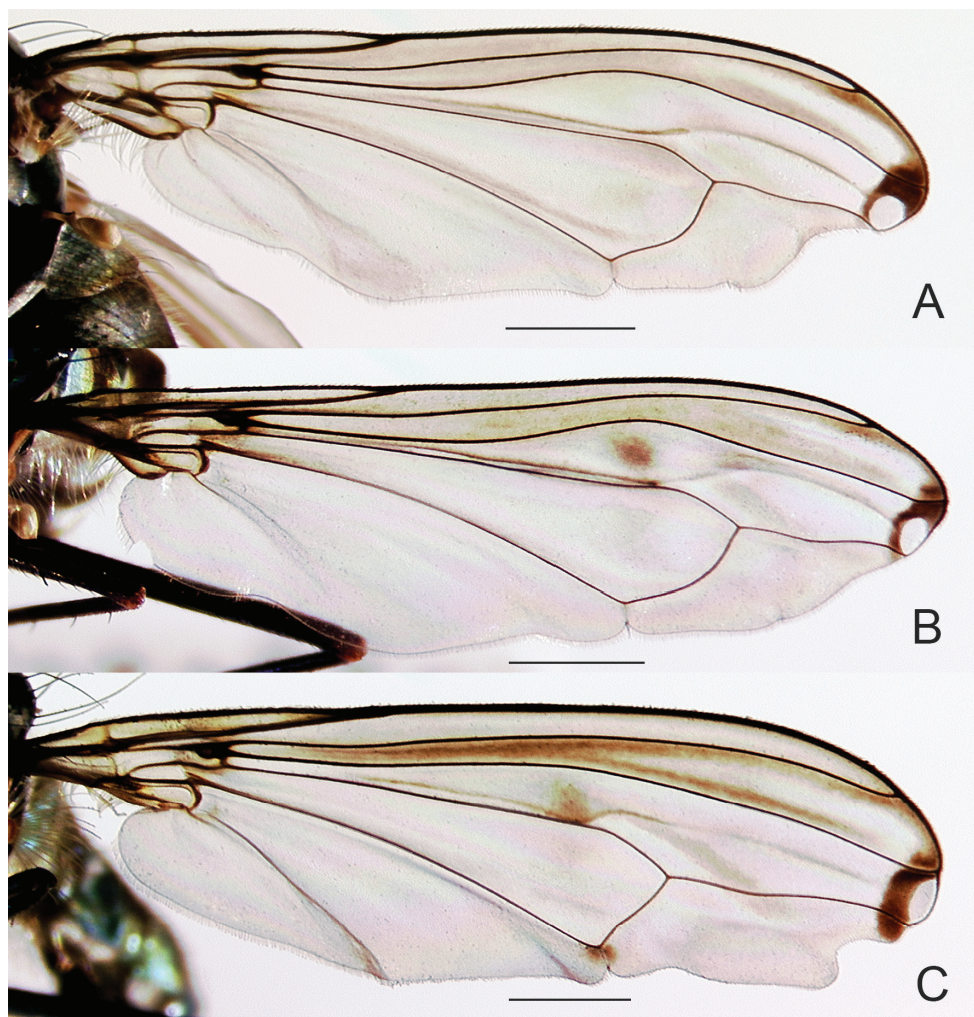


Figure 5. Wings of male **A** *Liancalus genualis* Loew **B** *L. sonorus* sp. n., and **C** *L. limbatus* Van Duzee. Scale bars = 1 mm.

pleural setae; postpronotum with 1–3 strong, black setae and often a few smaller white hairs; 2 presutural intra-alar setae (one near suture); 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum with 6 large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic green-bronze, covered with dense silver-gray pollen, without setae or hairs.

Legs: Legs concolorous with pleura, but with slightly less silver-gray pollen, femoral ‘knees’ very narrowly orange. Coxa I uniformly covered with white hairs on anterior surface (length of hairs subequal to width of coxa I), with a couple black, slender setae near apex. Coxa II with scattered white hairs anteriorly, a few white and black setae near apex, and a black *ad* seta just beyond 1/2. Coxa III with a few short, white hairs

on anterior surface and a black dorsal seta near 1/2. Femur I with row of short, black, *pd* setae on apical half (length \leq half width of femur) and scattered, short, white hairs near base. Femur II with row of posterior hairs/setae (length \leq width of femur), those on basal half white (longest near to just beyond middle of femur) and becoming black and shorter apically. Femur III with white hairs (length subequal to width of femur) dorsally to posteriorly at base. Tarsus I(2) very short, about as long as wide, with ventral row of setae/setulae (Fig. 3D). Ratios of tibia:tarsomeres for leg I: 16-8-2-4-3-2; for leg II: 26-20-8-4-2-2; for leg III: 37-20-17-6-2-2.

Wing (Fig. 5C): Hyaline, infuscated on anterior third, especially between R_{2+3} and R_{4+5} (mostly along veins apically); with a longitudinal spurious vein between R_{4+5} and M_1 that is arched anteriorly near 2/3 of wing and terminates near midpoint of a semicircular, translucent, area that is white in certain lights and enclosed within a small, brown cloud; with a diffuse brown spot just above spurious vein at arch and small brown spot on CuA_1 near dm-cu. Apex of wing shallowly excavated at M_1 , with a broad, blunt, apically-pointed lobe between M_1 and CuA_1 , this lobe without setae. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate, blunt at apex (Fig. 2C); T1 metallic green with dense silver pollen laterally becoming somewhat less dense dorsally. T2-T4 blue-green with dense silver pollen basally, bronze apically. T5 dark bronze with metallic green reflections and sparse silver pollen. T6 dark bronze with blue-green reflections and with dense silver pollen. T1-T3 with yellowish hair laterally, longest on T1 and T2, without black hairs or setae. Sternites bronze with dense silver-gray pollen. S1 bare except for lateral small tuft of yellow hairs at extreme base. S2 and S3 with sparse yellow hairs. S4 mostly bare. Hypopygium (Fig. 10C): cercus very long (as long as abdomen in unshriveled specimens), slender, cylindrical, with yellow hairs that are longest medially (Fig. 2C).

Female. Body length 7.0–8.0 mm, wing length 6.5–7.5 mm. Similar to male except for face twice as wide, dark green to violet obscured by moderate to dense brown pollen; palpus larger, black with silver pollen apically, with dense golden-brown pollen in middle at base, and black setae. Acrostichal setae large, stout, two-thirds to three-quarters size of dorsocentral setae. Femur I with *pd* row of black setae on apical half (longest subequal to half width of femur) and sparse, very short white hairs on posterior and ventral surface. Femur II posteriorly with row of white hairs/setae on basal half to two-thirds (longest at base and just beyond middle) and black setae on apical half to one-third (longest of these posterior hairs/setae subequal to width of femur). Wing (Fig. 16D) hyaline, with three to four diffuse brown clouds: one in cells r_{4+5} and $bm+dm$ near midpoint of wing (this often appears like two ‘spots’ but actually connected by sometimes light brown clouding), one light brown cloud on M_1 beyond crossvein dm-cu, and usually with very small light brown clouding on R_{4+5} at apex of wing; sometimes a small brown cloud is evident on CuA_1 .

Remarks. The type specimens were collected by Van Duzee (1917: 128) "at Berkeley, California, May 8th, on a wall of rock in a little canyon; the wall was covered with water-soaked moss". Specimens have commonly been collected on or near beaches and sea cliffs.

Copulation of this species was described by Peter Dyte (in litt. to Richard Hurley, 1988): "A pair of *Liancalus limbatus* V.D. were seen in copula on a seepage at Wreck Beach, Vancouver, B.C., Canada, on 5.vii.1988, at 16.18 hrs. They were captured by placing a 3×1 in[ch] tube over them and they remained in copula in the tube until 17.20 hrs...All her tarsi and his mid and hind tarsi were on the substrate, but his foretarsi were held against the sides of her third abdominal segment with their apices projecting slightly below her abdomen. Thus the modified second segment of his foretarsus would have been touching her abdomen, though the separate tarsal segments could not be distinguished with the hand lens available. His long genital lamellae pointed forwards below the female abdomen but not touching it".

Distribution. This species occurs primarily along or near the Pacific coast from central California to Alaska, but also inland in Idaho, Oregon, Washington and British Columbia (Fig. 14B).

Type material examined. **HOLOTYPE** ♂, labeled: "Berkeley, Cal./ May 8 1915/ MC Van Duzee"; "*Liancalus/ limbatus/* Holotype. Van Duzee" (CAS). **PARATYPE** ♀, same data as holotype (CAS).

Additional material examined. **CANADA. British Columbia:** Vancouver, 8.viii.1917, ALM (1 ♂, USNM), P Rupert, 11.ix.1921, W.B. Anderson (2 ♂, CNC), 27 mi. E Pr. Rupert, on tide flats, 24.vi.1960, R.J. Pilfrey (1 ♀, CNC), Vancouver, Point Grey, on seepage on earth cliff, 23.vii.1973, JRV (4 ♂, 4 ♀, CNC), same as previous, 26.vii.1973 (6 ♀, CNC), same as previous, 23.ii.1973 (1 ♀, CNC), same as previous, 15.v.1973 (1 ♀, CNC), Robson, 19.viii.1947, H.R. Foxlee (1 ♀, CNC), same as previous, 3.ix.1948 (1 ♀, CNC), same as previous, 21.x.1955 (1 ♂, UBCZ), Cultus Lake, 8.vii.1948, H.R. Foxlee (1 ♀, CNC), Vancouver, 28.iii.1902, C.W. Johnson (1 ♀, MCZ), Hwy 97, Bijoux Falls Park, mileage 115.3 miles (185.6 km) from Prince George, Stop-234, 6.viii.1989, PHA (1 ♀, CAS), Vancouver, University of British Columbia, Wreck Beach Trail, behind beach, 8.vii.1988, PHA (1 ♀, CAS). **USA. Alaska:** Juneau Co., Thane, 29.vii.1958 (1 ♂, WSU). **California:** Santa Cruz Mts., 24.vii.1895 (1 ♂, 1 ♀, LACM); Humboldt Co., Arcata, 19.v.1976, M. Terzich (1 ♀, MTEC), Arcata, 22.iii.1981, RLH (2 ♀, MTEC); Marin Co., Muir Woods, 7.viii.1915, ALM (1 ♂, 1 ♀, USNM), Ross, 22.vi.1955, H.L. Mathis (1 ♂, 1 ♀, UCDC), Stinson Beach SP, 2nd inlet S main beach, sweeping rocks and vegetation about waterfall at ocean beach, 21.vi.1970, I.A. Boussy (1 ♂, 1 ♀, CAS), Mt Tamalpais, 26.v.1974, D.G. Denning (1 ♂, UCDC), Point Reyes, 19.iv.1980, S.A. Marshall (2 ♂, 2 ♀, DEBU), Phoenix Lake Pk., 22.v.1949, C.H. Spitzer (1 ♀, EMEC), same as previous, 30.v.1949 (1 ♂, EMEC); Monterey Co., Pacific Grove, 5-8.v.1906, JMA (8 ♂, 8 ♀, USNM); Napa Co., Butts Cyn, 0.5 mi. S Napa Co. line, 7.v.1970, E.E. Grissell & R.F. Denno (1 ♀, UCDC); San Mateo Co., Martin's Beach, 9.ix.1969, T.W. Davies (1 ♂, 2 ♀, CAS), Memorial Park, 15.vii.1951, PHA (1 ♀, CSCA); Santa Barbara Co., Sta. Barbara, 6.vii.1917, JMA (1 ♂, 4 ♀, USNM); Santa Cruz Co., Capitola, 7-12.vi.1940, M.T. & H.B. James (14 ♂, 14 ♀, CSUC, WSU), Davenport, 1.ix.1948, W.W. Wirth (3 ♂, 1 ♀, EMEC, USNM), Santa Cruz, beach, 15-17.vi.1950, M.T. James (5 ♂, 11 ♀, WSU), 1 mi. N Davenport, on beach, 4.vii.1967, A. & A. Gillogly (1 ♂, UCR), Santa

Cruz, beach, 15-17.vi.1950, M.T. James (4 ♂, 12 ♀, WSU), Santa Cruz, 9.vii.1972, D.G. Denning (1 ♀, UCDC); Sonoma Co., Bodega Bay, 13.v.1963, C.G. Moore (1 ♂, UCDC), Stillwater Cove, 23.v.1954, E.I. Schlinger (2 ♂, 2 ♀, UCDC), same as previous, J.G. Downey (1 ♂, 1 ♀, UCDC). **Idaho:** Adams Co., Little Salmon R, 18 mi. N New Meadows, 8.viii.1979, RLH (1 ♀, MTEC); Boise Co., Canyon Crk, 30 mi. NE Lowman, 15.ix.1981, RLH (1 ♀, MTEC); Kootenai Co., Beauty Crk, near Lake CD'A, 31.viii.1976, D.F. Veirs (1 ♀, WFBM); Latah Co., Mts Moscow, 25.vii.1920, R.C. Shannon (1 ♂, 1 ♀, USNM), Moscow Mts, East Twin Peak, 19.vii.1983, R.S. Zack (2 ♂, 1 ♀, WSU), Lower Sand Crk, nr. Bonami Crk, 16 mi. E Potlatch, 2900 ft, 5.viii.1979, WJT (3 ♂, WSU), same as previous, 9.viii.1979 (2 ♂, 6 ♀, WSU), same as previous, 28.viii.1982 (1 ♂, 1 ♀, WSU), 7 mi. N Troy, near Big Meadow Recreation Area, 3000 ft, 31.vii.1979, WJT (1 ♂, 1 ♀, WSU), Big Meadow Recreation Area, 7 mi. NNE Troy, 3000 ft, 7.viii.1986, WJT (1 ♂, 1 ♀, WSU); Nez Perce Co., Juliaetta Falls, 5.2 mi. S. Juliaetta, 3.iii.1983, J. Jenkins (2 ♀, MTEC). **Oregon:** Mt Hood, 29.vii.1966, FCH (10 ♂, 4 ♀, EMUS, FSCA, MTEC); Benton Co., Mary's Peak, Parker Crk, roadside seepage, 26.ix.1967, KJG (1 ♂, ODAC), Marys Peak, Hwy 34, 4097', 16.vii.1968, B.V. Peterson (1 ♂, 1 ♀, CNC), Parker Crk, Marys Peak Rd, 1.vii.1971, G. Steyskal (1 ♂, 1 ♀, OSAC), Mary's Peak nr Corvallis, F.R. Cole (1 ♂, EMEC); Coos Co., Charleston, marine biological station, 9.vii.1954, M.T. James (1 ♀, WSU); Hood River Co., Hood River, seepage over road cut, 15.viii.1966, KJG (2 ♂, 1 ♀, CAS, OSAC), 8 mi. NW Mt Hood, Lolo Pass Rd, roadside seepage, 9.x.1966, KJG (1 ♂, OSAC), 20 mi. S Hood River, vertical roadside seepage, 16.viii.1966, KJG (1 ♂, 2 ♀, CAS, MTEC, OSAC), Hood River, 21.vi.1917, F.R. Cole (1 ♀, CAS); Jackson Co., 10 mi. S Ruch, stream margins, 22.v.1964, KJG (2 ♀, ODAC); Josephine Co., Grants Pass, black light trap, 15.ix.1965, KJG (1 ♂, ODAC); Lincoln Co., Agate Beach, base sea cliff, 16.v.1976, R.L. Westcott (1 ♀, ODAC), 15 mi. S Newport, seepage on sea cliffs, 13.vii.1966, KJG (1 ♂, 3 ♀, FSCA, OSAC), Newport, seeps along coastal cliffs, 22.vii.1983, WJT (1 ♂, 10 ♀, WSU), 20 mi. S Hood River, vertical roadcut seepage, 16.viii.1966, KJG (1 ♂, OSAC), Yachats, 20.vi.1939, G.E. Bohart (1 ♂, UCDC), 1 mi. N Depoe Bay, H₂O spring above beach, 24.vi.1956, J.D. Lattin (1 ♂, OSAC); Linn Co., 1 mi. S Marion Forks, 15.v.1967, KJG (2 ♀, ODAC), same as previous, seepage along road cut, 31.vii.1966 (5 ♂, 2 ♀, CAS, CSCA, ODAC, OSAC), same as previous, shaded vertical seepage, 24.viii.1967 (7 ♂, 4 ♀, ODAC, OSAC, MTEC), same as previous, 21.vii.1969, E.M. Fisher (1 ♀, CSCA); Multnomah Co., Larch Mt, 15.viii.1966, KJG (2 ♂, FSCA), Portland, 16.vi.1926, A. Spuler (1 ♂, SEMC), Troutdale, 1.viii.1965, FCH (2 ♂, 2 ♀, FSCA, MTEC), same as previous, 23.vi.1963, L.S. Miller (1 ♀, FSCA); Tillamook Co., Oceanside, seepage along ocean cliff, 29.vii.1966, KJG (2 ♀, ODAC). **Washington:** "Washington (state)" (♀ paralectotype of *L. similis*, SEMC), Mt Adams, 24.vii.1921, ALM (1 ♀, USNM); Asotin Co., 17 mi. S Anatone, nr. Grande Ronde River, 1950 ft, dripping spring, 10.viii.1976, WJT (1 ♂, WSU); Columbia Co., Tucanon RS, Blue Mts, 13.viii.1922, V.N. Argo (1 ♂, 2 ♀, USNM); King Co., Lake Washington, 12.viii.1917, ALM (7 ♂, 6 ♀, USNM); Okanogan Co., 9 mi. W Conconully, Salmon Mdws, 4500 ft, 3-6.vii.1975, N.E. Woodley (1 ♀,

WSU), Seattle (1 ♂, 2 ♀, OSAC); Pacific Co., Ilwaco, vii.1917, ALM (3 ♀, USNM); San Juan Co., Friday Harbor, 23.vii.1905, JMA (2 ♂, 2 ♀, USNM), same as previous, 27.vii.1905 (2 ♂, USNM), Olga, 17.v.1910 (2 ♀, USNM); Skagit Co., 2 mi. S Sedro-Woolley, 28.viii.1971, H.P. Stene (2 ♂, WSU); Stevens Co., Deer Lake, near Chewelah, 6-7.v.1972, M.T. James (1 ♀, WSU); Whatcom Co., 9 mi. N Concrete, 15.vii.1969, R. Turnbow (1 ♀, UGCA).

***Liancalus pterodactyl* Runyon & Hurley, sp. n.**

<http://zoobank.org/2C4A491C-2092-404D-B9E6-DEDB36EE233B>

Figs 1, 2D, 3A, 4A, 7, 11A, 13, 16A

Diagnosis. Males are most similar to *L. hydrophilus* but have a longer, more slender setae-bearing lobe on posteroapical wing margin (Figs 4, 7). Cerci of male *L. pterodactyl* have long setae confined mostly to apical half (Fig. 2D), whereas *L. hydrophilus* has long, evenly-spaced setae along the full-length of the cerci (Fig. 8). Females are distinguished by the dorsal one-quarter or more postcranial hairs dark brown to black (other Nearctic species have at most a few dark hairs).

Description. Male. Body length 9.0–12.0 mm, wing length 7.5–8.5 mm. **Head:** Face nearly parallel-sided on dorsal half, widening toward clypeus; frontoclypeal suture near mid-face, distinct; eyes with short hairs between facets; face green-bronze (more green immediately below antenna) with silver pollen most noticeable along eyes and on ventral half of face; ommatidia essentially the same size throughout. Vertex concolorous with face, usually with dense silver pollen. Vertical setae on small elevation; ocellar tubercle prominent with 2 large setae (subequal in size to vertical setae); with 2 postocellar setae which are two-thirds length ocellar setae; postocular setae approximately half length of vertical setae with dorsal two-thirds of postocular setae black (approximately 20 black setae), ventral third (approximately 10 setae) white and more slender and slightly longer than other postocular setae. Ventral postcranial hairs (beard) abundant, white with dorsal third to one-quarter black. Palpus black, covered with silver pollen and sparse black hairs. Antenna (Fig. 1) black, first flagellomere about as long as wide, rounded apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum blue-green with bronze stripes between acrostichal setae and dorsocentral setae, and along intra-alar setae; scutellum and posterior slope of scutum blue-green, posterior slope of scutum sometimes with bronze medially; notopleuron and postpronotum (humerus) covered with dense silver pollen, usually with some blue-green reflections; usually 6–10 dorsocentral setae; 8–14 long acrostichal setae ($\geq 2/3$ length of dorsocentral setae), in a single row; 2 notopleural setae; postpronotum with 1–2 strong setae and often a few smaller hairs or setae; 2 presutural intra-alar setae; 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum blue-green with 8 (rarely 9) large marginal setae (4 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic green-bronze, covered with dense silver-gray pollen, without setae or hairs (Fig. 1).

Legs: Legs concolorous with pleura. Coxa I (Fig. 1) uniformly covered with white, slender hairs on anterior surface (length of hairs subequal to width of coxa I), with a few black, slender setae at apex. Coxa II with white hairs anteriorly, a couple black setae near apex, and a black *ad* seta just beyond 1/2. Coxa III with scattered white hairs and a black dorsal seta near 1/2. Femur I with sparse white hairs on ventral surface (length \leq width of femur). Femur II with row of short (\leq width of femur) posterior to *pv* setae on distal half, those near middle of femur white, longest and becoming black and shorter apically; with a row of very short black *ad* setae preceding usual preapical seta. Femur III with scattered white hairs (length \leq width of femur) on dorsal and posterior surface at base. Tarsus I(2) short (length subequal to width), slightly thickened, with ventral brush of setulae (Fig. 3A). Ratios of tibia:tarsomeres for leg I: 18-7-2-5-3-2; for leg II: 26-22-7-4-2-2; for leg III: 38-17-13-4-2-2.

Wing (Figs 4A, 7): Hyaline, with light brown clouding between R_{2+3} and R_{4+5} apically, most distinct along veins; with a longitudinal spurious vein immediately above M_1 that ends near junction of M_1 with *dm-cu*; apical part of membrane between R_{4+5} and M_1 with a narrow, translucent area that is white in certain lights and enclosed within a small, brown cloud (Fig. 7). Fourth costal sector (between R_{4+5} and M_1) flattened with a cluster of 3–4 long, black setae at apex of M_1 that are usually fused apically; wing margin between M_1 and CuA_1 with a long (length $> 3 \times$ width), slender, finger-like projection bearing several black setae at apex. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow (Fig. 1).

Abdomen: Cylindrical, elongate (Fig. 2D); T1 metallic blue-green, covered with dense silver pollen. T2-T4 mostly metallic blue-green with silver pollen, with apical one-third bronze, usually bronze dorsally at base. T5 dark bronze with metallic green dorsally and sparse silver pollen. T6 dark metallic blue-green with sparse to moderate silver pollen. T1-T3 with long, white hair laterally, longest on T1 and T2. Sternites bronze with sparse silver-gray pollen. S1 bare except for lateral tuft of white hairs at extreme base. S2 and S3 with sparse long, white hairs. S4 mostly bare. Hypopygium (Fig. 11A): cerci as long or longer than abdomen, slender, cylindrical, with pale yellow setae on ventral surface that are most dense and longest on apical half (Fig. 2D).

Female. Body length 7.5–9.0 mm, wing length 7.0–7.5 mm. Similar to male except for face wider; palpus covered with golden brown pollen, with denser, black setae. Femur I with *pd* row of black setae/hairs and relatively long (subequal to width of femur), white hairs on ventral and posterior surface. Femur II with pale hair on posterior surface extending nearly to base; tarsus I(2) normal, not unusually short or thickened. Wing (Fig. 16A) hyaline, of normal shape; with diffuse brown clouding immediately above M_1 before junction with *dm-cu*, this clouding often continuing posteriorly into cell *bm+dm*.

Etymology. The epithet, a noun in apposition, is in reference to the large size of this species – reminiscent of the large pterosaurs from the Jurassic; and the Greek *pteron* "wing" + *daktylos* "finger" in reference to the finger-like lobe on the wing (Fig. 4A).

Remarks. This is perhaps the largest species of Dolichopodidae, at least in terms of body length.

Distribution. This species occurs in the Northern Rocky Mountains of U.S. and neighboring Canada; one male was collected in the Trinity Alps of northern California (Fig. 13).

Type material. **HOLOTYPE** ♂, labelled: "MONTANA: Gallatin Co./ Grotto Falls 7000'/ 22 mi S Bozeman/ 19-VIII-2001/ J. B. Runyon"; "HOLOTYPE/ ♂ *Liancalus/ pterodactyl/* Runyon & Hurley" [red label] (MCZ). **PARATYPES: CANADA. Alberta:** Lake Louise, 30.x.1923, Eric Hearle (1 ♂, CNC), Banff, 6.x.1926, Eric Hearle (1 ♂, CNC). British Columbia: Robson, 13.iii.1957, H.R. Foxlee (3 ♀, UBCZ), same as previous, 14.iii.1957 (1 ♀, UBCZ), same as previous, 18.iii.1957 (1 ♀, UBCZ), same as previous, 17.x.1961 (1 ♀, UBCZ). **USA. California:** Trinity Co., Siligo Mtn, 7000 ft, 11.viii.1967 (1 ♂, CAS). **Idaho:** Bonner Co., 14 mi. NW Samuels, 26.ix.1969, W.F. Barr (1 ♀, WSU). **Montana:** Flathead Co., seep on Going to the Sun Rd nr Haystack Crk, Glacier NP, 22.ix.2003, J. Giersch (1 ♂, MTEC), Cattle Queen Crk at Highline Trail, Glacier NP, 48.832221, -113.799051, 1845 m elev, 11.ix.2012, J. Giersch (1 ♂, MTEC); Gallatin Co., Bozeman, 3.ix.1960, S. Wiegand (1 ♂, MTEC), Silken Skein Falls, 3 mi. S Hyalite Rsvr., 8333 ft, 11.viii.2000, JBR (1 ♂, MTEC), Palisade Falls, 1 mi. S Hyalite Rsvr., 7685 ft, 12.viii.2000, RLH & JBR (1 ♂, 2 ♀, MTEC), same as previous, 19.x.2000, JBR (2 ♂, MTEC), same as previous, 20.iv.2002, JBR (1 ♀, MTEC), same as previous, 20.viii.2009, JBR (3 ♂, 1 ♀, MTEC), same as previous, 12.x.2012, JBR (1 ♂, MTEC); Glacier Co., Cracker Lake inlet far West stream, Glacier NP, 48.742317, -113.651581, 1845 m elev, 9.ix.2011, J. Giersch (1 ♂, MTEC).

Liancalus querulus Osten Sacken, 1877

Figs 2F, 3F, 6A, 12A, 15A, 16G

Diagnosis. This species is most similar to *L. similis*: males of both have tarsus I with tarsomere 2 long (Fig. 3F–G), wings with apical brown clouding (Fig. 6), and very short cerci (Fig. 2E–F), but *L. querulus* males have a smaller, semicircular brown cloud near wing apex and no black speck in cell m (Fig. 6A). Female wing with three distinct brown spots and with crossvein dm-cu meeting M_1 at nearly 45° angle (Fig. 16G).

Redescription. Male. Body length 6.5–8.0 mm, wing length 6.0–7.5 mm. **Head:** Face rather broad, uniformly covered with dense silver pollen. Ommatidia near face slightly larger than remaining ommatidia. Vertex covered with dense silver pollen, often with some metallic green or blue color near middle. Vertical setae on very small elevation; ocellar tubercle prominent with 2 large setae (subequal in size to vertical setae); with 2 postocellar setae which are three-quarters length ocellar setae; postocular setae slightly less than one-half length of vertical setae with dorsal one-third of postocular setae black (approximately 10 black setae), ventral two-thirds (approximately 15 setae) white and more slender and slightly longer than black postocular setae. Ventral postcranial hairs (beard) rather sparse, wholly white. Palpus black, covered with sparse to moderately dense silver pollen and sparse black hairs. Antenna black, first

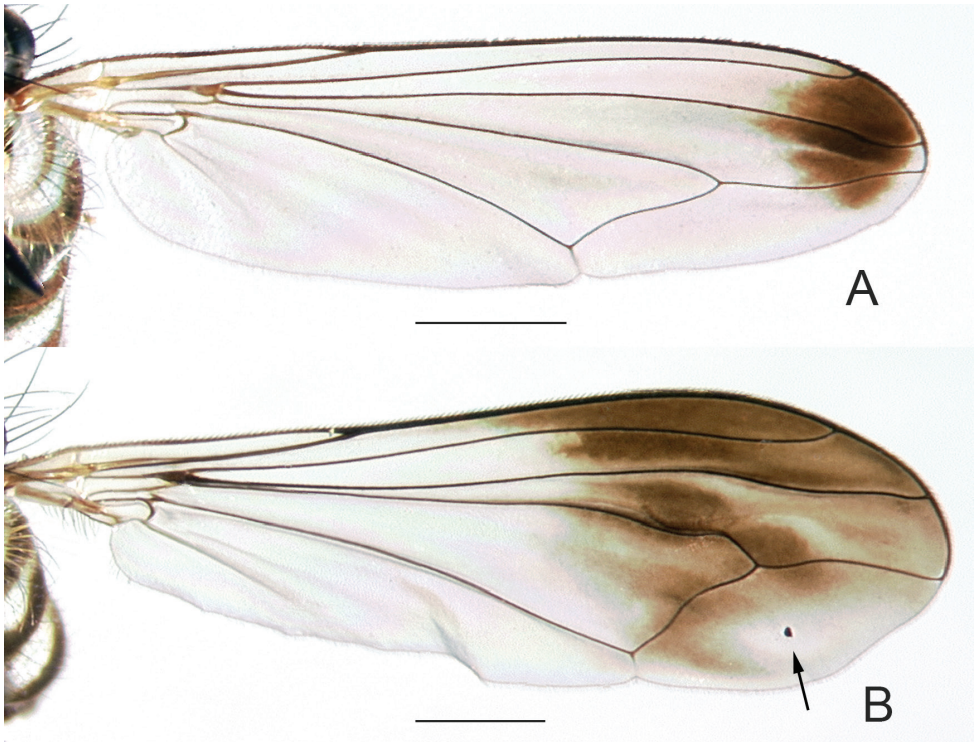


Figure 6. Wings of male **A** *Liancalus querulus* Osten Sacken, and **B** *L. similis* Aldrich. Scale bars = 1 mm. Note black speck in cell m of *L. similis*, indicated by arrow.

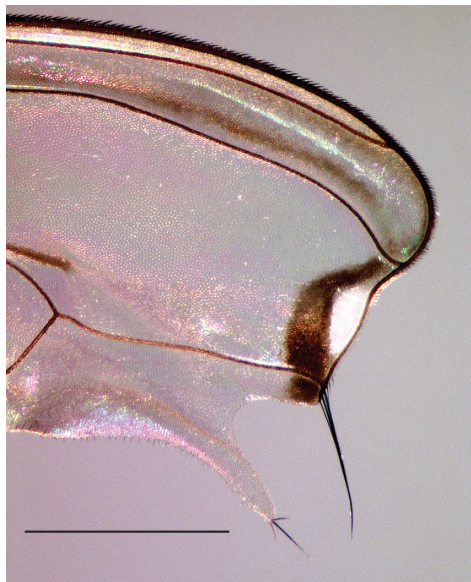


Figure 7. Wing tip of male *Liancalus pterodactyl* sp. n., showing white reflectance of apical spot in certain lights. Scale bar = 1 mm.



Figure 8. Habitus photograph of male *Liancalus hydrophilus* Aldrich taken at a waterfall in Utah County, Utah, N39.95963°, W111.2678°, on 13 September 2013. Note long cerci with nearly uniform row of long yellow setae. Photo taken by C. Riley Nelson.

flagellomere about as long as wide, broadly pointed apically, arista inserted just beyond midpoint of dorsal edge.

Thorax: Scutum green to green-blue with sparse to moderately dense silver-gray pollen, with bronze stripes between acrostichal and dorsocentral setae, and along intra-alar setae; scutellum and posterior slope of scutum green-blue with sparse silver pollen; notopleuron covered with silver pollen and postpronotum covered with sparse brown-gray pollen, both with some blue-green reflections; corner of postpronotum above anterior spiracle narrowly orange; 6 dorsocentral setae; 4–11 small acrostichal setae ($\leq 1/2$ length of dorsocentral setae), in a single row; 2 notopleural setae; postpronotum with 1–2 strong, black setae and often a few smaller white hairs; 2 presutural intra-alar setae (one near suture); 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum with 6 large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic green-bronze, covered with dense silver-gray pollen, without setae or hairs.

Legs: Legs concolorous with pleura, but less silver-gray pollen, femoral ‘knees’ narrowly orange. Coxa I uniformly covered with white hairs on anterior surface (length of hairs subequal to width of coxa I), with a few black, slender setae at apex. Coxa II with a few white hairs anteriorly, a couple white setae near apex, and a black *ad* seta just beyond $1/2$. Coxa III with a few white hairs and a black dorsal seta near $1/2$. Femur I and II with short, white hairs posteriorly to *pv* on basal half (length $<$ half width of femur). Femur III with some short white hairs (length \leq width of femur) on dorsal and posterior surface at base. Tarsus I(1) short, approximately one-third length of tarsus I(2) (Fig. 3F); tarsus I(2) long, flattened ventrally and covered with dense setulae full-length; tarsus I(3) slightly thickened near or just beyond middle (Fig. 3F); tarsus I(3–4)

with black, felt-like setulae on *pv* surface. Ratios of tibia:tarsomeres for leg I: 11-3-8-3-2-2; for leg II: 23-22-11-3-2-2; for leg III: 27-14-16-4-2-2.

Wing (Fig. 6A): Hyaline, with semicircular brown cloud near apex (clouding very faint in a few specimens). Wing relatively slender, rounded at apex, without outstanding hairs or setae. Veins R_{4+5} and M_1 closely approximated and nearly parallel at apex of wing. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate, slightly enlarged and rather blunt at apex (Fig. 2F); T1 metallic green-blue, with dense silver pollen laterally becoming less dense dorsally, with bronze along posterior edge and usually a narrow bronze stripe dorsally. T2-T4 bronze with large lateral blue-green spots covered with dense silver pollen. T5 dark bronze with metallic green reflections and sparse silver pollen. T6 bronze with blue-green reflections and with moderately dense silver pollen. T1-T3 with white hair laterally, longest on T1 and T2. Sternites bronze with silver-gray pollen. S1 bare except for lateral small tuft of white hairs at extreme base. S2 and S3 with sparse white hairs. S4 mostly bare. Hypopygium (Fig. 12A): cerci small, lacking long tubular filaments of other species, but with minute papilla where filaments originate in other species.

Female. Body length 5.0–7.5 mm, wing length 5.5–7.0 mm. Similar to male except for face slightly wider, dark blue-green covered with moderate golden-brown pollen that is most dense along eyes; palpus black with sparse silver pollen apically, dense golden-brown pollen in middle basally, and black setae. Femur II usually with posterior row of short (length less than half width of femur) white hairs on basal half, these hairs becoming black on apical half. Tarsus I(1) normal, about twice as long as tarsus I(2). Wing (Fig. 16G) hyaline, with three brown spots: one between R_{4+5} and M_1 near midpoint of wing, one apically in cell $bm+dm$ but not reaching crossvein $dm-cu$, and a spot on or just above M_1 beyond crossvein $dm-cu$. Crossvein $dm-cu$ meeting M_1 at a nearly 45° angle.

Remarks. Harmston and Knowlton (1945) found *L. querulus* "in large numbers during late summer about masonry dams in the canyons near Logan and Ogden, Utah".

Distribution. This species is rather uncommon, but widely distributed in the western U.S. (Fig. 15).

Type material examined. LECTOTYPE (designated here to fix identity of the species) ♂, labelled: "Type/ 870" [red label]; "The Geysers, Cal./ May 5-7./ R. Osten Sacken."; "O. Sacken./ West. Dipt."; "Liancalus querulus O.S." [hand-written]; "MCZ-ENT/ 00302771" [with barcode]; "LECTOTYPE ♂/ Liancalus querulus/ Osten Sacken/ des. Runyon & Hurley" [red label] (MCZ). **PARALECTOTYPE:** Same data as lectotype, MCZ-ENT/ 00000870 (1 ♀, MCZ).

Additional material examined. USA. Arizona: Cochise Co., Portal, S.W. Res. Sta. AMNH, 23.vi.1968, V.D. Roth & FCH (2 ♂, 2 ♀, MTEC); Coconino Co., Oak Crk Cyn, 25.vi.1986, J. Jenkins (3 ♂, MTEC). **California:** Contra Costa Co., Jewel L, 11.v.1948, W.W. Wirth (1 ♀, EMEC), Danville, 23.vi.1951, by small waterfall, F.X. Williams (2 ♂, CAS), same as previous, 3.vii.1952, by rapids at creek (1 ♂, CAS), same as previous, 24.vi.1952, by rapids (1 ♂, CAS); Humboldt Co., Orick,

3.vii.1950, L.W. Quate (1 ♀, EMEC); Los Angeles Co., Monrovia Cyn, 18.v.1966, J.C. Hall (1 ♂, UCR), Topanga Cyn, 10.v.1953 (1 ♀, LACM), Big Dalton Cyn, 19-23.vii.1952, S. Miyagawa (22 ♂, 8 ♀, CUIC, UCDC), same as previous, 23.vii.1952, H.L. Mathis (2 ♂, 2 ♀, UCDC), same as previous, 14-23.vii.1952, A.T. McClay (2 ♂, 3 ♀, UCDC), same as previous, 19.vii.1952, A.A. Grigarick (3 ♂, 1 ♀, UCDC), Tanbark Flat, 15.vi.1956, R.C. Bechtel (1 ♂, UCDC); Marin Co., Phoenix Lake Pk., 22.v.1949, C.H. Spitzer (1 ♂, 1 ♀, EMEC), same as previous, 30.v.1949 (1 ♂, EMEC); Monterey Co., Big Creek, 4.vi.1982, J. Powell (1 ♂, EMEC); Sierra Co., Hwy 49, creek at Rosasco Ravine, 2.4 km W Downieville, 890 m, 4.vii.1975, PHA (1 ♂, CAS); Stanislaus Co., Del Puerto Cyn, Frank Raines Park, 335m, 17.v.1970, PHA (1 ♂, CAS); Sutter Co., Sutter Buttes, 5.v.1940, G.E. Bohart (3 ♂, 2 ♀, UCDC). **Idaho:** Gooding Co., Hagerman, Thousand Springs, JMA (1 ♂, USNM). **Oregon:** Hood River Co., Hood River, 1.x.1917, F.R. Cole (1 ♂, CAS); Jackson Co. Beaver Sulfur Campground, 10 mi. S Ruch, resting on rock in stream, 28.vii.1967, KJG (1 ♂, 1 ♀, MTEC); Malheur Co., 9 mi. E Juntura, runoff from hot spring, 16.vi.1964, KJG (1 ♂, ODAC). **Utah:** Cache Co., Logan Meadows, 15.x.1939, G.F. Knowlton & FCH (3 ♂, CAS), Logan Cyn, 15.viii.1940, FCH (1 ♂, 2 ♀, MTEC); Kane Co., Grand Staircase-Escalante National Monument, Sheep Crk jct., Skutumpah Rd., 5531 ft, 37°29'43N 112°03'59W, 29.ix.1999, R.W. Baumann, K.T. Huntzinger, C.R. Nelson (1 ♂, BYU); Rich Co., Lakota, 5.vii.1957, FCH (3 ♂, 2 ♀, MTEC); Washington Co., Leeds, 27.iv.1940, G.F. Knowlton & FCH (2 ♂, CMNH, EMUS), same as previous, 9.vi.1940 (1 ♂, MTEC), Leeds Cyn, 13-16.ix.1984, Hansen & Youssef (1 ♂, 2 ♀, EMUS), same as previous, 15-18.vii.1980, malaise trap (1 ♂, EMUS), same as previous, 21.viii-4.ix.1985, W.J. Hansen (1 ♀, EMUS), same as previous, 29.vii.1965 (1 ♂, EMUS); Weber Co., Ogden Cyn, 10.x.1939, G.F. Knowlton & FCH (7 ♂, 4 ♀, CNC, CUIC, EMUS, MTEC, OSU), same as previous, 9.x.1937 (1 ♂, EMUS). **Washington:** Grant Co., O'Sullivan Dam, 25.x.1953, H.G. Davis (1 ♂, WSU); Whitman Co., Lyle Grove, near Pullman, malaise trap, 1.vii.1968, H.S. Telford (1 ♀, WSU), Steptoe Cyn, 10 mi. SW Colton, 3.viii.1974, WJT (1 ♀, WSU).

Liancalus similis Aldrich, 1893

Figs 2E, 3G, 6B, 9, 12B, 15B, 16E

Diagnosis. Males are easily distinguished by having the apical third of wing mostly brown and with a slightly raised, black speck near middle of cell m (Fig. 6B). Female wing has three distinct brown spots, one of which intersects M_1 beyond crossvein dm-cu, and with crossvein dm-cu meeting M_1 at nearly 90° angle (Fig. 16E).

Redescription. Male. Body length 6.5–8.0 mm, wing length 6.0–7.5 mm. Habitus (Fig. 9). **Head:** Face rather narrow, nearly parallel-sided, slightly widening toward clypeus, uniformly covered with dense silver pollen. Ommatidia near vertex slightly smaller than remaining ommatidia. Vertex covered with dense silver pollen, often with some metallic blue-green color visible near middle. Vertical setae on small elevation;



Figure 9. Habitus photograph of male *Liancalus similis* Aldrich taken at Palisade Falls in Gallatin County, Montana on 12 October 2012. Note very short cerci. Photo taken by Justin Runyon.

ocellar tubercle prominent with 2 large setae (subequal in size to vertical setae); with 2 postocellar setae which are two-thirds length ocellar setae; postocular setae approximately one-third size of vertical setae with dorsal one-third of postocular setae black (approximately 10 black setae), ventral two-thirds white (approximately 12 setae) and more slender and slightly longer than black postocular setae. Ventral postcranial hairs (beard) rather sparse, wholly white. Palpus black, covered with dense silver pollen and sparse white hairs. Antenna black, first flagellomere about as long as wide, broadly pointed apically, arista inserted near midpoint of dorsal edge.

Thorax: Scutum blue-green obscured with dense silver-gray pollen, with bronze stripes between acrostichal and dorsocentral setae, and along intra-alar setae; scutellum and posterior slope of scutum green-blue with sparse gray or brown pollen; notopleuron and postpronotum (humerus) covered with dense silver pollen, usually with some blue-green reflections; usually 6 dorsocentral setae; 2–6 short acrostichal setae ($\leq 1/2$ length of dorsocentral setae), in a single row; 2 notopleural setae; postpronotum with 1–2 strong, black setae and often a few smaller white hairs; 2 presutural intra-alar se-

tae (one near suture); 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum with 6 large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic green-bronze, covered with dense silver-gray pollen, without setae or hairs.

Legs: Legs concolorous with pleura, but with less silver-gray pollen. Coxa I uniformly covered with white hairs on anterior surface (length of hairs subequal to width of coxa I); with a few black, slender setae at apex. Coxa II with a few white hairs anteriorly, a couple white setae near apex, and a black *ad* seta just beyond 1/2. Coxa III with a few white hairs and a black dorsal seta near 1/2. Femur I and II with some short, white hairs ventrally at base (length < half width of femur). Femur III with white hairs (length \leq width of femur) on dorsal and posterior surface at base. Tarsus I(1) short, approximately one-quarter length of tarsus I(2) (Fig. 3G); tarsus I(2) long, flattened ventrally with dense row of red-brown *av* setulae full-length and slightly longer row of *pv* setae/setulae. Ratios of tibia:tarsomeres for leg I: 14-2-8-3-3-3; for leg II: 29-20-11-3-2-2; for leg III: 33-14-15-4-2-2.

Wing (Fig. 6B): Hyaline, with extensive brown clouding on most of apical half; cell m (beyond crossvein bm-cu) with a minute, raised, black speck near middle – the area surrounding this speck usually lacks brown clouding. Veins R_{4+5} and M_1 widely separated and parallel to slightly diverging at apex of wing. Wing broadly and rather evenly rounded apically, without outstanding hairs or setae. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate (Fig. 2E); T1 metallic blue-green, with dense silver pollen laterally, sparser pollen dorsally and often with diffuse narrow bronze stripe. T2-T4 with large lateral blue-green spots covered with dense silver pollen, with apical one-third to one-half bronze, narrowly bronze dorsally. T5 dark bronze with metallic green reflections and sparse silver pollen. T6 bronze with some blue-green reflections and with dense silver pollen. T1-T3 with white hair laterally, longest on T1 and T2. Sternites bronze with dense silver-gray pollen on S1 and S2, sparser pollen apically. S1 bare except for lateral small tuft of white hairs at extreme base. S2 and S3 with sparse white hairs. S4 mostly bare. Hypopygium (Fig. 12B): cerci broad basally with very short slender, cylindrical lobe (subequal in length to first flagellomere of antenna), with small white hairs.

Female. Body length 5.0–7.5 mm, wing length 5.5–7.0 mm. Similar to male except for face wider, dark blue-green covered with moderate golden-brown pollen; palpus dark brown-black with sparse golden-brown pollen and black setae. Femur II with row of short (length less than half width of femur) hairs full-length posteriorly to *pv*, those on basal half white, those on apical half black. Tarsus I(1) normal, distinctly longer than tarsus I(2). Wing (Fig. 16E) hyaline, with three distinct brown spots: one between R_{4+5} and M_1 just beyond midpoint of wing, one near apex of cell bm+dm and just crossing crossvein dm-cu, and a spot on M_1 beyond crossvein dm-cu. Cell m without black speck near middle. Crossvein dm-cu meeting M_1 at nearly 90°.

Remarks. Aldrich (1893) states the type specimens are from "Washington (state)" and described *L. similis* from one male and two females, and noted that "the wings of

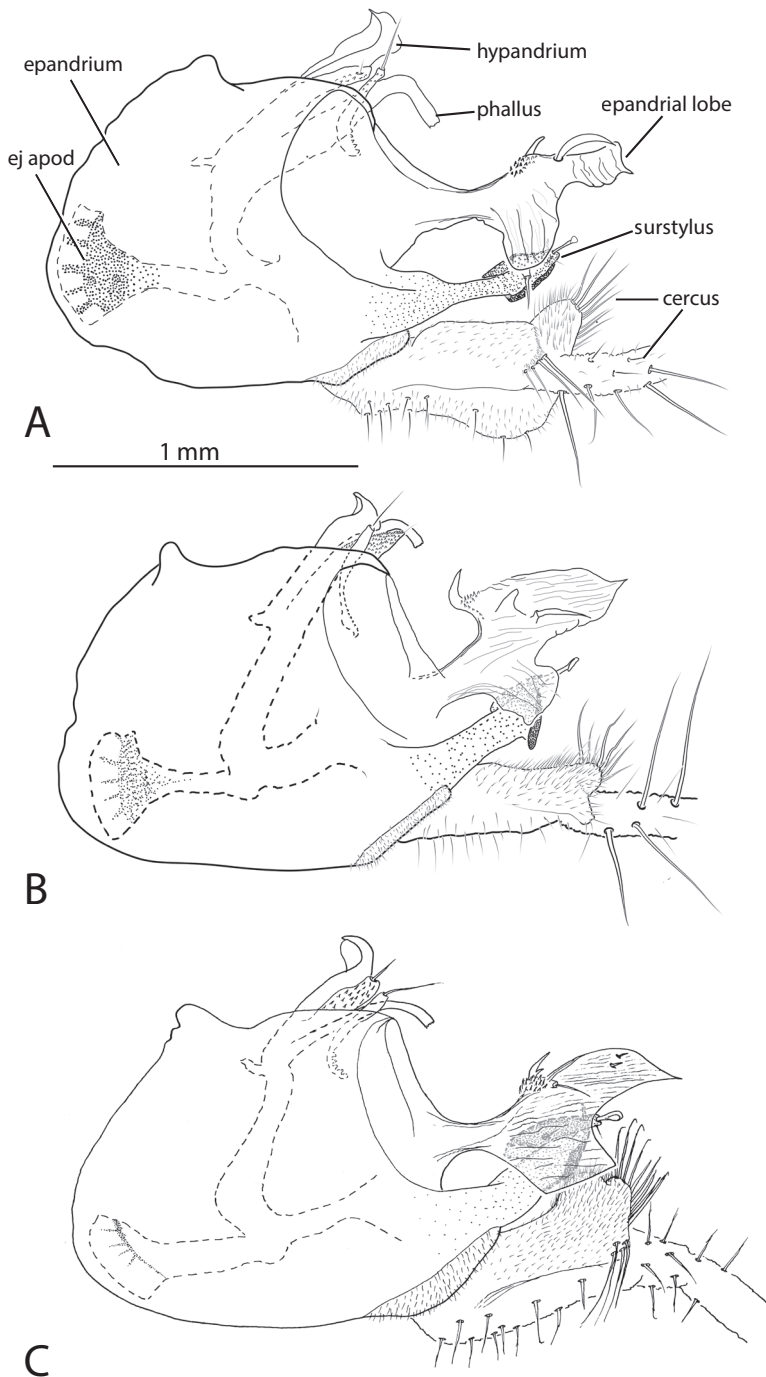


Figure 10. *Liancalus* male terminalia, right lateral view of **A** *L. genualis* Loew **B** *L. sonorus* sp. n., and **C** *L. limbatus* Van Duzee. ej apod = ejaculatory apodeme. Scale bar = 1 mm. Only base of cercus shown, see Fig. 2 for photographs of entire cerci.

one [female] specimen have more brown, which takes the form of three well defined spots, but this is evidently variable". The female specimen with three well defined spots is *L. similis*, but the other female is a specimen of *L. limbatus* which co-occurs with *L. similis* in Washington State.

This species is common at Palisade Falls in Gallatin County, Montana where the senior author (JBR) has observed females feeding (Suppl. material 1) and males interacting (Suppl. materials 2–3). Suppl. material 3 shows the typical looping flight of *Liancalus* species.

The immature stages of *L. similis* were described by Corpus (1986). Mouthparts of *L. similis* were described and illustrated by Cregan (1941).

Distribution. This species is common from southern California north through the Cascades and east to the Northern Rockies, but generally absent from the Great Basin (Fig. 15B).

Type material examined. **LECTOTYPE** (designated here to fix identity of the species) ♂, labelled: "W.J." [hand-written]; "COTYPE/ *Liancalus/ similis/* Ald." [red label, one wing on pin below this label]; "LECTOTYPE/ *Liancalus/ similis* Aldrich/ des. Runyon & Hurley 2014" [red label] (SEMC). **PARALECTOTYPE** ♀, same data as lectotype (SEMC).

Additional material examined. **CANADA. British Columbia:** 13 km N Revelstoke-Hwy 23, cascading stream over roadcut, 2.vii.1989, B.J. Sinclair (1 ♂, 3 ♀, CNC), Robson, H.R. Foxlee, numerous dates between 1955 and 1969 (2 ♂, 49 ♀, UBCZ), Harrison Mills, 16.vii.1953, W.R.M. Mason (1 ♀, CNC), Langford, 30.iii.1957, D. Evans (1 ♀, CNC), Summerland, Shingle Crk, 7.x.1932, A.N. Gartrell (1 ♀, CNC). **MEXICO. Baja California:** Sierra San Pedro Martir, 17 km. E Park entrance, 2900 m, 7.ix.1980, DDW (3 ♂, 1 ♀, CAS), San Pedro Martir, La Grulla, 12.vii.1953, PHA (1 ♀, CAS). **USA. California:** Yosemite NP, 1.viii.1940, D.E. Hardy (3 ♂, 2 ♀, MTEC, SEMC); Santa Cruz Mts., 24.vii.1895 (1 ♀, LACM), same as previous, 27.viii.1895 (1 ♂, LACM); Mt Saint Helena, 28.vii.1940, B. Brookman (1 ♂, CAS); Yosemite, 12.vi.1935, ALM (1 ♂, USNM); Alameda Co., Berkeley, 16.v.1951, R. Morgan (1 ♂, LACM); Amador Co., Forest Home, 26.viii.1944, ALM (2 ♂, 2 ♀, USNM); Contra Costa Co., Mt Diablo, 2.viii.1951, F.X. Williams (1 ♂, CAS), same as previous, 2000 ft, 23.viii.1951 (1 ♀, CAS), same as previous, wet wall of spring, 18.vii.1951 (1 ♀, CAS); Del Norte Co., 6 mi. N Gasquet, 11.i.1986, RLH (1 ♀, MTEC); El Dorado Co., Fred's Place, 20.viii.1950, L.W. Quate (1 ♂, EMEC); Fresno Co., Glen Meadow Crk, above Dinkey Crk Ranger Station, 1755 m, 3.viii.1975, PHA (1 ♂, CAS), Bolsillo Crk at Bolsillo cmgrd, SW Mono Hot Springs, 2270 m, 8.viii.1975, PHA (1 ♂, 1 ♀, CAS); Humboldt Co., Crk 1/3 mi. W Ruby Crk above Willow Crk, 25.iv.1987, Baumann, Stark, Nelson & Wells (1 ♀, BYU); Kern Co., Mt Pinos, Iris Meadow, 2670m, malaise, 2–3.vi.1992, J. Skevington, A. Goering (1 ♂, DEBU); Lake Co., Kelseyville, 9.v.1953, W.H. Lange (1 ♀, UCDC); Los Angeles Co., Singing Sprs, 29.viii.1958, Menke & Stange (7 ♂, 9 ♀, LACM), Ranch - 2.5 mi. SSW Valyermo, 4800', 18.viii.1962, N. McFarland (2 ♂, OSAC), Angeles Nat. Forest, Windy Spr, 27.vi.1974, DDW (3 ♂, 8 ♀, CAS), July, Collection Coquillett (1

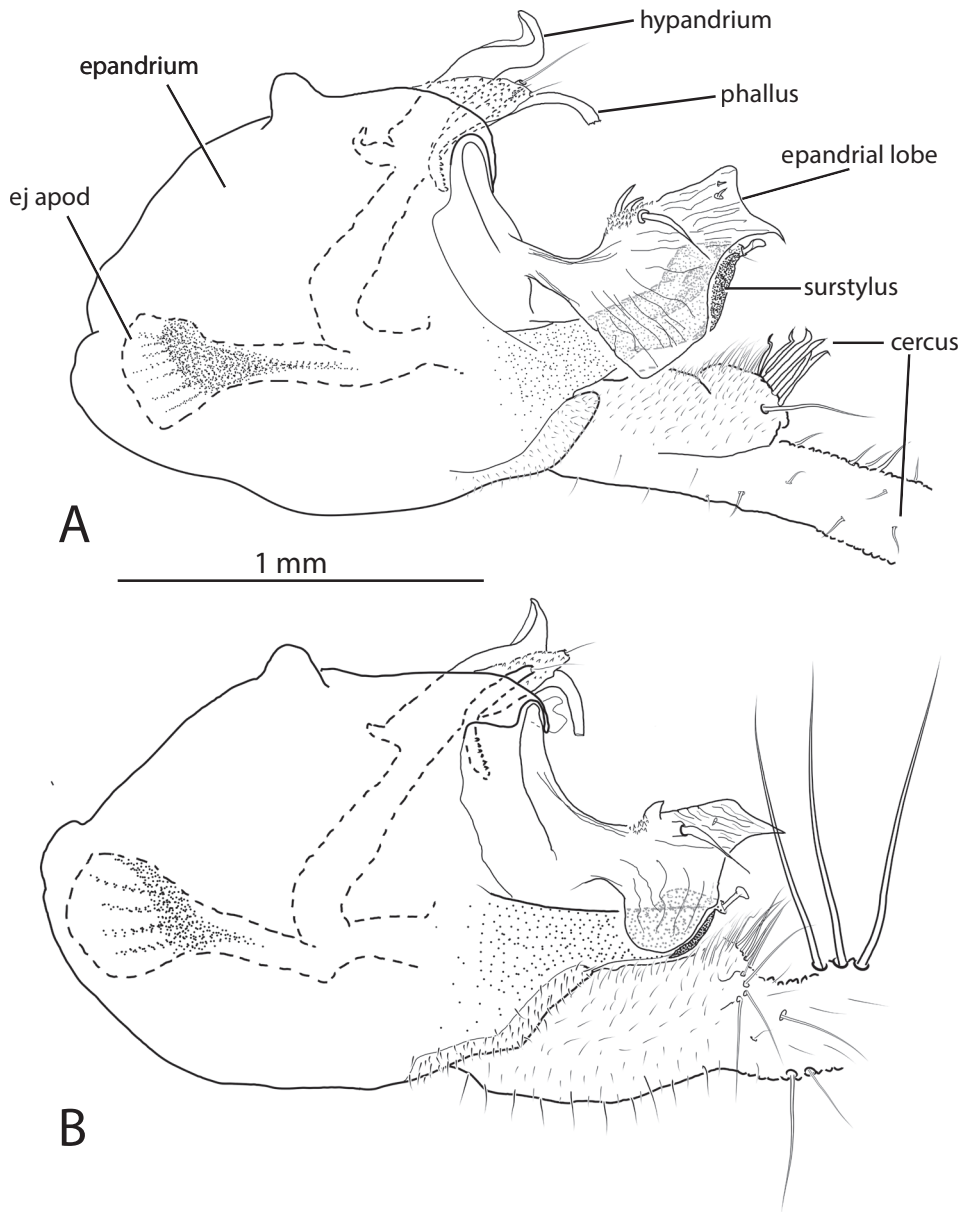


Figure 11. *Liancalus* male terminalia, right lateral view of **A** *L. pterodactyl* sp. n., and **B** *L. hydrophilus* Aldrich. ej apod = ejaculatory apodeme. Scale bar = 1 mm. Only base of cercus shown, see Figures 2D and 8 for photographs of entire cerci.

♂, USNM), San Gabriel Mts, Cloudburst Cyn, T2N, R12W, Sec. 14, 4000 ft, 30. iv.1972, J.P. & K.E. Donahue (1 ♂, LACM), Big Dalton Cyn, 23.vii.1952, S. Miyagawa (1 ♀, LACM), Tanbark Flat, 12.vii.1952, S. Miyagawa (1 ♂, 3 ♀, FSCA, UCDC), same as previous, 24.vi.1952 (1 ♀, UCDC), same as previous, 5.vii.1952,

R.L. Anderson (1 ♀, UCDC), same as previous, 16.vii.1952, D.E. Barcus (2 ♂, 2 ♀, UCDC), same as previous, 10.vii.1950, F.X. Williams (5 ♀, CAS), Monrovia Cyn, 18.v.1966, J.C. Hall (1 ♀, UCR), Tujunga Cyn, 12.vii.1962 (2 ♂, 1 ♀, MTEC), 0.5 mi. E Islip Saddle, Cortelyou Spr on Hwy 2, Angeles N.F., 25.iv.1977, DDW (2 ♀, CAS), N Fk. San Gabriel R, along Hwy 39, 2 mi. S Coldbrook Stn., 25.iv.1977, DDW (1 ♀, CAS), San Antonia Cyn, Ontario, 25.vii.1907 (12 ♂, 12 ♀, CAS, OSU), 1/4 mi. down Cooper Cyn Trail, near Mt Waterman Ski Area, 31.iii.1981, S.M. Clark (1 ♀, MTEC), 1 mi. NE Crystal Lake, 1.vii.1962, J.F. Lawrence (2 ♀, MCZ); Marin Co., Point Reyes National Seashore, 22.vi.1975, D.G. Denning (1 ♂, 1 ♀, UCDC), Mill Valley, Blithedale Ridge, Lee Street, 110 m, 27.iv.1965, PHA (1 ♀, CAS), Alpine Lake, 18.v.1958, D.C. Rentz (1 ♂, CAS), Mt Tamalpais, vicinity of Rock Sprs, ca. 610 m, 13.v.1978, PHA (1 ♂, CAS); Mariposa Co., Yosemite NP, Boundary Hill, Research Res. Area, 4.vii.1971, R.P. Allen (1 ♂, CSCA), seepage along Hwy 49 between Bear Valley and Coulterville, 3.v.1978, D.D. Wilder (1 ♂, 1 ♀, CAS), Summerdale Forest Camp on Big Crk, 1520m, 28.vi.1973, PHA (1 ♀, CAS); Monterey Co., Willow Crk, 7.viii.1962, E.I. Schlinger (1 ♀, UCR), Big Crk, 4.vi.1982, J. Powell (1 ♀, EMEC), Los Padres Nat. Forest, Escondido Cpgd, 22.v.1976, DDW (1 ♀, CAS); Nevada Co., Sagehen Crk, 19.vii.1978, R.B. Kimsey (3 ♂, UCDC), same as previous, L.D. French (3 ♀, UCDC), same as previous, 8.vii.1980, R.M. Bohart (1 ♀, UCDC); Plumas Co., Squirrel Crk, 8 mi. E Quincy, 3900', 15.v.1982, J.A. Powell (2 ♀, EMEC), Upper Jamison Crk, 3 mi. SW Johnsville, 5800', 27.vi.1989, RLH (1 ♂, 5 ♀, MTEC), Wolf Crk, 6 km NW Greenville, 1180 m, 15.viii.1977, PHA (1 ♂, 1 ♀, CAS); Riverside Co., Lake Hemet, 29.vii.1964, M.E. Irwin (1 ♂, 1 ♀, LACM), Fuller Mill Crk., 23.vii.1964, near stream under rocks, M.E. Irwin (1 ♂, 4 ♀, LACM), same as previous, vii.28.1965, P. Rauch (1 ♀, LACM), Idyllwild, 7.vii.1940, ALM (10 ♂, 16 ♀, USNM), Strawberry Crk., 3000', San Jacinto Mts., 19.v.1966, C.L. Hogue (3 ♂, 2 ♀, LACM), San Jacinto Peak, 7,000-10,000 ft, 20.viii.1914, J.C. Bradley (1 ♀, CUIC), Idyllwild, 13.vii.1940, Timberlake (2 ♀, UCR), San Jacinto Mts, 21.vii.1929, P.W. Oman (1 ♂, EMUS), Cottonwood Cyn, 7.iii.1967, S. Frommer, H. Nakakihara, T. Plichta (2 ♀, UCR), San Jacinto Mts, 10 road mi. from Hwy 74 toward Pine Cove, Jct N Fork San Jacinto R, 4.vi.1978, S. Frommer & W. Kramer (2 ♀, UCR), Agua Caliente Indian Res., Palm Cyn, 25.ii.1970, PHA (2 ♀, CAS); San Bernardino Co., Camp O-onga, nr. Running Spgs, San Bdn Mts, 11.viii.1966, C.L. Hogue (11 ♂, 7 ♀, LACM), Mt Home Cyn, 16.viii.1920, F.R. Cole (2 ♂, 9 ♀, CMNH, EMEC), same as previous, 16.vii.1921 (1 ♀, EMEC), same as previous, 20.ix.1922 (3 ♀, EMEC), same as previous, 16.vii.1922 (1 ♀, EMEC), Mill Crk Cyn, 17.vii.1922 (1 ♂, FSCA), Mt San Gorgonio, Vivian Crk, 6500', 2.vii.1968, Truxal (1 ♂, LACM), Vivian Crk., 6500', S. Gorgonio, 2.vii.1968, C.L. Hogue (1 ♀, LACM), Forest Home, 29.v.1972, G.R. Ballmer (1 ♀, UCR), Bear Valley, San Bernardino Mts, 6700 ft, JMA (1 ♂, USNM), same as previous, N. Banks (1 ♂, 1 ♀, MCZ), Glen Martin, 16.viii.1920, F.R. Cole (1 ♀, EMEC); San Mateo Co., 2 mi. N Pebble Beach, intertidal zone, 8.v.1965, A.J. Slater (1 ♀, EMEC), Corte de Madera Crk near Portola, 22.viii.1957, PHA (1 ♀, CAS); Santa Barbara Co., Cueva Valdez, Santa Cruz Is.,

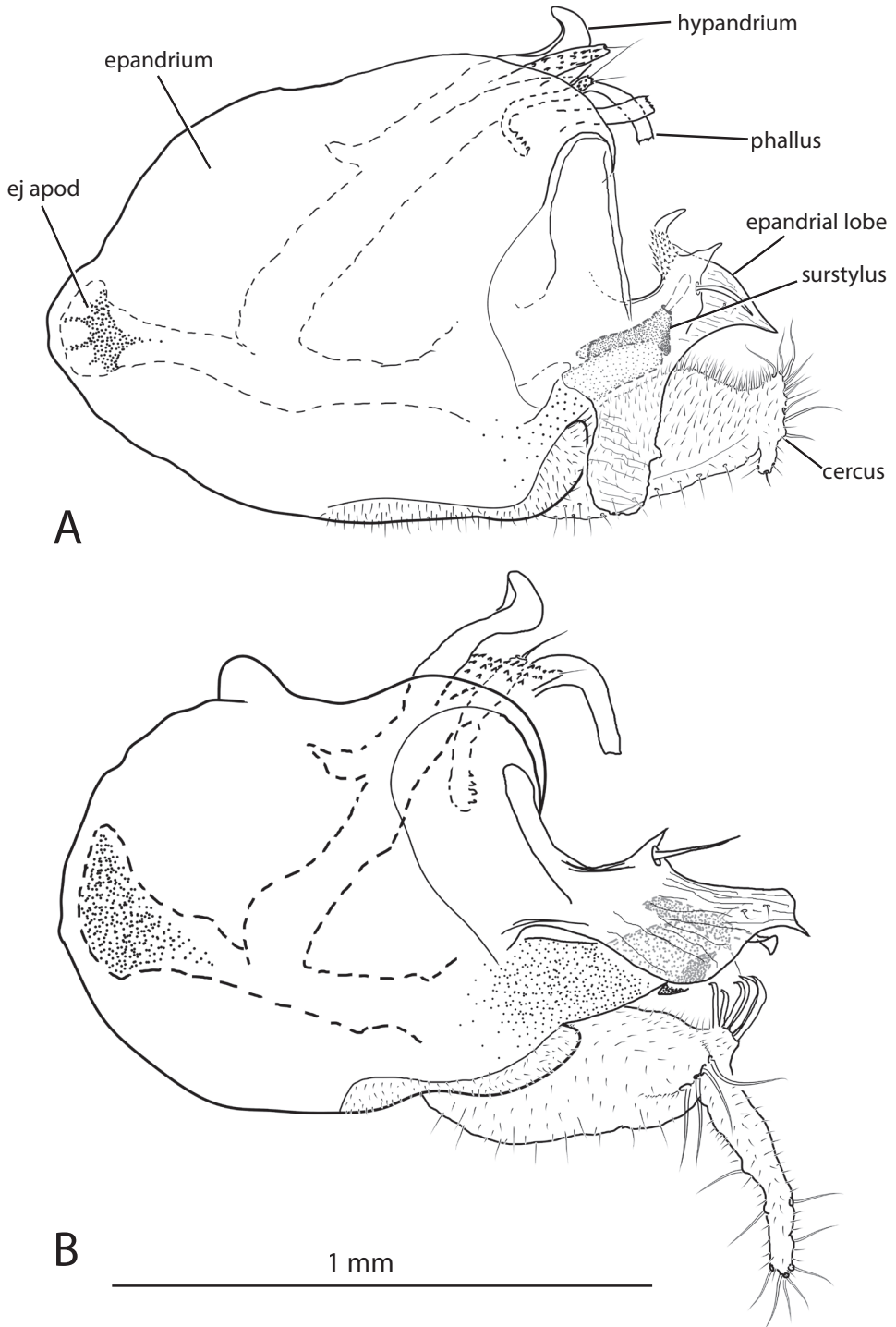


Figure 12. *Liancalus* male terminalia, right lateral view of **A** *L. querulus* Osten Sacken, and **B** *L. similis* Aldrich. ej apod = ejaculatory apodeme. Scale bar = 1 mm.

31.viii.1980, RLH (3 ♀, MTEC), Fryes Harbor, Santa Cruz Is., 1.ix.1980, RLH (1 ♀, MTEC); Santa Clara Co., Uvas Cyn County Park, 2.vii.1971, D.G. Denning (10 ♂, 2 ♀, UCDC), same as previous, 9.iii.1973 (2 ♂, 4 ♀, UCDC), same as previous, 15.vi.1975 (1 ♂, 1 ♀, UCDC), Alum Rock Park, 3.xi.1975, S. Fend (1 ♀, CAS), same as previous, 21.iv.1951, R.L. Usinger (2 ♂, EMEC), same as previous, 22.vii.1979, rocks over creek, L.G. Bezark (14 ♂, 18 ♀, CSCA), Stevens Crk, 23.vii.1940, T.G.H. Aitken (1 ♀, CAS); Santa Cruz Co., Santa Cruz, 8.vii.1948, W.W. Wirth (1 ♂, EMEC); Shasta Co., McArthur Burney Falls Memorial SP, 2900', 1.viii.1970, PHA (1 ♀, CAS); Sierra Co., Hwy 49, Crk at Rosasco Ravine, 2.4 km W Downieville, 890m, 4.vii.1975, PHA (1 ♂, CAS); Siskiyou Co., S Fork Sacramento R, 4000 ft, 4.viii.1953, H.P. Chandler (4 ♂, 1 ♀, CAS); Sonoma Co., Kenwood, Sonoma Crk, Morton's Warm Sprs, ca. 105m, 20.ix.1975, PHA (1 ♀, CAS); Stanislaus Co., Del Puerto Cyn, 900-1200', 6.vi.1970, E.I. Schlinger (1 ♀, EMEC); Tehama Co. Deer Crk, Hwy 32, 30.vii.1972, D.G. Denning (2 ♂, 3 ♀, UCDC), S Fork Battle Crk, 23.v.1952, H.P. Chandler (1 ♂, CAS); Trinity Co., 4 mi. W Forest Glen, 3400', 15.viii.1985, RLH (1 ♀, MTEC); Tuolumne Co., Pinecrest, 2-3.ix.1947, PHA (2 ♂, CNC), same as previous, 9.vii.1947 (1 ♀, CAS), same as previous, 19.vii.1948 (1 ♂, 1 ♀, CNC, FSCA), Lyon's Dam, 8.vii.1937, T.G.H. Aitken (1 ♂, CAS), Brightman Flat, 18.ix.1974, DDW (1 ♂, 1 ♀, CAS), Lions Dam, 7.viii.1937, M.A. Cazier (1 ♂, AMNH); Tulare Co., Mineral King, 30.vii.1935 (2 ♂, 1 ♀, LACM, UCDC), same as previous, 13.viii.1956, Simonds (3 ♂, 3 ♀, CSCA), same as previous, 1964, W.E. Simonds (1 ♀, CSCA), Sequoia NP, Giant Forest, 22.viii.1917, R.C. Shannon (2 ♀, CUIC), California Hot Springs, 20.vii.1994 (1 ♂, CSCA). **Idaho:** Adams Co., Little Salmon R., 18 mi. N New Meadows, 8.viii.1979, RLH (1 ♂, 1 ♀, MTEC); Boundary Co., 5 mi SW Bonners Ferry, 16.ix.1969, W.F. Barr (1 ♀, WFBM); Idaho Co., Holly Crk, Hwy 12, 33 mi. NE Lowell, 2600 ft, 19.viii.1969, E.M. Fisher (1 ♀, CSCA), Lightning Crk, 3 mi. N Riggins, 25.iii.1966, W.F. Barr (7 ♀, WFBM), same as previous, S.D. Smith (1 ♀, WFBM), Whitebird, 3.vii.1907, JMA (2 ♂, 1 ♀, USNM), Fiddle Crk, 5 mi. N Riggins, 25.iii.1966, W.F. Barr (1 ♀, WFBM); Kootenai Co., Beauty Crk, near Lake Cd'A., 15.ix.1975, D.F. Veirs (1 ♂, WFBM); Latah Co., Moscow Mt (5 ♀, WSU), Juliaetta (2 ♀, CNC, USNM), Juliaetta, 12.viii.1904 (1 ♂, USNM), Juliaetta, 12.vii.1904, JMA (1 ♂, 3 ♀, USNM), Kendrick, JMA (2 ♂, 1 ♀, USNM), same as previous, 28.iii.1902 (4 ♀, USNM), Mtn Moscow, 25.vii.1920, R.C. Shannon (2 ♂, 5 ♀, CNC, CUIC, WSU), Lower Sand Crk, nr. Bonami Crk, 16 mi. E Potlatch, 2900 ft, 9.viii.1979, WJT (2 ♂, WSU), same as previous, 5.viii.1979 (1 ♂, WSU), Big Meadow Recreation Area, 7 mi. NNE Troy, 3000 ft, 7.viii.1986, WJT (3 ♂, WSU), same as previous, 31.vii.1979 (1 ♂, WSU), 4.1 mi. S Juliaetta, 14.iii.1975, D.F. Veirs (4 ♀, WFBM), Moscow Mt, 4.vi.1910, JMA (1 ♀, USNM), 4.1 mi. S Juliaetta, 14.iii.1975, D.F. Veirs (6 ♀, WFBM); Lemhi Co., 5 mi. N Gibbonsville, 21.vii.1963, W.F. Barr (1 ♂, WFBM), same as previous, 1.ix.1967 (1 ♀, WFBM); Lewis Co., Five Mile Crk at Clearwater R., 14.vii.1992, RLH (1 ♂, 3 ♀, MTEC); Nez Perce Co., Lewiston Hill, 25.vi.1923, ALM (4 ♂, 2 ♀, USNM), Lake Waha, 9.vi.1918, ALM (2 ♂, 1 ♀, USNM), Juliaetta Falls, 11.iv.1975, D.F. Veirs (3 ♀, WFBM), Lewiston, 9.vi.1923,

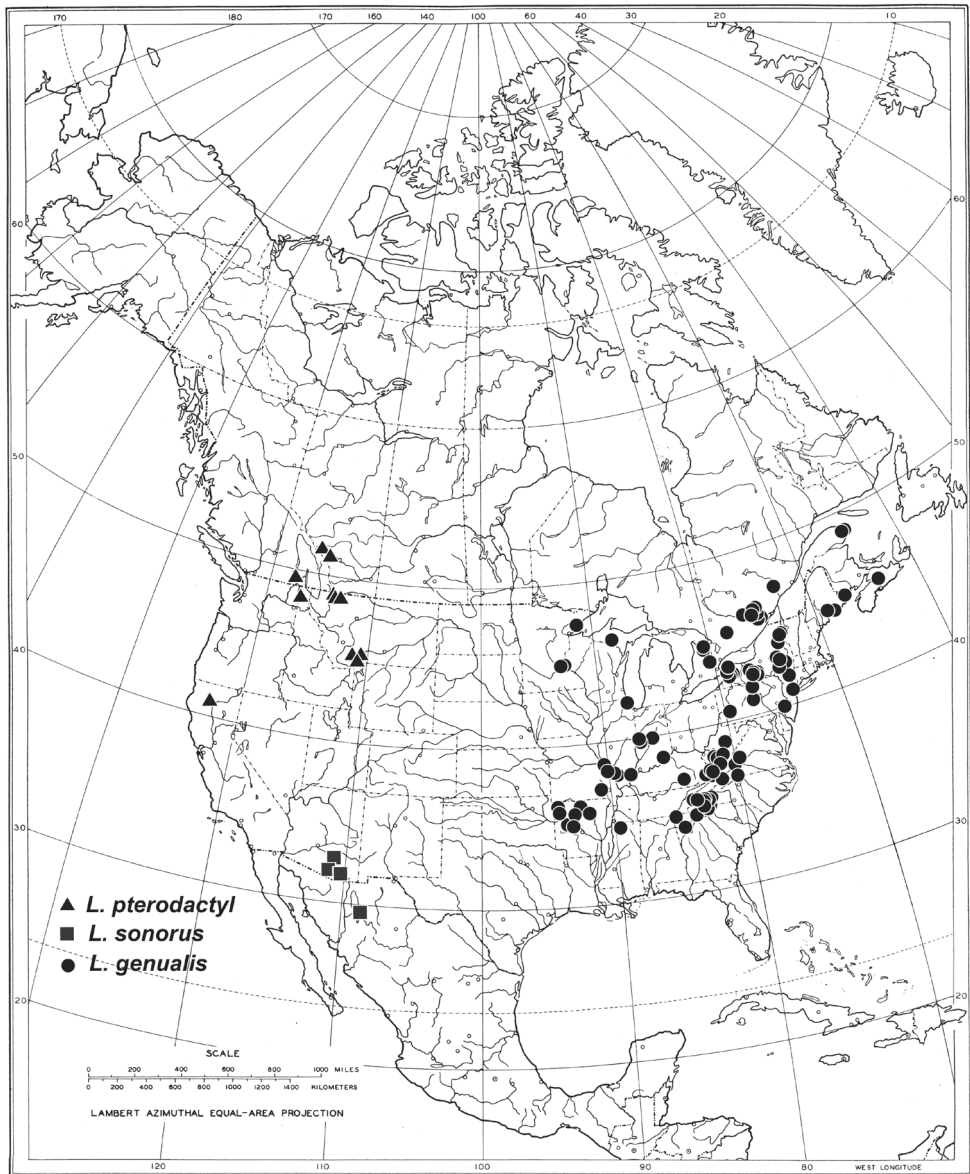


Figure 13. Known distributions of *Liancalus pterodactyl* sp. n., *L. sonorus* sp. n., and *L. genualis* Loew.

ALM (6 ♂, 2 ♀, USNM); Twin Falls Co., 20 mi. S Hansen, 27.vii.1973, RLH (6 ♂, 8 ♀, MTEC). **Montana:** Cascade Co., Memorial Falls, 2 mi. SE Neihart, 6150 ft, N46°54.78', W110°41.63', 12.ix.2009, JBR (3 ♂, 3 ♀, MTEC); Flathead Co., Cooram, Badrock Cyn, Shepard Memorial Fountain, swept from rocks and vegetation of seepage, 28.viii.1981, PHA (2 ♀, CAS); Gallatin Co., Silken Skein Falls, 3 mi. S. of Hyalite Rsvr., 8333', 11.viii.2000, JBR (1 ♂, MTEC), Palisade Falls, 1 mi. S. Hyalite

Rsvr., 7685', 12.viii.2000, RLH & JBR (1 ♂, 2 ♀, MTEC), same as previous, 19.x.2000, JBR (1 ♂, 2 ♀, MTEC), same as previous, 20.iv.2002 (1 ♀, MTEC), same as previous, 20.viii.2009 (1 ♂, MTEC); Glacier Co., Glacier NP, Sun Point Trail, Crk below Baring Falls, 26.viii.1981, PHA (1 ♀, CAS); Park Co., Pine Crk Falls, 15 mi. S Livingston, 6000', 6.viii.2000, RLH & JBR (3 ♂, 7 ♀, MTEC), same as previous, 28.vii.2001, JBR (2 ♂, 1 ♀, MTEC). **Nevada:** Elko Co., Ruby Mts, Thomas Cyn, 7500', 15.viii.1989, RLH (6 ♂, MTEC), Ruby Mts, Lamoille Crk, 8900', 18.viii.1989, RLH (4 ♂, 3 ♀, MTEC), same as previous, 25 mi. SE Elko, 8800 ft, 11.viii.2005, JBR & RLH (3 ♂, 2 ♀, MTEC). **Oregon:** Mt Hood, 29.vii.1966, FCH (5 ♂, 8 ♀, CAS, FSCA, MTEC, EMUS); Benton Co., Parker Crk., Mary's Peak Rd, 26.vi.1985, R.W. Baumann, C.R. Nelson & M.F. Whiting (1 ♀, BYU), Siuslaw Nat. For., Mary's Peak, Parkers Crk. & falls, 14.vii.1989, B.J. Sinclair (2 ♂, CNC), same as previous, Alder Falls (2 ♂, CNC), Marys Peak, Parker Crk., 3100', 24.vii.1969, E.M. Fisher (2 ♂, 2 ♀, CSCA), Mary's Peak, Parker Crk., 26.ix.1967, KJG (1 ♂, 3 ♀, MTEC, OSAC), Mary's Peak, 19.iii.1968, KJG (1 ♀, OSAC), Marys Peak, 14 mi., 20.v.1979, K. West (5 ♀, OSAC), Mary's Peak, Parker Crk Falls, 3500', 27.ii.1964, J.D. Lattin (1 ♀, OSAC), Marys Peak, 11.viii.1953, V. Roth (1 ♀, OSAC), same as previous, 21. viii.1952 (1 ♀, OSAC), Cary's Grove, 2.ix.1974, W.N. Mathis (2 ♂, OSAC), Mary's Peak, 3.x.1978, G.L. Parsons (1 ♂, OSAC), Mary's Peak, Parker Crk, roadside seepage, 26.ix.1967, KJG (1 ♂, CAS); Clackamas Co., Still Crk., Mt. Hood, Timberline Lodge Rd., 27.vi.1985, C.R. Nelson (1 ♂, BYU), Eagle Crk, 15.vi.1925, ALM (1 ♀, USNM), same as previous, 2.viii.1921 (2 ♀, USNM); Clatsop Co., Saddle Mt, 2500-3000', 2.ix.1966, KJG (1 ♂, ODAC); Hood River Co., Starvation Crk. St. Pk., cascading stream below falls, 10.vii.1989, B.J. Sinclair (1 ♀, CNC), Cloud Cap Inn, Mt Hood, 11.vii.1932, JMA (2 ♂, 1 ♀, USNM), Homestead Inn, Mt Hood, 12.vii.1932, JMA (1 ♂, 5 ♀, USNM), Hood River, seepage over road cut, 15.viii.1966, KJG (1 ♀, FSCA), 20 mi. S Hood River, seepage vertical roadcut, 16.viii.1966, KJG (1 ♀, OSAC); Jackson Co., 10 mi. S Ruch, stream margins, 22.v.1964, KJG (1 ♀, ODAC); Lake Co., Deep Crk, 1.5 mi. W Adel, 4850', 17.viii.1992, RLH (2 ♀, MTEC), Ana Sprs Reservoir, sweeping margin of springs, 3.viii.1966, KJG (1 ♀, ODAC) St. Helena Crk, stream margin, 17.viii.1948, W.W. Wirth (1 ♀, USNM); Linn Co., 1 mi. S Marion Forks, shaded vertical seepage, 24.viii.1967, KJG (2 ♂, 2 ♀, ODAC); Multnomah Co., Troutdale, 1.viii.1965, FCH (5 ♂, 4 ♀, EMUS, MTEC, ODAC); Tillamook Co., Neskowin, 10-19.viii.1948, M.T. James (3 ♂, 3 ♀, WSU), 4 mi. W of summit of Coast Range, Hwy 6, small crk flowing down face of road cut, 29.vii.1966, KJG (1 ♂, CAS); Umatilla Co., Dead Man Pass, 30.vii.1966, FCH (1 ♂, 3 ♀, FSCA); Union Co., North Powder, 25.vii.1965, FCH (6 ♂, 5 ♀, CAS, FSCA, MTEC, USNM), 4 mi. W Elgin, bank of Crk, vertical rock, 10.viii.1967, KJG (2 ♂, 2 ♀, ODAC, OSAC); Wallowa Co., 39 mi. N Enterprise, Hwy 3, 3400 ft, seep area, 28. vi.1976, WJT (8 ♀, WSU), 39 mi. N Enterprise, Hwy 3, 3400 ft, seep area, 28. vi.1976, WJT (1 ♂, WSU), 9 mi. S Imnaha, 1.vii.1969, KJG (2 ♀, ODAC, OSAC), 10 mi. N Imnaha, waterfall, 1.vii.1969, KJG (2 ♂, 1 ♀, ODAC); Wasco Co., The Dalles, 27.vii.1965, FCH (3 ♀, CAS, EMUS, MTEC). **Washington:** E. Washington

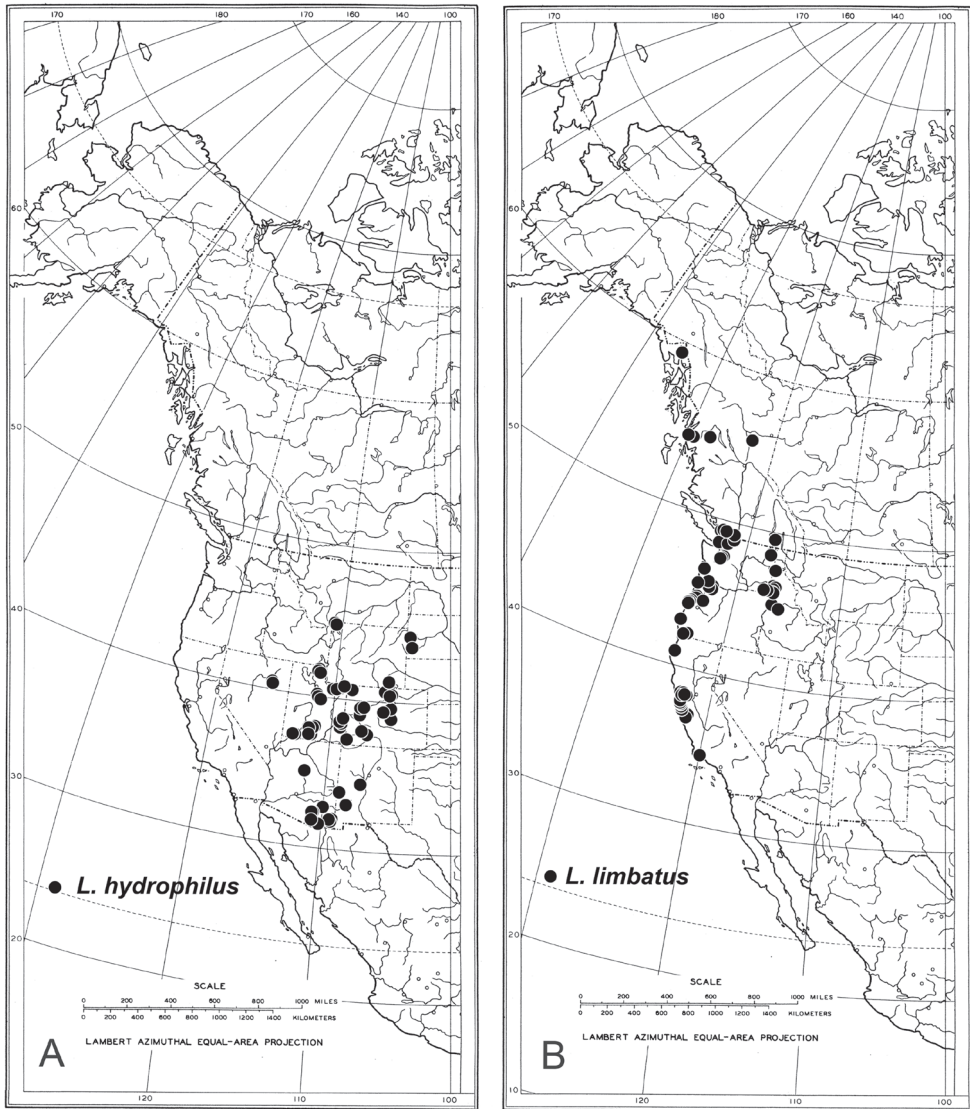


Figure 14. Known distributions of **A** *Liancalus hydrophilus* Aldrich and **B** *L. limbatus* Van Duzee.

(1 ♀, USNM); Mt Adams, 24.vii.1921, ALM (1 ♂, USNM); Asotin Co., Fields Spring S.P., 4 mi. S Anatone, 3500–4000 ft, 12–13.vi.1974, WJT (2 ♀, WSU), same as previous, 31.v.1975 (1 ♀, WSU), same as previous, 3600 ft, 26.vi.1979 (1 ♂, 1 ♀, WSU), 17 mi. S Anatone, nr. Grande Ronde River, 1950 ft, dripping spring, 31.v.1976, WJT (1 ♀, WSU), same as previous, 11.vi.1976 (3 ♂, 1 ♀, WSU), Clarkston, 8.vi.1923, V. Argo (1 ♂, USNM), Asotin, 19–20.v.1923, V. Argo (4 ♀, USNM), Asotin, 4.vi.1930, JMA (2 ♀, USNM); Columbia Co., Tucanon RS, Blue Mts, 13.viii.1922, V. Argo (1 ♀, USNM); Lewis Co., Stevens Crk at Stevens Cyn Rd, Mt Rainier NP, 4000–4500

ft, 24.viii.1973, WJT (1 ♂, WSU); Pierce Co., Mt Rainier, 31.vii.1966, FCH (5 ♂, 4 ♀, CAS, FSCA, MTEC, EMUS), Mt Rainier, Christine Falls, 16.viii.1917, ALM (2 ♂, CNC, USNM), Mt Rainier, Summerland, 29.viii.1934, ALM (1 ♀, USNM); San Juan Co., Friday Harbor, 23.vii.1905, JMA (1 ♂, 2 ♀, USNM), Olga, 15.vii.1909, JMA (1 ♀, USNM); Skamania Co., Stevenson, 20.vii.1906 (1 ♀, USNM); Whitman Co., Pullman, 2100 ft, 28.viii.1984, WJT (1 ♂, WSU), Rock Lake (1 ♀, USNM); Yakima Co., Bear Crk, 8 mi. SW Tieton RS, nr Rimrock Lk. 3000 ft, 24-25.vi.1974, malaise/CO₂, WJT (1 ♀, WSU).

***Liancalus sonorus* Runyon & Hurley, sp. n.**

<http://zoobank.org/82101701-D65F-4434-BD93-6A7B51F16720>

Figs 2B, 3E, 5B, 10B, 13, 16F

Diagnosis. Males and females are most similar to *L. genualis*, but can be distinguished by having 2 intra-alar setae, whereas *L. genualis* only has 1 intra-alar seta. Males are further distinguished by having tarsus I with tarsomere 2 very short (Fig. 3E), cerci long (Fig. 2B), and wing as in Fig. 5B.

Description. Male. Body length 7.5–8.25 mm, wing length 6.5–7.0 mm. **Head:** Face nearly parallel-sided above frontoclypeal suture, slightly widening below suture; with dense silver-gray pollen along eyes that is otherwise sparse revealing violet and green-blue reflections. Frontoclypeal suture near mid-face, distinctly bulging. Eyes with minute hairs between facets; ommatidia the same size throughout. Vertex with dense silver-gray pollen along eyes that is sparser medially revealing violet, green-blue, and coppery reflections. Ocellar tubercle prominent with 2 large setae; vertical setae two-thirds size of ocellar setae, on a small elevation; 2 postocellar setae similar in size to vertical setae; postocular setae half the length of vertical setae with approximately dorsal one-half black (approximately 12 black setae), remainder white and more slender and slightly longer. Ventral postcranial hairs (beard) wholly white. Palpus black, with rather dense silver pollen and black setae that are most dense basally, with brown pollen around insertion of these basal setae. Antenna black, first flagellomere a little longer than wide, rounded apically, arista inserted just before midpoint of dorsal edge.

Thorax: Scutum with bronze ground color that is mostly obscured by blue-green-violet stripes along acrostichal setae, dorsocentral setae, and around postalar area; stripe along acrostichal setae pale green and narrower than stripes along dorsocentral setae; posterior slope of scutum with two large lateral blue-green-violet spots; notopleuron and postpronotum (humerus) covered with dense silver pollen, humerus usually with some violet-green reflections; 6 dorsocentral setae; 1–13 acrostichal setae in a single row; 2 notopleural setae; postpronotum with 1–2 strong setae and often a few smaller hairs or setae; 2 presutural intra-alar setae; 1 presutural and 2 postsutural supra-alar setae; 1 postalar seta; scutellum dark metallic bronze with 6 (rarely 7) large marginal setae (3 per side), no additional hairs; proepisternum with 1 dorsal and 1 ventral tuft of white hairs. Pleura metallic green-bronze, covered with dense silver-gray pollen, without setae or hairs.

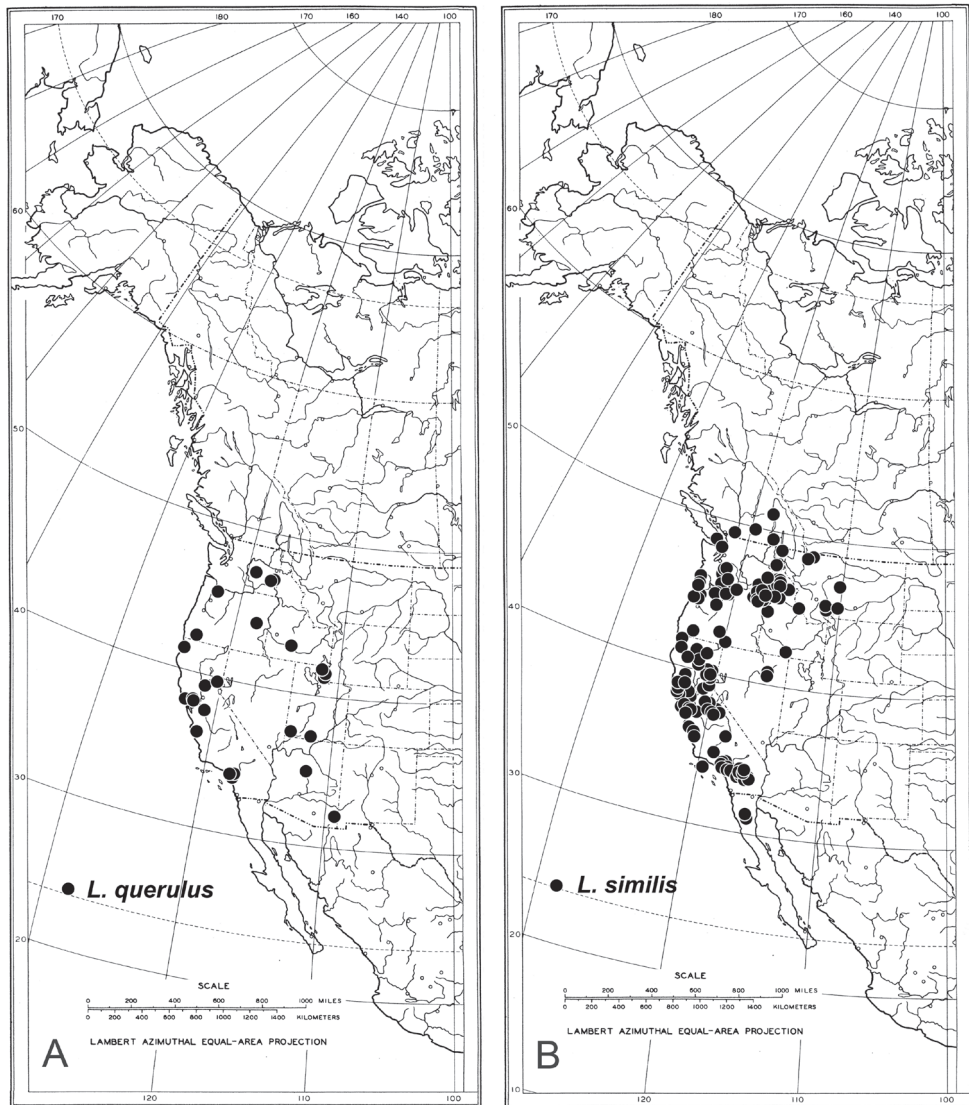


Figure 15. Known distributions of **A** *Liancalus querulus* Osten Sacken and **B** *L. similis* Aldrich.

Legs: Coxae concolorous with pleura; remainder of legs dark metallic green-bronze, dusted with silver pollen; femoral ‘knees’ narrowly orange. Coxa I uniformly covered with white, slender hairs on anterior surface (length of hairs subequal to width of coxa I), with a few black, slender setae at apex. Coxa II with scattered white hairs anteriorly (those at apex longer and stouter), a couple black setae at apex, and a black *ad* seta just beyond 1/2. Coxa III with a black dorsal seta near 1/2. Femur II with row of short (\leq width of femur) posterior to *pv* setae on distal half, those near middle of femur white, longest and becoming black and shorter apically. Tarsus I(2) short (length subequal to width), slightly thickened, with ventral brush of setulae (Fig. 3E). Ratios of tibia:tarsomeres for leg I: 18-8-2-4-3-2; for leg II: 26-23-9-4-2-2; for leg III: 33-16-15-4-2-2.

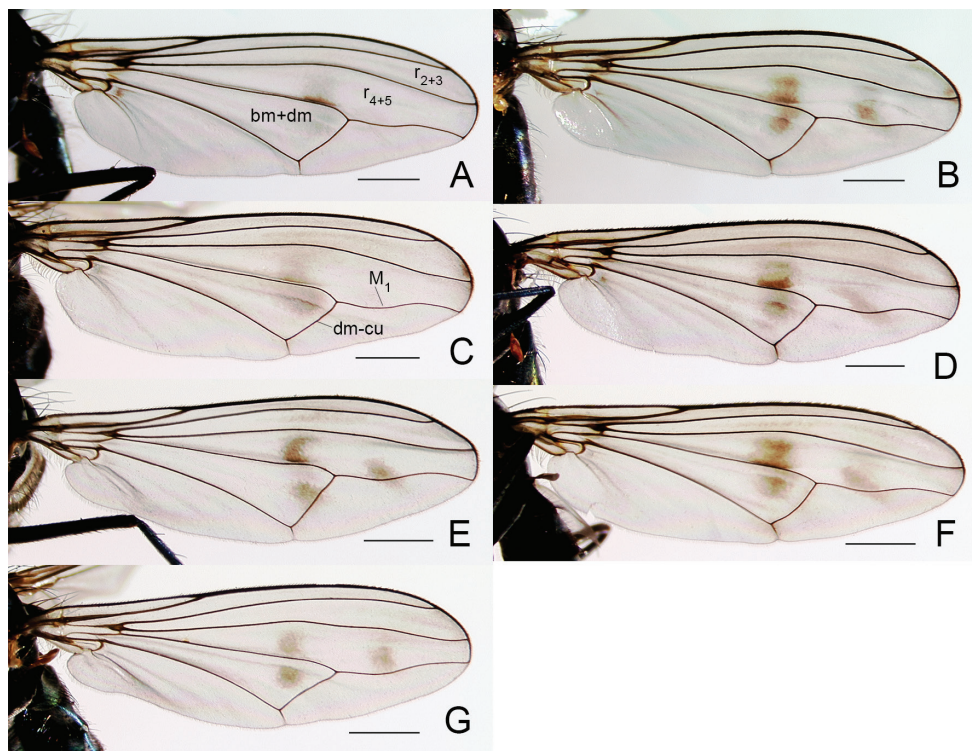


Figure 16. Wings of female species of *Liancalus*, **A** *L. pterodactyl* sp. n. **B** *L. genualis* Loew **C** *L. hydrophilus* Aldrich **D** *L. limbatus* Van Duzee **E** *L. similis* Aldrich **F** *L. sonorus* sp. n. **G** *L. querulus* Osten Sacken. Wing cells $bm+dm$, r_{2+3} and r_{4+5} are labeled in (**A**); wing veins $dm-cu$ and M_1 are labeled in (**B**).

Wing (Fig. 5B): Hyaline, with anterior third somewhat brownish and a diffuse brown spot near $2/3$ between R_{4+5} and M_1 ; with a longitudinal spurious vein between R_{4+5} and M_1 that is arched on apical third of wing and terminates near midpoint of a nearly circular, translucent, apical spot that is white in certain lights; this spot enclosed within a small, brown, apical cloud. Calypter yellow with a fan of long, pale yellow setae at apex. Halter pale yellow.

Abdomen: Cylindrical, elongate (Fig. 2B), bronze with large metallic blue-green spots with dense silver pollen laterally at base of T1-T4 which do not meet dorsally (except occasionally on T1 which is largely blue-green). T5 metallic green dorsally with sparse silver pollen. T6 wholly metallic green with sparse silver pollen. T1-T3 and base of T4 with white hair laterally, longest on T1 and T2. Sternites bronze with silver-gray pollen. S1 bare except for lateral tuft of 3–5 white hairs at extreme base. S2 and S3 with sparse white hairs. S4 mostly bare. T5 with a few white hairs ventrally and a row of black setae along posterior margin. Hypopygium (Fig. 10B): cerci almost as long as abdomen, slender, cylindrical (though often shriveled when dried), sparsely covered with whorls of long, pale yellow setae.

Female. Body length 6.5–7.0 mm, wing length 6.5–7.0 mm. Similar to male except for face wider; palpus slightly larger and more uniformly covered with black setae. Tarsus I(2) normal, not unusually short or thickened. Wing as in Fig. 16F.

Etymology. This species is named for its known distribution: most specimens were collected in the Sky Island mountain ranges in the Sonoran Desert region (Fig. 13).

Remarks. Specimens were collected in April–June prior to onset of the summer monsoon.

Robinson (1970b: 57) reports *L. genualis* from Mexico (Guerrero) but this single specimen "differs from the eastern North America material by...the presence of a row of small acrostichal setae". This specimen could not be located, but is probably *L. sonorus*.

Distribution. *Liancalus sonorus* is known from the southwestern U.S. and neighboring Mexico (Fig. 13).

Type material. **HOLOTYPE** ♂, labeled: "ARIZONA: Cochise Co./ Ramsey Canyon/ Huachuca Mtns. 5500'/ 23-IV-2002/ R. Hurley & J. Runyon"; "HOLOTYPE/ ♂ *Liancalus/ sonorus/* Runyon & Hurley" [red label] (MCZ). **PARATYPES: MEXICO:** CHIHUAHUA: Radiola Spring, tributary Rio Chuhuichupa, 23.vi.1987, Baumann, Kondratieff, Sargent & Wells (1 ♀, BYU). **USA:** same data as holotype (3 ♀, MTEC); Pima Co., Catalina Mts, Marshall Gulch near Summerhaven, 28.v.1986, J. Jenkins (1 ♂, 2 ♀, MTEC); Santa Cruz Co., Coronado National Forest, Santa Rita Mts, Madera Cyn, 3-4.vi.1991, B.J. Sinclair (1 ♂, 2 ♀, CNC), same as previous, 27.iv.1979, K.N. Barber (1 ♂, DEBU), same as previous, 5100 ft, 25.iv.2001, RLH & JBR (1 ♂, MTEC).

Acknowledgements

Michael Ivie (MTEC) is especially thanked for help elucidating the nomenclature of *Liancalus*; Neal Evenhuis (BPBM) and Frank Krell (DMNS) also provided helpful discussion on this issue. Scott Brooks (CNC) kindly provided the blank map template used for distribution figures. Crystal Maier (SEMC) is thanked for providing tips on preparing illustrations using a graphics tablet. Riley Nelson is thanked for allowing us to use the excellent photo taken of *L. hydrophilus* (Fig. 8). Martin Hauser (CSCA) and an anonymous reviewer provided comments that improved the manuscript. Thanks to the following curators and their respective institutions for the loan of specimens: Tam Nguyen and David Grimaldi (AMNH), Shawn Clark and Nelson Riley (BYU), Norm Penny (CAS), Chen Young (CMNH), Scott Brooks (CNC), Steve Gaimari and Martin Hauser (CSCA), Boris Kondratieff (CSUC), Rick Hoebeke (CUIC); Steve Marshall (DEBU), Cheryl Barr (EMEC), Carol von Dohlen (EMUS), Gary Steck (FSCA), Paul Tinerella (INHS), Greg Courtney (ISUI), Brian Brown (LACM), Philip Perkins (MCZ), Gary Parsons (MSUC); Margaret Rusch and Timothy McCabe (NYSM); Josh Vlach (ODAC), Chris Marshall (OSAC), Creighton Freeman (OSU), Zack Falin (SEMC), Carl Olson (UAIC), Karen Needham (UBCZ); Steve Heydon (UCD), Doug Yanega (UCR), Cecil Smith (UGCA); Phil Clausen (UMSP), Norman Woodley (USNM), Frank Merickel (WFBM), Rich Zack (WSU), Mark O'Brien (UMMZ).

References

- Aldrich JM (1893) The dolichopodid genus *Liancalus* Loew. *Psyche* 6: 569–571. doi: 10.1155/1893/26053
- Aldrich JM (1904) A contribution to the study of American Dolichopodidae. *Transactions of the American Entomological Society* 30: 269–286.
- Aldrich JM (1905) A catalogue of North American Diptera. *Smithsonian Miscellaneous Collections* 46: 1–680.
- Banta AM (1907) The Fauna of Mayfield's Cave. *Carnegie Institution of Washington* 67: 1–114.
- Barnes JK, Slay ME, Taylor SJ (2009) Adult Diptera from Ozark Caves. *Proceedings of the Entomological Society of Washington* 111: 335–353. doi: 10.4289/0013-8797-111.2.335
- Becker T, Bezzi M, Bischof J, Kertész K, Stein P (1903) Katalog der paläarktischen Dipteren. Band II. Orthorrhapha Brachycera. Budapest, 396 pp. doi: 10.5962/bhl.title.9240
- Becker T (1917–1918) Dipterologische Studien. Dolichopodidae. A. Paläarktischen Region. *Nova Acta Academiae Caesarum Leopoldinisch-Carolinæ Germanicæ Naturæ Curiosorum* 102(2)(1917): 113–361, 103(3)(1918): 203–315, 104(2)(1918): 35–214.
- Becker T (1922a) Dipterologische Studien, Dolichopodidae. B. Nearktische und Neotropische Region. *Abhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 13(1): 1–394.
- Becker T (1922b) Dipterologische Studien. Dolichopodidae der Indo-Australische Region. *Capita Zoologica* 1(4): 1–247.
- Bickel DJ (2009) Family Dolichopodidae. In: Brown BV et al. (Eds) *Manual of Central American Diptera*. Volume 1. NRC Press, Ottawa, 671–694.
- Bigot JMF (1859) Essai d'une classification générale et synoptique de l'ordre des Insectes Diptères. VII mémoire. Tribus des Raphidi et Dolichopodi (Mihi). VIIe. *Annales de la Société entomologique de France* (ser. 3) 7: 201–231.
- Bigot JMF (1890) Diptères nouveaux ou peu connus, 36e partie XLV: Dolichopodidae, Essai d'une classification générale. *Annales de la Société entomologique de France* 10(6): 261–296.
- Cole FR, Schlinger EI (1969) *The Flies of Western North America*. University of California Press, Berkeley, 693 pp.
- Coquillett DW (1910) The type-species of the North American genera of Diptera. *Proceedings of the United States National Museum* 37: 499–647. doi: 10.5479/si.00963801.37-1719.499
- Corpus LD (1986) Immature stages of *Liancalus similis* (Diptera: Dolichopodidae). *Journal of the Kansas Entomological Society* 59: 635–640.
- Cregan MB (1941) Generic relationships of the Dolichopodidae (Diptera), based on a study of the mouth parts. *Illinois Biological Monograph* 18: 1–68.
- Crossley R (1988) Mating behaviour of *Liancalus virens* (Scop.), (Dolichopodidae). *Dipterists Digest* 1: 45–46.
- Curran CH (1926) The Dolichopodidae of the South African Museum. *Annals of the South African Museum* 23: 377–416.
- Curran CH (1934) The families and genera of North American Diptera. *American Museum of Natural History*, New York, 512 pp. doi: 10.5962/bhl.title.6825

- D'Assis Fonseca ECM (1978) Diptera. Orthorrhapha. Brachycera. Dolichopodidae. Handbooks for the Identification of British Insects 9(5): 1–90.
- Dyte CE (1967) The genus *Liancalus* Loew (Diptera: Dolichopodidae) in the Ethiopian Region. Proceedings of the Royal Entomological Society of London (B) 36: 123–127.
- Dyte CE (1975) Family Dolichopodidae. In: Delfinado MD, Hardy DE (Eds) A catalog of the Diptera of the Oriental Region (Volume II). Suborder Brachycera through Division Aschiza, Suborder Cyclorrhapha. University of Hawaii Press, Honolulu, 212–258.
- Evenhuis NL (2013) The insect and spider collections of the World. <http://hbs.bishopmuseum.org/codens/codens-inst.html> [accessed 28 April 2014]
- Evenhuis NL, Bickel DJ (2011) A new species of the endemic Hawaiian genus *Paraliancalus* Parent, with notes on the genus *Liancalus* Loew (Diptera: Dolichopodidae). Bishop Museum Occasional Papers 109: 3–13.
- Frey R (1915) Zur Kenntnis der Dipterenfauna Finnlands. III. Dolichopodidae. Acta Societas pro Fauna et Flora Fennica 40(5): 1–80.
- Guérin-Ménéville FE (1844) Iconographie du Règne Animal de G. Cuvier, ou représentation d'après nature de l'une des espèces les plus remarquables et souvent non encore figurées, de chaque genre d'animaux Insectes. JB Baillière, Paris, 576 pp.
- Gobert E (1887) Catalog des Diptères de France. Revue D'Entomologie 6: 1–88.
- Harmston FC, Knowlton GF (1945) On the status of *Liancalus limbatus* Van Duzee (Diptera-Dolichopodidae). Bulletin of the Brooklyn Entomological Society 40: 55–56.
- Hurley RL, Runyon JB (2009) A review of *Erebomyia* (Diptera: Dolichopodidae), with descriptions of three new species. Zootaxa 2054: 38–48.
- Hurley RL (1985) Dolichopodidae: Hydrophorinae. In: Griffiths GCD (Ed.) Flies of the Nearctic Region (Volume VI) – Orthogenya (Part 6, Number 1). E Schweizerbart, Stuttgart, 1–112.
- Hurley RL (1995) Dolichopodidae: Hydrophorinae. In: Griffiths GCD (Ed.) Flies of the Nearctic Region (Volume VI) – Orthogenya (Part 6, Number 2). E Schweizerbart, Stuttgart, 113–224.
- ICZN (1999) International Code of Zoological Nomenclature (Fourth Edition). The International Trust for Zoological Nomenclature, London, 306 pp.
- Kahanpää J (2014) Checklist of the Empidoidea of Finland (Insecta, Diptera). Zookeys 441: 183–207. doi: 10.3897/zookeys.441.7154
- Loew H (1857) Neue Beiträge zur Kenntniss der Dipteren. Fünfter Beitrag. Programme der Königlichen Realschule zu Meseritz 1857: 1–56.
- Loew H (1861) Neue Beiträge zur Kenntniss der Dipteren. Achter Beitrag. Programme der Königlichen Realschule zu Meseritz 1861: 1–100.
- Loew H (1864) Monographs of the Diptera of North America, Part II. Smithsonian Institution, Smithsonian Miscellaneous Collections 6(2): 1–360.
- Lundbeck W (1912) Diptera Danica, Part IV: Dolichopodidae. S. Gad, Copenhagen, 416 pp.
- Masunaga K (2001) Redescription of *Liancalus zhenzhuristi* Negrobov (Diptera: Dolichopodidae) from Japan, with descriptions of immature stages and biological notes. Entomological Science 4: 109–119.
- McAlpine JF (1981) Morphology and terminology – adults. Chapter 2. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual

- of Nearctic Diptera, Volume 1, Monograph No. 27. Research Branch, Agriculture Canada, Ottawa, 9–63.
- Negrobov OP (1978) Fliegen der Palaearktischen Region Supplement 29(319), 387–418.
- Negrobov OP (1979) Species of the genus *Liancalus* (Dolichopodidae, Diptera) in South Korea and Taiwan. Zoologicheskii Zhurnal 58: 928–931.
- Negrobov OP, Grootaert P, Coulibaly B (1987) Description d’une espece nouvelle du genre *Liancalus* Loew, 1857 (Diptera, Dolichopodidae) du Zaïre. Bulletin de l’Institut Royal des Sciences Naturelles de Belgique Entomologie 57: 157–159.
- Negrobov OP (1991) Family Dolichopodidae. In: Soos A, Papp L (Eds) Catalogue of Palaearctic Diptera (Vol. 7. Dolichopodidae – Platypezidae). Elsevier, Amsterdam, 11–139.
- O’Hara JE, Cerretti P, Pape T, Evenhuis NL (2011) Nomenclatural studies toward a world list of Diptera genus-group names. Part II: Camillo Rondani. Zootaxa 3141: 1–268.
- Osten Sacken CR (1877) Western Diptera: Descriptions of new genera and species of Diptera from the region west of the Mississippi and especially from California. [U.S. Department of the Interior] Bulletin of the United States Geological and Geographical Survey of the Territories 3: 189–354.
- Parent O (1932) Dolichopodides de l’expédition du Dr. Rensch aux petites îles de la Sonde. Encyclopédie Entomologique (B II) Diptera 6: 103–123.
- Parent O (1938) Diptères Dolichopodides. Faune de France 35: 1–720.
- Parent O (1939) Diptères Dolichopodides de la région éthiopienne. Revue de Zoologie et de Botanique Africaines 32: 256–282.
- Pollet MA, Brooks SE, Cumming JM (2004) Catalog of the Dolichopodidae (Diptera) of America north of Mexico. Bulletin of the American Museum of Natural History 283: 1–114. doi: 10.1206/0003-0090(2004)283<0001:COTDDO>2.0.CO;2
- Reeves WK, Jensen JB, Ozier JC (2000) New faunal and fungal records from caves in Georgia, USA. Journal of Cave and Karst Studies 62: 169–179.
- Robinson H (1964) A synopsis of the Dolichopodidae (Diptera) of the southeastern United States and adjacent regions. Miscellaneous Publications of the Entomological Society of America 4: 103–192.
- Robinson H (1970a) The subfamilies of the family Dolichopodidae in North and South America (Diptera). Papéis Avulsos do Departamento de Zoologia (São Paulo) 23(6): 53–62.
- Robinson H (1970b) 40 Family Dolichopodidae. In: Papavero N (Ed.) A catalogue of the Diptera of the Americas south of the United States (Volume 40). Universidade de São Paulo, Museu de Zoologia, 92 pp.
- Robinson H, Vockeroth JR (1981) Dolichopodidae [Chapter 48]. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera, Volume 1. Agriculture Canada Monograph 27: 625–639.
- Rondani C (1856) Dipterologiae italicae prodromus. Vol: I. Genera italica ordinis dipterorum ordinatim disposita et distincta et in familias et stirpes aggregata. A Stocchi, Parma, 226 pp.
- Rondani C (1857) Dipterologiae italicae prodromus. Vol: II. Species italicae ordinis dipterorum in genera characteribus definita, ordinatim collectae, methodo analitica distinctae, et novis vel minus cognitis descriptis. Pars prima. Oestridae: Syrphidae: Conopidae. A. Stocchi, Parmae (Parma), 264 pp.

- Runyon JB (2008) New species of long-legged flies (Diptera: Dolichopodidae) from central Pennsylvania. *Proceedings of the Entomological Society of Washington* 110: 363–373. doi: 10.4289/07-021.1
- Runyon JB, Hurley RL (2003) Revision of the Nearctic species of *Nepalomyia* Holis (= *Neurigonella* Robinson) (Diptera: Dolichopodidae: Peloropecodinae) with a world catalog. *Annals of the Entomological Society of America* 96: 403–414. doi: 10.1603/0013-8746(2003)096[0403:ROTNOS]2.0.CO;2
- Runyon JB, Hurley RL (2004) A new genus of long-legged flies displaying remarkable wing directional asymmetry. *Proceedings of the Royal Society of London Series B (Supplement)* 271: S114–S116. doi: 10.1098/rsbl.2003.0118
- Runyon JB, Ivie MA, Evenhuis NL (submitted) Case 3681. *Liancalus* Loew, 1857 and *Scellus* Loew, 1857 (Insecta, Diptera, Dolichopodidae): proposed conservation of the names by designation of *Dolichopus regius* Fabricius, 1805 as type species for *Anoplomerus* Rondani, 1856. *Bulletin of Zoological Nomenclature*.
- Sinclair BJ (1992) A phylogenetic interpretation of the Brachycera (Diptera) based on the larval mandible and associated mouthpart structures. *Systematic Entomology* 17: 233–252. doi: 10.1111/j.1365-3113.1992.tb00335.x
- Sinclair BJ, Cumming JM (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). *Zootaxa* 1180: 1–172.
- Ulrich H (2004) Predation by adult Dolichopodidae (Diptera): a review of literature with an annotated prey-predator list. *Studia Dipterologica* 11: 369–403.
- Vaillant F (1948) Les premier stades de *Liancalus virens* Scop. (Dolichopodidae). *Bulletin de la Société zoologique de France* 73: 118–130.
- Van Duzee MC (1917) New North American species of Dolichopodidae (Dip.). *Entomological News* 28: 123–128.
- Wagler J (1830) *Natürliches System der Amphibien, mit vorangehender Classification der Säugethiere und Vögel*. München, Stuttgart & Tübingen, 354 pp.
- Wahlgren E (1912) *Svensk Insektfauna* 11. Diptera. 1. Orthorapha. 2. Brachycera, Fam. 25–26 (Dolichopodidae, Lonchopteridae). *Entomologisk Tidskrift* 33: 1–56.
- Wei LM, Liu G (1995) Studies on the family Dolichopodidae in southwest China, a new species of *Liancalus* from Guizhou Province (Diptera). *Journal of Guizhou Agricultural College* 14: 35–38.
- Yang D (1998) New and little known species of Dolichopodidae from China (I). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique Entomologie* 68: 151–164.
- Yang D, Zhu Y, Wang M, Zhang L (2006) *World Catalog of Dolichopodidae* (Insecta: Diptera). China Agricultural University Press, Beijing, 704 pp.
- Yang D, Zhang L, Wang M, Zhu Y (2011) Diptera, Dolichopodidae. In: *Fauna Sinica, Insecta*, Vol. 53. Science Press, Beijing, 1912 pp.
- Zimmer M, Diestelhorst O, Lunau K (2003) Courtship in long-legged flies (Diptera: Dolichopodidae): function and evolution of signals. *Behavioral Ecology* 14: 526–530. doi: 10.1093/beheco/arg028

Supplementary material 1

Supplemental Video 1

Authors: Justin B. Runyon, Richard L. Hurley

Data type: MPEG video file

Explanation note: Adult female *Liancalus similis* feeding on nematoceros dipteran larva (Tipulidae?) on Palisade Falls, Gallatin County, Montana on June 27, 2013.

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

Supplementary material 2

Supplemental Video 2

Authors: Justin B. Runyon, Richard L. Hurley

Data type: MPEG video file

Explanation note: Two adult males of *Liancalus similis* on Palisade Falls, Gallatin County, Montana on October 12, 2012. This video was taken looking upwards on vertical basalt column near water of falls.

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

Supplementary material 3

Supplemental Video 3

Authors: Justin B. Runyon, Richard L. Hurley

Data type: MPEG video file

Explanation note: Two males of *Liancalus similis* showing the typical looping flight of *Liancalus* adults. This video was taken looking upwards on vertical basalt column on Palisade Falls, Gallatin County, Montana on October 12, 2012.

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

Halechiniscidae (Heterotardigrada, Arthrotardigrada) of Oura Bay, Okinawajima, Ryukyu Islands, with descriptions of three new species

Shinta Fujimoto¹

¹ Department of Zoology, Division of Biological Science, Graduate School of Science, Kyoto University, Kitashirakawa-Oiwakecho, Sakyo-ku, Kyoto 606-8502, Japan

Corresponding author: Shinta Fujimoto (shintaf@water-bears.com)

Academic editor: Sandra McInnes | Received 12 November 2014 | Accepted 9 February 2015 | Published 24 February 2015

<http://zoobank.org/58EC3A1C-7439-4C15-9592-ADEA729791B3>

Citation: Fujimoto S (2015) Halechiniscidae (Heterotardigrada, Arthrotardigrada) of Oura Bay, Okinawajima, Ryukyu Islands, with descriptions of three new species. ZooKeys 483: 149–166. doi: 10.3897/zookeys.483.8936

Abstract

Marine tardigrades of the family Halechiniscidae (Heterotardigrada: Arthrotardigrada) are reported from Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan, including *Dipodarctus* sp., *Florarctus wunai* sp. n., *Halechiniscus churakaagii* sp. n., *Halechiniscus yanakaagii* sp. n. and *Styraconyx* sp. The attributes distinguishing *Florarctus wunai* sp. n. from its congeners is a combination of two characters, the smooth dorsal cuticle and two small projections of the caudal alae caestus. *Halechiniscus churakaagii* sp. n. is differentiated from its congeners by the combination of two characters, the robust cephalic cirrophores and the scapular processes with flat oval tips, while *Halechiniscus yanakaagii* sp. n. can be identified by the laterally protruded arched double processes with acute tips situated dorsally at the level of leg I. A list of marine tardigrades reported from the Ryukyu Islands is provided.

Keywords

Meiobenthos, northwestern Pacific, subtidal, subtropic, Tardigrada, taxonomy

Introduction

Halechiniscidae (Heterotardigrada: Arthrotardigrada) is a group of unarmoured marine tardigrades possessing cephalic appendages, including the median cirrus, and legs with four digits terminating in distal claws. More than half of the described marine species are assigned to this family, which comprises 29 genera in seven subfamilies.

In January 2014, the first Umisawa-kai (Field Workshop for Young Marine Biologists) was held to survey the invertebrate fauna of Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan. During this survey, the following five species of Halechiniscidae were encountered: *Dipodarctus* sp., *Florarctus wunai* sp. n., *Halechiniscus churakaagii* sp. n., *Halechiniscus yanakaagii* sp. n. and *Styraconyx* sp.

Materials and methods

Specimens were found in five sediment samples (each sample was approximately 1L in volume) collected from Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan by SCUBA diving. The geographical coordinates, water depth, sediment type and date of collection are listed for each sediment sample in Table 1.

The samples were freshwater-shocked (Kristensen 1983), sieved through a 32-μm-mesh net and fixed in 3% formaldehyde. To extract specimens from the remaining sediment the fixed samples were treated using a modified density separation method from Burgess (2001). The sample was rinsed with distilled water to remove formaldehyde. Subsequently, the sample was thoroughly mixed with distilled water-diluted LUDOX® HS-40 colloidal silica (density slightly above 1.15 g cm⁻³) before allowing the sediment to settle (for at least 15 minutes). The supernatant was sieved through a 32-μm-mesh net to collect the specimens, and the procedure repeated three times per sample. The specimens were sorted under a stereomicroscope before being mounted in glycerol and observed under a phase-contrast microscope (Olympus BX53). The terminology for the genus *Florarctus* follows Hansen (2011).

Table 1. Sediment samples collected from Oura Bay, Okinawajima, Ryukyu Islands.

Sediment sample number	Dive site	Geographical coordinates of dive site	Water depth	Sediment type	Date	Species collected (Number of specimens)
1	Off Sedake	26°32'39.06"N, 128°2'52.8"E	6 m	Coarse sand	24th Jan. 2014	<i>Halechiniscus churakaagii</i> sp. n. (1)
2	Off Camp Schwab	26°31'51.78"N, 128°3'10.74"E	9 m	Coarse sand	25th Jan. 2014	<i>Florarctus wunai</i> sp. n. (2)
3	Off Camp Schwab	26°31'51.78"N, 128°3'10.74"E	6 m	Coarse sand	25th Jan. 2014	<i>F. wunai</i> sp. n. (2)
4	Off Futami	26°32'42.47"N, 128°2'26.34"E	6 m	Muddy sand	27th Jan. 2014	<i>Dipodarctus</i> sp. (2) <i>H. churakaagii</i> sp. n. (1) <i>Styraconyx</i> sp. (2)
5	Off Thima	26°32'0.81"N, 128°3'49.61"E	6 m	Coarse sand	28th Jan. 2014	<i>F. wunai</i> sp. n. (1) <i>H. yanakaagii</i> sp. n. (1)

Systematics

Order ARTHROTARDIGRADA Marcus, 1927

Family Halechiniscidae Thulin, 1928

Subfamily Dipodarctinae Pollock, 1995

Genus *Dipodarctus* Pollock, 1995

Dipodarctus sp.

Fig. 1

Material examined. Two four-clawed juveniles found in sediment sample 4 (Table 1).

Remarks. The species resembles *Dipodarctus borrori* Pollock, 1995 and *D. susannae* Jørgensen, Boesgaard, Møbjerg & Kristensen, 2014 by having digits of unequal length on legs I–III and the lack of lateral processes between legs III and IV. It is distinguished from the two species by the lateral cirrus lack of scapus, which is present in the both *D. borrori* and *D. susannae*. It is also distinguished from *D. borrori* by the shorter digit 1 of legs I–III and from *D. susannae* by its shorter papillate leg IV sense organ. These observations are based on comparing juveniles with descriptions of adults so while this species is probably an undescribed species observation of an adult specimen is required for confirmation.



Figure 1. Phase contrast micrograph of *Dipodarctus* sp. Scale bar = 20 μ m.

Subfamily Florarctinae Renaud-Mornant, 1982**Genus *Florarctus* Delamare, Deboutteville & Renaud-Mornant, 1965*****Florarctus wunai* sp. n.**

<http://zoobank.org/39C064FF-3B9A-44D7-9B44-AE96EFA9C337>

Figs 2–3, Table 2

Diagnosis. *Florarctus* with smooth dorsal cuticle; six alae with continuous caestus; frontal ala with no caestus; antero-lateral alae caestus with small projection at levels of leg I and II and developed projection at posterior end; postero-lateral alae caestus with parallelogram-shaped projection at posterior end; caudal ala divided into four lobes; caudal alae caestus with pair of small projections; longitudinally elongate secondary clava with internally directed weak swelling.

Material examined. *Holotype*: KUZ Z705: adult female found in sediment sample 3 (Table 1).

Paratypes: KUZ Z706: adult female found in sediment sample 2 (Table 1); KUZ Z707: adult male found with holotype; KUZ Z708: four-clawed specimen of undetermined status found from sediment sample 5 (Table 1); KUZ Z709: four clawed juvenile found from sediment sample 2 (Table 1).

Type locality. Water depth of 6 m, off Camp Schwab, Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan (26°31'51.78"N, 128°3'10.74"E). Collected by the author on 25th January 2014.

Type depository. The type series is deposited in the Zoological Collection of Kyoto University (KUZ).

Description of holotype. Adult female, body length: 257 μm , excluding alae (Fig. 2A, 3A). Cephalic region clearly separated from trunk. Dorsal surface smooth with folds. Ventral surface smooth. Lateral margin of body surrounded by aliform expansions with continuous caestus, which consists of frontal ala, pair of antero-lateral alae, pair of postero-lateral alae and caudal ala. Frontal ala spreads across entire anterior margin of cephalic region. Scapi of internal cirri continuous with ala. Base of lateral cirri and primary clavae enveloped together in ala. Antero-lateral ala spreads from approximately level with median cirrus to level of leg III with four slight indentations. Antero-lateral alae caestus with small projections at level of leg I and leg II and developed projection at posterior end. Slightly overlapping antero-lateral ala, postero-lateral ala spreads from level of leg III to level of cirrus E with two indentations: anterior slight indentation and posterior relatively strong indentation. Postero-lateral alae caestus with developed projection parallelogram-shaped at posterior end. Caudal ala spread between pair of cirri E with pair of lateral indentations (26 μm deep) and medial indentation (40 μm deep). Caudal caestus with pair of small projections. Unpaired median cirrus (36 μm) with scapus (10 μm), tubular portion (22 μm) and flagellum (4 μm) inserted dorsally 27 μm from frontal margin. Pair of internal cirri (46 μm) each with scapus (13 μm) tubular portion (30 μm) and flagellum (3 μm) inserted at anterior margin. Internal structure of internal cirrus arise

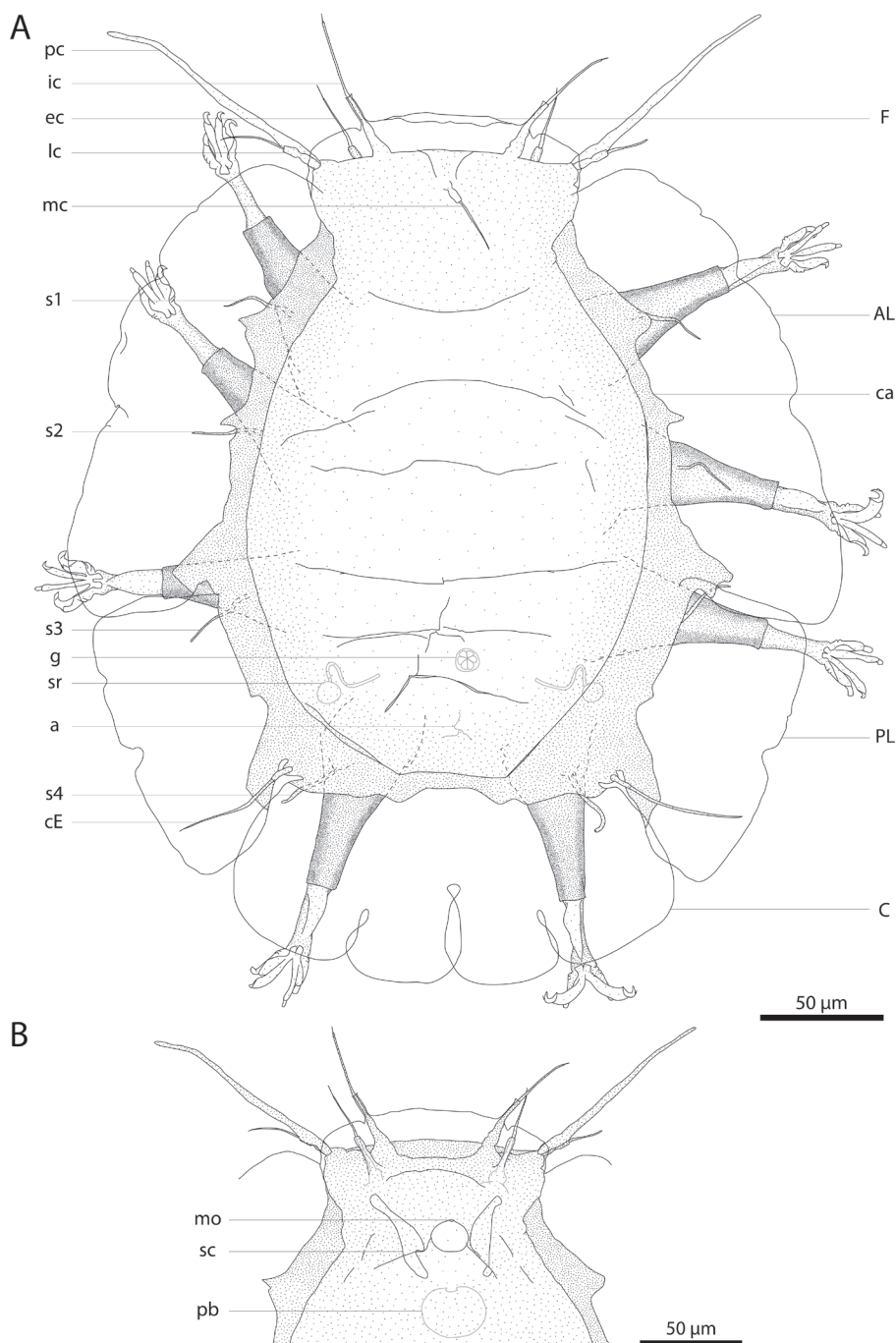


Figure 2. Drawing of *Florarctus wunai* sp. n., holotype KUZ Z705. **A** dorsal view **B** ventral view of cephalic region. a anus; AL anterolateral ala; C caudal ala; ca caestus; cE cirrus E; ec external cirrus; F frontal ala; g gonopore; ic internal cirrus; lc lateral cirrus; mc median cirrus; mo mouth; pb pharyngeal bulb; pc primary clava; PL postero-lateral ala; sc secondary clava; sr seminal receptacle; s1–4 leg I–IV sense organs.

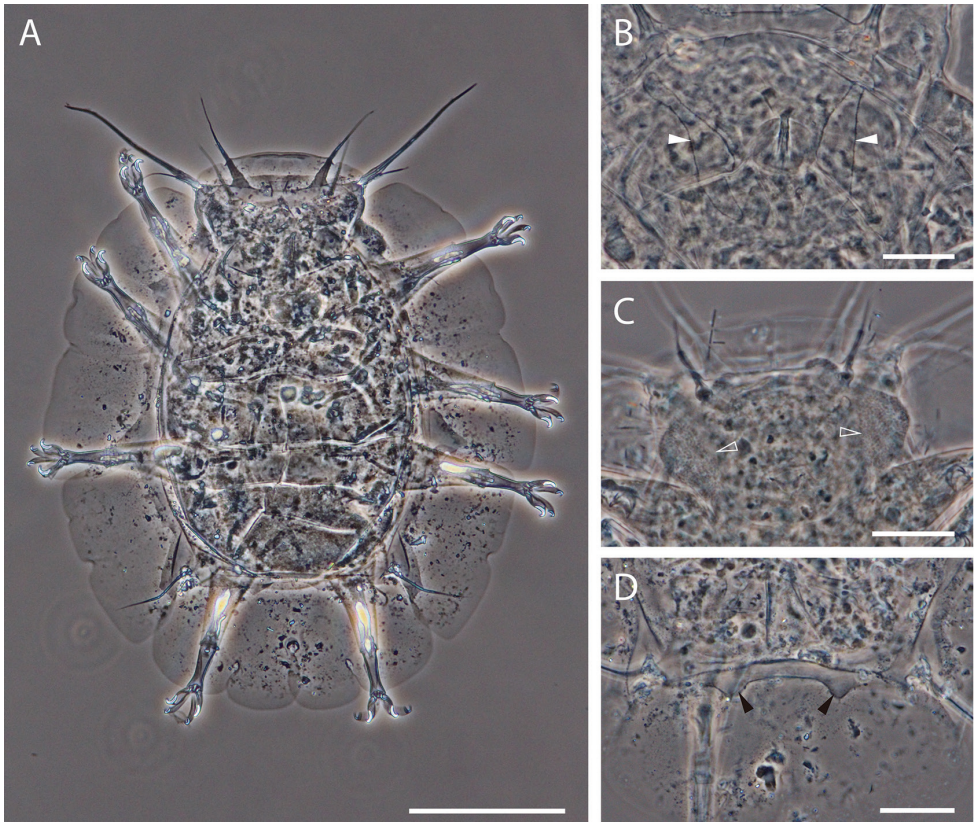


Figure 3. Phase contrast micrograph of *Florarctus wunai* sp. n. **A** dorsal view, holotype KUZ Z705, scale bar = 100 µm **B** secondary clavae (white arrowhead), holotype KUZ Z705, scale bar = 20 µm **C** bacterial vesicles (white, hollow arrowhead), paratype KUZ Z709, scale bar = 20 µm **D** caudal alae caestus with pair of small projections (black arrowhead), paratype KUZ Z708, scale bar = 20 µm.

25 µm from frontal margin. Pair of external cirrus (44 µm) with scapus (18 µm), tubular portion (20 µm) and flagellum (6 µm) inserted ventrally 30 µm from frontal margin. Internal structure of external cirrus arise 39 µm from frontal margin. Lateral cirrus (43 µm) with scapus (15 µm), tubular portion and flagellum and primary clava arise from same cirrophore. Boundary between tubular portion and flagellum of lateral cirrus indistinct in holotype. Lateral cirrus inserted dorso-posteriorly to primary clava. Primary clava (101 µm) thicker near base with basal van der Land's body. Secondary clavae in shape of longitudinally elongated, flat sac with internally directed weak swelling on each side of ventrally protruded mouth cone (Figs 2B, 3B). Bucco-pharyngeal apparatus not visible except for pharyngeal bulb (32 µm × 24 µm). No bacterial vesicles visible. Leg I sense organ (29 µm) consists of tapering spine and distal flagellum. Leg II and leg III sense organ (28 µm and 24 µm respectively) each consists of unsegmented tapering spine. Leg IV sense organ (29 µm) consists of tapering spine with basal van der Land's body, distal constricted portion and distal

Table 2. Morphometrics of the three new species (measurements in μm). Dashes indicate unmeasured trait.

Species	<i>Florarctus wunai</i> sp. n.					<i>Halechiniscus churakaagii</i> sp. n.		<i>Halechiniscus yanakaagii</i> sp. n.
	Holotype	Paratype	Paratype	Paratype	Paratype	Holotype	Paratype	Holotype
KUZ No.	Z705	Z706	Z707	Z708	Z709	Z710	Z711	Z712
Status	Female	Female	Male	?	Four-clawed juvenile	Female	Female	Female
Body length	257	241	125	132	122	170	183	170
Median cirrus	36	34	22	19	19	66	-	35
Internal cirrus	46	49	32	29	24	37	40	26
External cirrus	44	42	32	28	19	23	24	18
Lateral cirrus	43	46	32	-	32	68	52	41
Primary clava	101	101	78	-	-	34	38	21
Cirrus E	46	54	37	36	39	86	-	41
Leg I sense organ	29	31	19	18	14	11	12	14
Leg II sense organ	28	29	14	16	12	36	36	21
Leg III sense organ	24	28	15	-	17	32	33	21
Leg IV sense organ	29	25	17	17	15	16	17	15
Scapular process	absent	absent	absent	absent	absent	42	44	absent
Double process (anterior)	absent	absent	absent	absent	absent	absent	absent	23
Double process (posterior)	absent	absent	absent	absent	absent	absent	absent	26

pore. Pair of cirri E (46 μm) each with proximal portion and flagellum arise from between postero-lateral and caudal alarum caesti. Rosette-like female gonopore opens 27 μm anterior to anus. Pair of seminal receptacles sited laterally at a level between gonopore and anus. Seminal receptacle consists of sinuous duct, which opens 29 μm laterally from gonopore and terminates in spherical vesicle 9 μm in diameter. Each

leg terminates in four digits with proximal wrinkles and distal claws. External digits with hook-shaped peduncle. Internal digits longer than external digits. Internal claws with dorsal spur. External claws with calcar and avicularia. Internal claws smaller than external claws.

Etymology. The specific epithet, *wunai*, is a Ryukyuan word for “sister” (Nakamoto 1981) referring to the new species as a sister of *Florarctus antillensis* Van der Land, 1968, a species with similar morphology.

Remarks on paratypes. The adult male, KUZ Z707, was smaller than adult females, KUZ Z705 and Z706, but had longer primary clavae relative to its body length (Table 2). The male gonopore of KUZ Z707 opens 10 μ m anterior to the anus. The precise shape of male gonopore was not visible but spermatozoa were present inside the body. Excluding the lack of the genital structure, the paratypic four-clawed juvenile, KUZ Z709, was identical to the adults. A pair of bacterial vesicles is present in the paratypic four-clawed juvenile (Fig. 3C). For antero-lateral and postero-lateral alae, the number of slight indentations varied among specimens. There are two projections at the level of leg II in the paratypic specimen, KUZ Z708. The pair of small projections of the caudal alae caestus was better observed in the paratypes (Fig. 3D).

Differential diagnosis. The presence of the continuous caestus and the absence of dorsal mammilla-like ornamentation, are shared by *Florarctus antillensis*, *F. glareolus* Noda, 1987, *F. pulcher* De Zio Grimaldi, Lamarca, D’addabbo Gallo & Pietanza, 1999 and *F. wunai* sp. n. The new species is distinguished from these three species by the two small projections of the caudal alae caestus, which are long projections in *F. glareolus*, long projections with swollen tips in *F. pulcher* and absent in *F. antillensis* (using Renaud-Mornant [1970] for information on the caestus morphology of *F. antillensis*).

Subfamily Halechiniscinae Thulin, 1928

Genus *Halechiniscus* Richters, 1908

Halechiniscus churakaagii sp. n.

<http://zoobank.org/1BDD532C-501A-4D6B-9B2D-B4520618DB88>

Figs 4–5, Table 2

Diagnosis. *Halechiniscus* with cephalic region consisting of antero-medial lobe and dorsal lobe; median cirrus inserted on long robust cirrophore; dorsal internal cirrus inserted on robust cirrophore; ventral external cirrus inserted on short cirrophore; lateral cirrus and primary clava inserted on large lateral cirrophore; large scapular process with flat oval tip; cirrus E with proximal portion with distal dark portion and distal flagellum; bipartite leg I sense organ; large, unsegmented legs II and III sense organs; papillate leg IV sense organ; all claws with calcar.

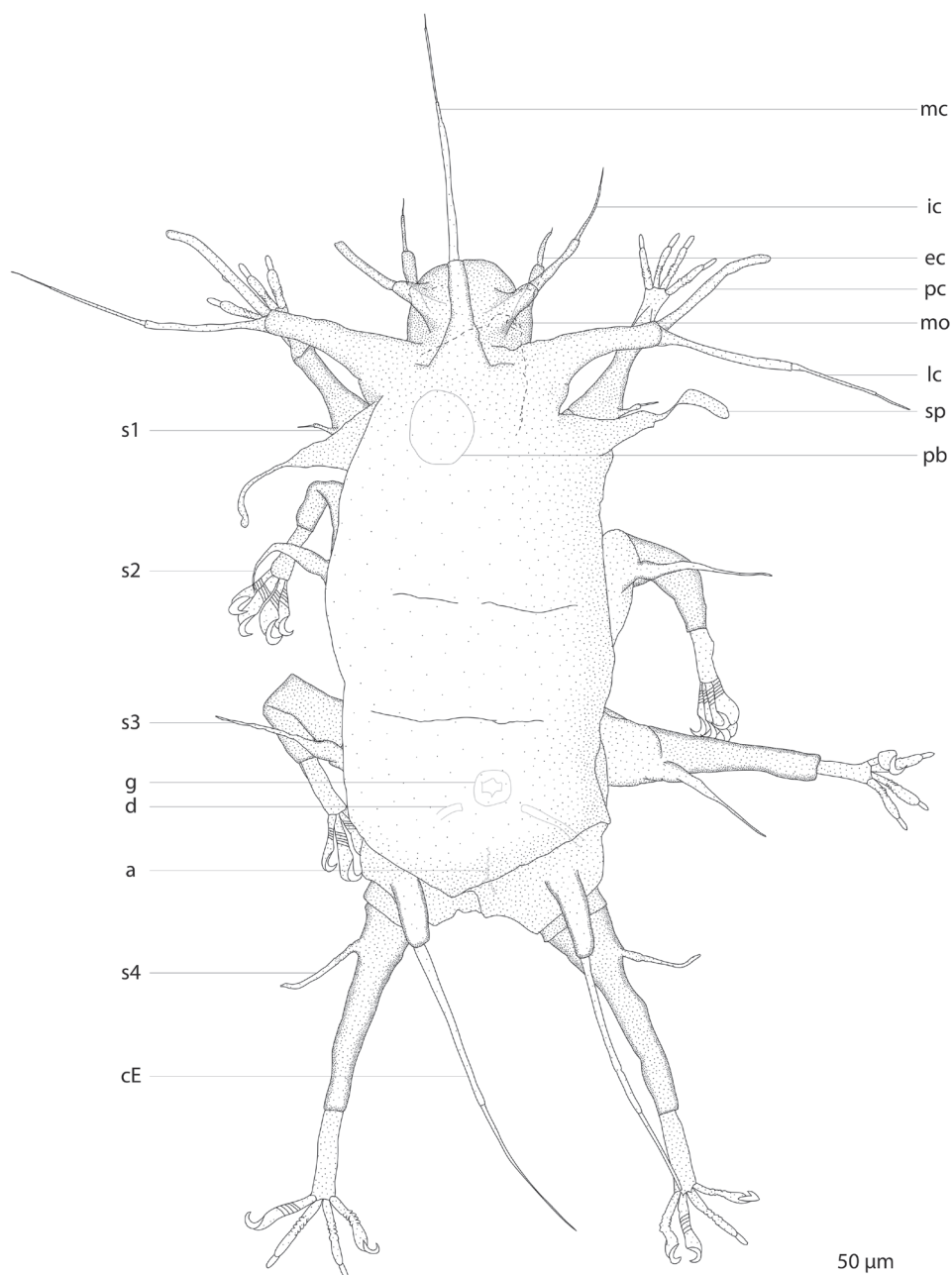


Figure 4. Drawing of *Halechiniscus churakaagii* sp. n., holotype KUZ Z710 (dorsal view). a anus; cE cirrus E; d seminal receptacle duct; ec external cirrus; g gonopore; ic internal cirrus; lc lateral cirrus; mc median cirrus; mo mouth; pb pharyngeal bulb; pc primary clava; sc scapular process; s1–4 leg I–IV sense organs.

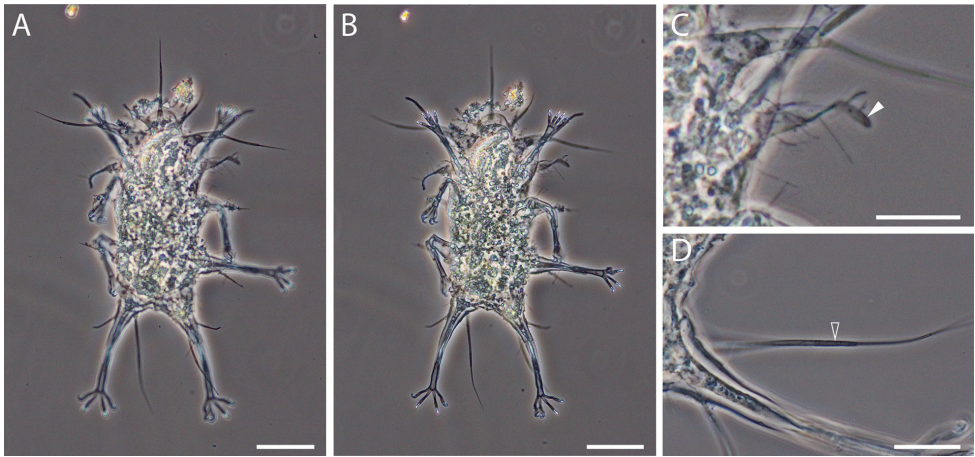


Figure 5. Phase contrast micrograph of *Halechiniscus churakaagii* sp. n., holotype KUZ Z710. **A** dorsal view, scale bar = 50 µm **B** ventral view, scale bar = 50 µm **C** scapular process (white arrowhead), scale bar = 10 µm **D** cirrus E with dark region (white, hollow arrowhead), scale bar = 20 µm.

Material examined. *Holotype*: KUZ Z710: adult female found in sediment sample 1 (Table 1).

Paratype: KUZ Z711: adult female found in sediment sample 4 (Table 1).

Type locality. Water depth of 6 m, off Sedake, Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan (26°32'39.06"N, 128°2'52.8"E). Collected by the author on 24th January 2014.

Type depository. The type series is deposited in the Zoological Collection of Kyoto University (KUZ).

Description of holotype. Adult female, body length: 170 µm (Figs 4, 5A, B). Dorsal and ventral surface smooth. Cephalic region divided into two lobes: antero-ventrally protruded round medial lobe and dorsal lobe. Unpaired median cirrus with scapus (42 µm) constricted at distal end, tubular portion (20 µm) and flagellum (4 µm) inserted on robust cirrophore (28 µm); positioned dorsally 28 µm from frontal margin on dorsal lobe. Pair of internal cirri each with scapus (16 µm), tubular portion (16 µm) and flagellum (5 µm) inserted on cirrophore; positioned dorsally on basal margin of medial lobe. Base of internal cirri arise postero-internal to base of scapi beneath cuticle. Pair of external cirri each with scapus (9 µm), tubular portion (9 µm) and flagellum (4 µm) inserted on cirrophore; positioned ventrally on medial lobe. Base of external cirri arise posterior to scapi beneath cuticle. Lateral cirrus with scapus (35 µm), tubular portion (23 µm) and flagellum (10 µm) and elongate primary clava (34 µm) inserted on each large, lateral cirrophore; positioned slightly anterior to level of median cirrus on dorsal lobe. Primary clava with basal van der Land's body inserted antero-ventrally to lateral cirrus. Secondary clava absent. Mouth cone protruded antero-ventrally. Bucco-pharyngeal apparatus not visible except for pharyngeal bulb (17 µm × 19 µm). Laterally protruded scapular process (42 µm)

with flat oval tip (Figs 4, 5C). No other process present. Cirrus E (86 μ m) segmented into proximal portion and distal flagellum. Under phase contrast microscopy distal end of proximal portion appears dark (Fig. 5D). This could be a distinct portion with accordion-like folds but scanning electron microscopy is required for confirmation. Rosette-like female gonopore opens ventrally 20 μ m anterior to anus. Seminal receptacle ducts open postero-lateral to gonopore. Vesicles of seminal receptacles not visible. Leg I sense organ (11 μ m) consists of scapus and flagellum. Leg II and III sense organs (36 μ m, 32 μ m) each consists of unsegmented, large spine. Papillate leg IV sense organ (16 μ m) with basal van der Land's body and terminal constriction inserted on slender cirrophore. Each leg terminates in digits with wrinkles and distal claws. All claws with small calcar.

Etymology. The specific epithet, *churakaagii*, is a Ryukyuan word for “beautiful woman” (Tojo 1930) referring to the well-defined cephalic morphology of the new species.

Differential diagnosis. The robust cirrophores of the median and lateral cirri are present in *Halechiniscus chafarinensis* De Zio Grimaldi & Villora Moreno, 1995, *H. macrocephalus* Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1988, *H. paratuleari* Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1988, *H. tuleari* Renaud-Mornant, 1979 and *H. churakaagii* sp. n. Among these species, *H. paratuleari* and the new species are the only species with large scapular processes. The new species is distinguished from *H. paratuleari* by the flat oval tip of the scapular process, which is acute in the latter and by the dark portion on cirrus E, which is absent in the latter.

I have interpreted the dorsally positioned cirrus as internal cirrus and the ventrally positioned cirrus as external cirrus in the new species, which is opposite to the interpretation of these features in the original descriptions of *H. tuleari* and *H. paratuleari*.

***Halechiniscus yanakaagii* sp. n.**

<http://zoobank.org/AEFB03E6-3BB7-401F-A85A-E3F3A666DB90>

Figs 6–7, Table 2

Diagnosis. *Halechiniscus* with no distinct cephalic lobes; only lateral cirrus and primary clava inserted on cirrophore; laterally protruded arched, double processes with acute tips at level of leg I; unsegmented cirrus E; bipartite leg I sense organ; unsegmented legs II and III sense organs; papillate leg IV sense organ; claws of internal digits with dorsal spur.

Material examined. *Holotype*: KUZ Z712: adult female found in sediment sample 5 (Table 1).

Type locality. Water depth of 6 m, Off Thima, Oura Bay, Okinawajima, one of the Ryukyu Islands, Japan (26°32'0.81"N, 128°3'49.61"E). Collected by the author on 28th January 2014.

Type depository. The holotype is deposited in the Zoological Collection of Kyoto University (KUZ).

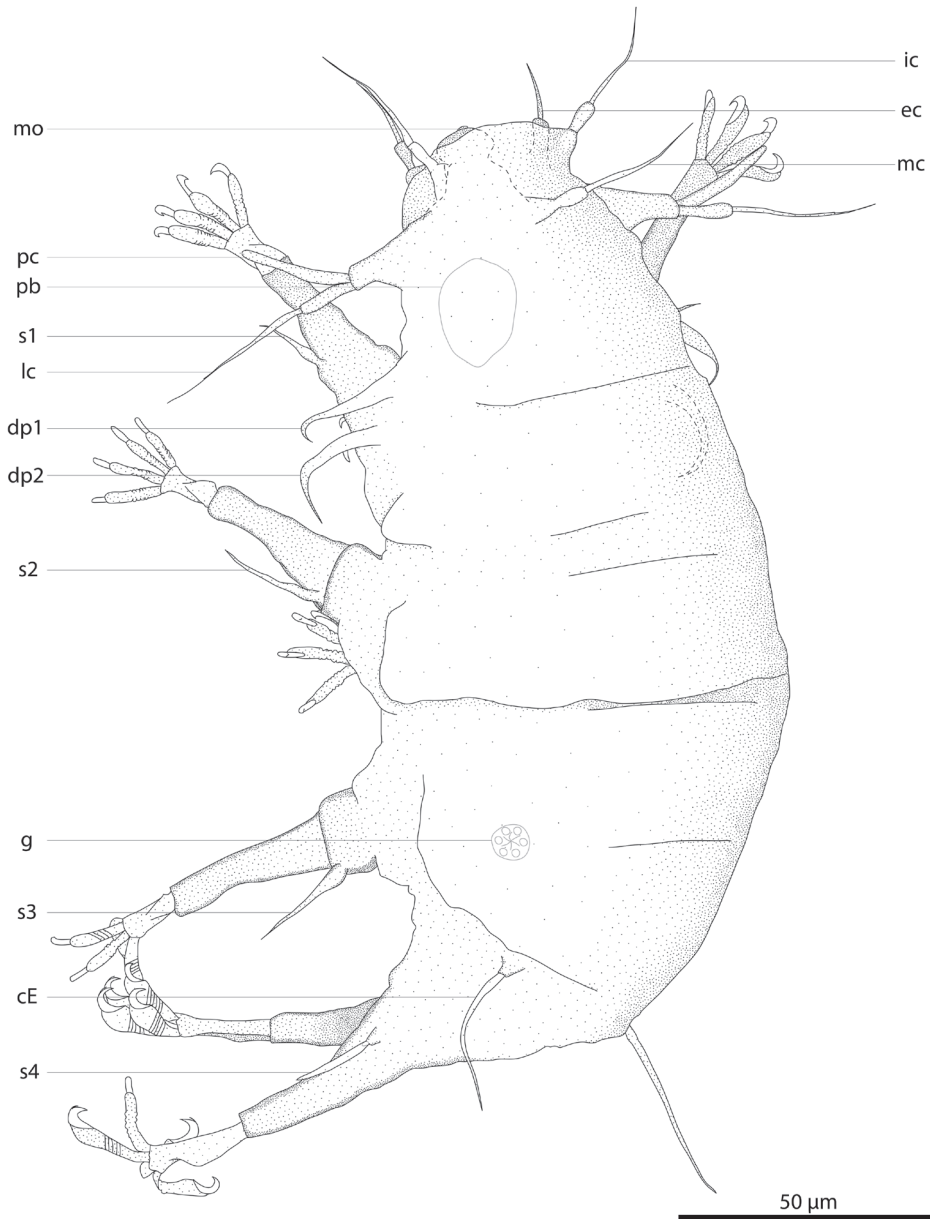


Figure 6. Drawing of *Halechiniscus yanakaagii* sp. n., holotype KUZ Z712 (dorso-lateral view). cE cirrus E; dp1–2 anterior and posterior double processes; ec external cirrus; g gonopore; ic internal cirrus; lc lateral cirrus; mc median cirrus; mo mouth; pb pharyngeal bulb; pc primary clava; s1–4 leg I–IV sense organs.

Description of holotype. Adult female, body length: 170 μm (Figs 6, 7A). Dorsal and ventral surface smooth. Cephalic region not divided into distinct lobes. Tubular portions of cephalic cirri indistinct from flagellum for median, internal and external

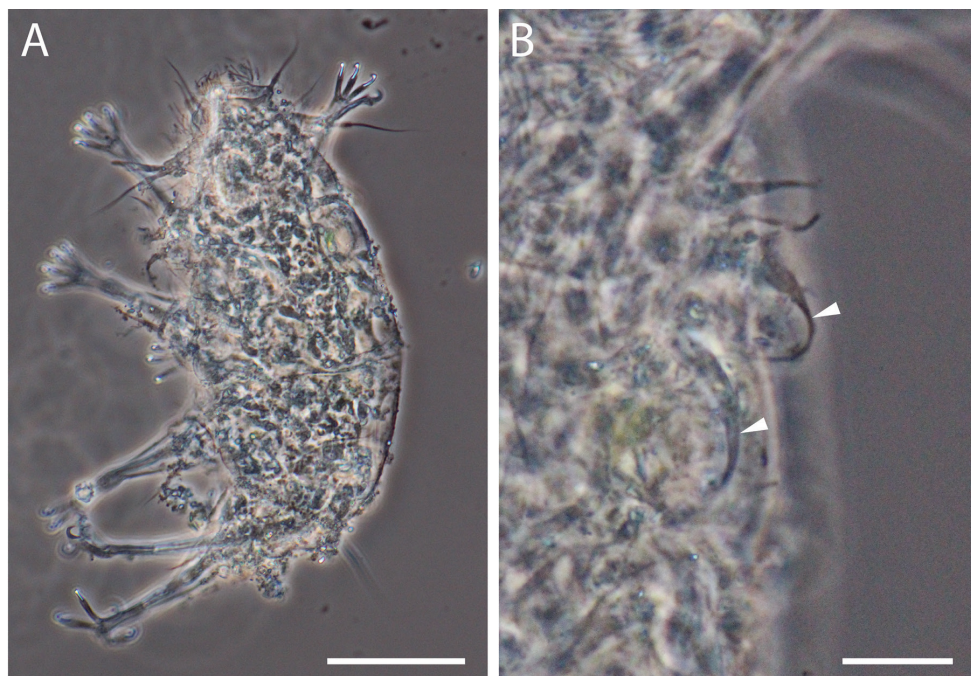


Figure 7. Phase contrast micrograph of *Halechiniscus yanakaagii* sp. n., holotype KUZ Z712. **A** dorso-lateral view, scale bar = 50 μ m **B** double processes (white arrowhead), scale bar = 10 μ m.

cirri. Unpaired median cirrus with scapus (11 μ m) and flagellum (24 μ m); inserted dorsally 16 μ m from frontal margin. Pair of internal cirri each with scapus (6 μ m) and flagellum (20 μ m); inserted dorsally close to frontal margin. Pair of external cirri each with scapus (7 μ m) and flagellum (11 μ m); inserted ventrally close to frontal margin. Lateral cirrus with scapus (11 μ m), tubular portion (22 μ m) and flagellum (8 μ m) and elongate primary clava (21 μ m); inserted on each lateral cirrophore positioned at same level as median cirrus. Primary clava with basal van der Land's body inserted antero-ventrally to lateral cirrus. Secondary clava absent. Mouth cone protruded antero-ventrally. Buccopharyngeal apparatus not visible except for pharyngeal bulb (14 μ m \times 20 μ m). Laterally protruding arched, double processes (23 μ m, 26 μ m) with acute tip situated dorsally at level of leg I (Figs 6, 7B). Unsegmented cirrus E (41 μ m) inserted on short cirrophore. Rosette-like female gonopore present. Seminal receptacles not visible. Leg I sense organ (14 μ m) consists of tapering spine and distal flagellum. Leg II and III sense organs (both 21 μ m) each consists of unsegmented spine. Papillate Leg IV sense organ (15 μ m) with basal van der Land's body inserted on small cirrophore. Each leg terminates in digits with wrinkles and distal claws. Claws of internal digits with dorsal spur.

Etymology. The specific epithet, *yanakaagii*, is a Ryukyuan word for “ugly woman” (Tojo 1930) referring to dirty appearance of the holotype.

Differential diagnosis. *Halechiniscus yanakaagii* sp. n. and *H. tuleari* are the only two *Halechiniscus* species with double processes at the level of leg I. The new species

is distinguished from *H. tuleari* by the absence of distinct cephalic lobes and robust cephalic cirrophores (which are present in the latter species), the similar length, arched, double processes (23 μm , 26 μm) in contrast with a short, straight, anterior process (holotype female: 8 μm ; paratype male: 4 μm) and a long, straight, posterior process (holotype female: 19 μm ; paratype male: 10 μm) (see: Renaud-Mornant 1979), and the absence of processes at level of leg II and III, which are present in *H. tuleari*.

Subfamily Styraconyxinae Kristensen & Renaud-Mornant, 1983

Genus *Styraconyx* Thulin, 1942

Styraconyx sp.

Fig. 8

Material examined. One female adult and one four-clawed juvenile found in sediment sample 4 (Table 1).

Remarks. The individuals found resemble *Styraconyx nanoqsunguak* Kristensen & Higgins, 1984 by the dorsal ridges (Fig. 8A, B). However, these specimens are distinguished by the lateral cirrus with no scapus (which is present *S. nanoqsunguak*), longer peduncles of the external digits and leg IV sense organs consisting of a spheri-

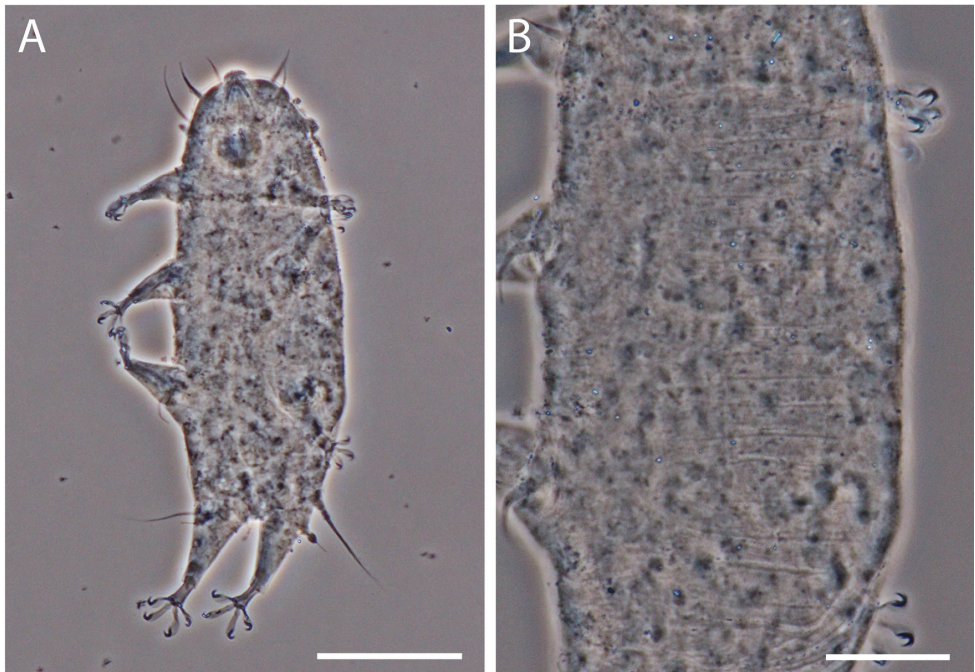


Figure 8. Phase contrast micrograph of *Styraconyx* sp. **A** ventral view, scale bar = 50 μm **B** dorsal cuticle with ridges, scale bar = 20 μm .

cal papilla and a distal spine (which is an elongate papilla and a shorter distal spine in *S. nanoqsunguak*). While I believe this is a new undescribed species, lack of visible taxonomic characters has hindered providing a complete species description.

Discussion

With the addition of the three new species and two unidentified species reported in this study, two orders, five families, 15 named and two unidentified genera, 13 named and 14 unidentified species of marine heterotardigrades are known from the Ryukyu Islands (Table 3). Sudzuki (1979) reported the first species as *Actinarctus* sp., which I deem a misidentification of *Florarctus* sp. according to the micrograph in his paper. Subsequently, Noda (1993, 1994a–c, 1998) reported 21 species but, with the exception of four species, with neither exact sampling localities nor remarks on species morphology. He noted that *Renaudarctus psammocryptus* Kristensen & Higgins, 1984 accorded well with the original description (Noda 1994b) and considered three species to be undescribed: Stygarctidae gen. (?) sp. (Noda 1993), Renaudarctidae gen. (?) sp. (Noda 1994b) and *Anisonyches* sp. (Noda 1994c). Recently, Fujimoto and Miyazaki (2013) described a new species from a submarine cave off Shimoji Island, Miyako Islands.

Table 3. Marine tardigrades reported from the Ryukyu Islands.

Taxon		Sampling locality	References
Order ARTHROTARDIGRADA			
Family Batillipedidae			
	<i>Batillipes pennaki</i> Marcus, 1946	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>B. similis</i> Schulz, 1955	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
Family Halechiniscidae			
Dipodartinae	<i>Dipodartus borrori</i> Pollock, 1995	Kuroshima	Noda (1998)
	<i>D.</i> sp.	Oura Bay, Okinawajima	This study
Florarctinae	<i>Florarctus wunai</i> sp. n.	Oura Bay, Okinawajima	This study
	<i>Florarctus</i> sp. 1 (Originally reported as <i>Actinarctus</i> sp.)	Taketomijima and Okinawajima	Sudzuki (1979)
	<i>F.</i> sp. 2	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>F.</i> sp. 3	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>Wingstrandartus</i> sp.	Tsunami, Okinawajima	Noda (1994a,b)
	<i>Halechiniscus chafarinensis</i> De Zio Grimaldi & Villora Moreno, 1995	Kuroshima	Noda (1998)
Halechiniscinae	<i>H. churakaagii</i> sp. n.	Oura Bay, Okinawajima	This study
	<i>H. yanakaagii</i> sp. n.	Oura Bay, Okinawajima	This study
	<i>H.</i> sp. 1	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>H.</i> sp. 2	Tsunami, Okinawajima	Noda (1994a)

Taxon		Sampling locality	References
Styraconyxinae	<i>Angursa clavifera</i> Noda, 1985	Tsunami, Okinawajima	Noda (1994a)
	<i>Raiarctus</i> sp.	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>Styraconyx nanoqsunguak</i> Kristensen & Higgins, 1984	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>S.</i> sp.	Oura Bay, Okinawajima	This study
	<i>Tholoarctus natans</i> Kristensen & Renaud-Mornant, 1983	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
Tanarctinae	<i>Tanarctus</i> sp.	Tsunami, Okinawajima	Noda (1994a)
Family Renaudarctidae			
	<i>Renaudarctus psammocryptus</i> Kristensen & Higgins, 1984	Kabira, Ishigakijima	Noda (1994b)
	Gen. (?) sp.	Kabira, Ishigakijima	Noda (1994b)
Family Stygarctidae			
Stygarctinae	<i>Neostygarctus lovedeluxe</i> Fujimoto & Miyazaki, 2013	Twin Cave, off Shimojijima	Fujimoto and Miyazaki (2013)
	<i>Parastygarctus higginsii</i> Renaud-Debyser, 1965	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	<i>Stygarctus</i> sp.	Kabira, Ishigakijima and/or Tsunami, Okinawajima	Noda (1994a,b)
	Gen. (?) sp.	Off Kuroshima	Noda (1993)
Order ECHINISCOIDEA			
Family Echiniscoididae			
	<i>Anisonyches</i> sp.	Kabira, Ishigakijima	Noda (1994b,c)

As noted above, at best the identifications are ambiguous, and verifying the identity of the species across published papers is difficult. Nonetheless, the data shows that Ryukyu Islands harbour a rich marine tardigrade fauna. With more research we can expect further species discoveries as many of the islands are unexplored and there are currently only seven species reported for the usually species-rich sub-littoral zone.

Acknowledgments

The author's thanks are due to the participants of the first Umisawa-kai, especially the two hosts, Daisuke Uyeno and Hiroshi Yamasaki, and the members of the diving team Snack Snufkin for facilitating the opportunity to survey Oura Bay. Thanks are also due to Tsutomu Hikida for helpful comments on the manuscript. This work was supported by Japan Society for the Promotion of Science Grant-in-Aid for JSPS fellows (Grant No. 25987).

References

- Burgess R (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Marine Ecology Progress Series* 214: 161–165. doi: 10.3354/meps214161
- Delamare Deboutteville C, Renaud Mornant J (1965) Un remarquable genre de Tardigrades des sables coralliens de Nouvelle-Calédonie. *Comptes Rendus de l'Académie des Sciences de Paris* 260: 2581–2583.
- De Zio Grimaldi S, Villora-Moreno S (1995) *Halechiniscus chafarinensis* n. sp. (Halechiniscidae), a new marine Tardigrada from the Alboran Sea (SW Mediterranean Sea). *Cahiers de Biologie Marine* 36(4): 285–289.
- De Zio Grimaldi S, Lamarca A, D'Addabbo Gallo M, Pietanza R (1999) Florarctinae of Asdhu Island, Maldives, Indian Ocean (Tardigrada, Heterotardigrada). *Italian Journal of Zoology* 66(4): 383–391. doi: 10.1080/11250009909356282
- Fujimoto S, Miyazaki K (2013) *Neostygartus lovedeluxe* n. sp. from the Miyako Islands, Japan: The First Record of Neostygartidae (Heterotardigrada: Arthrotardigrada) from the Pacific. *Zoological Science* 30(5): 414–419. doi: 10.2108/zsj.30.414
- Grimaldi de Zio S, D'Addabbo Gallo M, Morone De Lucia RM (1988) Two new Mediterranean species of the genus *Halechiniscus* (Tardigrada, Heterotardigrada). *Bolletino di Zoologia* 55(3): 205–211. doi: 10.1080/11250008809386618
- Hansen JG (2011) The phylogeny of Arthrotardigrada. PhD Thesis, University of Copenhagen, Copenhagen, Denmark.
- Jørgensen A, Boesgaard TM, Møbjerg N, Kristensen RM (2014) The tardigrade fauna of Australian marine caves: With descriptions of nine new species of Arthrotardigrada. *Zootaxa* 3802(4): 1–43. doi: 10.11646/zootaxa.3802.4.1
- Kristensen RM (1983) Loricifera, a new phylum with Aschelminthes characters from the meiobenthos. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 21: 163–180. doi: 10.1111/j.1439-0469.1983.tb00285.x
- Kristensen RM, Higgins RP (1984a) Revision of *Styraconyx* (Tardigrada: Halechiniscidae), with description of two new species from Disko Bay, West Greenland. *Smithsonian Contributions to Zoology* 391: 1–40. <http://hdl.handle.net/10088/5620>
- Kristensen RM, Higgins RP (1984b) A new family of Arthrotardigrada (Tardigrada: Heterotardigrada) from the Atlantic Coast of Florida, U.S.A. *Transactions of the American Microscopical Society* 103(3): 295–311. doi: 10.2307/3226191
- Kristensen RM, Renaud-Mornant J (1983) Existence d'Arthrotardigrades semi-benthiques de genres nouveaux de la sous-famille des Styraconyxinae subfam. n. *Cahiers de Biologie Marine* 24: 337–353.
- Marcus E (1927) Zur Anatomie und Ökologie mariner Tardigraden. *Zoologische Jahrbücher. Abteilung für Systematik* 53: 487–558.
- Marcus E (1946) *Batillipes pennaki*, a new marine tardigrade from the North and South American Atlantic coast. *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo* 2: 1–3.
- Nakamoto M (1981) *Zusetsu Ryukyugo jiten*. Kinkeisha, Tokyo, 463 pp.

- Noda H (1985) Description of a New Subspecies of *Angursa bispicis* Pollock (Heterotardigrada, Halechiniscidae) from Tanabe Bay, Japan. Publications of the Seto Marine Biological Laboratory 30(4/6): 269–276. <http://hdl.handle.net/2433/176110>
- Noda H (1987) A new species of marine Tardigrada of the genus *Florarctus* (Heterotardigrada, Halechiniscidae) from Japan. Publications of the Seto Marine Biological Laboratory 32(4/6): 323–328. <http://hdl.handle.net/2433/176140>
- Noda H (1993) Stygarctid tardigrade showing neoteny from Kuroshima Island, Ryukyu Archipelago. Zoological Science 10 (Supplement): 175. [Published conference abstract]
- Noda H (1994a) Tardigrades from sand beaches in Okinawa. Proceedings of the Japanese Society of Systematic Zoology 51: 79. [Published conference abstract in Japanese]
- Noda H (1994b) Two renaudarctids (Arthrotardigrada) from Ryukyu Archipelago, Japan. Sixth International Symposium on Tardigrada. Selwyn College, Cambridge, 42. [Unpublished conference abstract] http://www.tardigrada.net/newsletter/symposia_06.htm#Proceedings [accessed 14 January 2015]
- Noda H (1994c) An undescribed *Anisonyches* sp. (Tardigrada) with a large basal spur on the external claw from Ryukyu Islands. Zoological Science 11 (Supplement): 33. [Published conference abstract]
- Noda (1998) Two halechiniscid tardigrades from Japan and a similarity in marine tardigrade fauna between Japan and the Mediterranean. Zoological Science 15 (Supplement): 37. [Published conference abstract]
- Pollock LW (1995) New marine tardigrades from Hawaiian beach sand and phylogeny of the family Halechiniscidae. Invertebrate Biology 114: 220–235. doi: 10.2307/3226877
- Renaud-Debyser J (1965) *Parastygarctus higginsi* n.g., n.sp. Tardigrade marin interstitiel de Madagascar. Comptes Rendus de l'Académie des Sciences de Paris 260: 955–957.
- Renaud-Mornant J (1970) Tardigrades marines des Bermudes. Bulletin du Muséum National d'Histoire Naturelle, Paris, 2e série 42(6): 1268–1276.
- Renaud-Mornant J (1979) Tardigrades marins de Madagascar. I. Halechiniscidae et Batillipedidae. Bulletin du Muséum National d'Histoire Naturelle, Paris, Série 4e 1: 257–277.
- Renaud-Mornant J (1982) Sous-famille et genre nouveaux de Tardigrades marins (Arthrotardigrada). Bulletin du Museum National d'Histoire Naturelle Paris, Série 4e 4: 89–94.
- Richters F (1908) Marine Tardigraden. Zoologischer Anzeiger 33: 77–85.
- Schulz E (1955) Studien an marinen Tardigraden. Kieler Meeresforschung 11: 73–79.
- Sudzuki M (1979) Some aspects of the haline interstitial biota from Ryukyu Shotō, subtropical chain islands, southwest Japan. Sesoko Marine Science Laboratory Technical Report 6: 37–50, plate I–IV.
- Thulin G (1928) Über die phylogenie und das system der Tardigraden. Hereditas 11: 207–266. doi: 10.1111/j.1601-5223.1928.tb02488.x
- Thulin G (1942) Ein neuer mariner Tardigrad. Meddelanden från Göteborgs Musei Zoologiska Avdelning 99: 1–10.
- Tojo M (1930) Nantou Hougen Shiryou. Tokoshoin, Tokyo, 236 pp.
- Van der Land J (1968) *Florarctus antillensis*, a new tardigrade from the coral sands of Curaçao. Studies on the Fauna of Curaçao and other Caribbean Islands 25: 140–146.